SIZE-BASED RESPONSES OF PREY TO PISCIVORE EXCLUSION IN A SPECIES-RICH NEOTROPICAL RIVER

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Abstract. Characteristics used to group species, and thus generalize ecological interactions, can aid in constructing predictive models in species-rich food webs. We tested whether size could be used to predict a behavioral response of multiple prey species ($n >$ 50) to exclusion of large-bodied fishes, including seven abundant piscivore species, in a lowland Neotropical river. A randomized block design ($n = 6$) included three experimental treatments constructed on sandbank habitats: large fish exclusion, cage control (barrier with gaps), and natural reference plot (no barrier). Exclosures prevented passage of all large-bodied fishes, but the mesh size allowed passage of prey fishes. After two weeks, experimental areas were sampled once during the day and once at night. Total abundance of prey fishes was not significantly different among treatments, and effects on species density were variable. Analyses based on fish size class, however, demonstrated significant size-based effects of large-fish exclusion. Abundance of medium fishes (40–110 mm) in exclusion treatments increased significantly relative to controls in day (248%) and night (91%) samples, and this trend was apparent for many species ($n > 13$). Species density of medium fishes increased significantly in exclusion treatments. There was evidence of an intraspecific, size-dependent response for the three most common species. Ninety percent of prey in stomach contents of seven common large-bodied piscivores (collected from river sandbanks) were 40–110 mm, corresponding to size of fishes that responded to large-fish exclusion. Behavioral responses of medium prey likely resulted from exclusion of these large-bodied piscivores. These results extend size-based predator avoidance behavior demonstrated in temperate systems to a highly connected tropical river food web. In this species-rich web, size is a strong predictor of behavioral responses of multiple prey species to large piscivores, and it can be used to generalize outcomes of multiple species interacting simultaneously.

Key words: complexity; diversity; fish; food webs; indirect effects; predator–prey interactions; river; size structure; tropics; Venezuela.

INTRODUCTION

Developing predictive models of species interactions is challenging, especially in diverse communities. Much of the world's species diversity is located in tropical ecosystems, and a better understanding of species interactions is necessary to help stem biodiversity loss and assess community-level responses to human-induced habitat change. In species-rich food webs, extending the logic of pair-wise predator–prey interactions often will not predict outcomes of multiple species interactions (Wilbur and Fauth 1990, Polis and Strong 1996, Schmitz 1998). For example, effects of multiple predators on prey populations might not be additive (Wootton 1994, Sih et al. 1998, Eklöv and VanKooten 2001). Indirect effects become increasingly complex in speciose food webs (Fox and Olsen 2000), rendering it difficult to make predictions when many species interact simultaneously (Abrams 1992, Kle-

banoff and Hastings 1994, Yodzis 2000, Wootton 2001, Relyea and Yurewicz 2002).

Body size is an important determinant of predator–prey interactions and is used to predict behavioral responses to predation threat in aquatic systems. Body size predicted avoidance behavior by bluegill, *Lepomis macrochirus*, in response to presence of predatory largemouth bass, *Micropterus salmoides* (Werner et al. 1983, Werner and Hall 1988, Turner and Mittelbach 1990). In streams, small prey fishes move into shallow water in the presence of largemouth bass, but larger fishes do not alter their distribution patterns (Harvey 1991). In Trinidad, body size of the killifish *Rivulus hartii* is a determinant of movements within a river and among tributaries in the presence of the piscivore *Hoplias malabaricus* (Gilliam and Fraser 2001). Steinmetz et al. (2003) demonstrated in two temperate streams that fish response to bird predation is size dependent. The importance of such induced behavioral responses at both community and ecosystem levels is becoming increasingly clear (Luttbeg and Schmitz 2000, Lima 2002).

Few studies have manipulated multiple predators and evaluated behavioral responses of multiple prey (Woot-

FIG. 1. Experimental exclosure on a Río Cinaruco sandbank.

ton 1993, Marquis and Whelan 1994, Dial and Rough-garden 1995, Greenberg et al. 2000, Nyström et al. 2001, Relyea and Yurewicz 2002), and none of this work has been conducted in tropical aquatic systems. Here, we tested for a behavioral response of multiple prey species ($n > 50$) to multiple piscivore species ($n > 7$) using large experimental exclosures ($\sim$500 m²). We examined if prey alter their spatial distribution in the absence of piscivores (e.g., peacock cichlids *Cichla* spp.) in a species-rich tropical river with a highly connected food web. All large-bodied fishes were excluded, but prey were able to pass in and out of experimental areas. To test if size is a useful predictive variable of piscivore effects on prey fish assemblages, we a priori divided potential prey fish into size categories and evaluated results based on these groupings. We tested the null hypothesis that there would be no difference in fish abundance or species density among experimental treatments, regardless of fish size.

STUDY SITE

The study was conducted in the Río Cinaruco, a blackwater, floodplain river in southwestern Venezuela (6°32′ N, 67°24′ W). The river is strongly seasonal with water levels fluctuating >5 m in an annual hydroperiod. During the dry season (January–April), the main river channel contains long ($\leq$2 km), broad sandbanks that constitute a large proportion of river shoreline. River width in the dry season is 40–200 m, water temperatures typically range from 28° to 36°C, Secchi depths are $\sim$1 m in the main river channel adjacent to beaches, and dissolved oxygen is always near saturation in the main channel.

The river supports $\geq$260 fish species that span an extremely wide range of ecological attributes and life history strategies. In previous (Jepsen et al. 1997, Winemiller and Jepsen 1998) and ongoing research, seven species have been identified as the most common large-bodied (total length >350 mm) piscivores of sandbank habitats where experiments were conducted: peacock cichlids (*Cichla intermedia*, *C. orinocensis*, and *C. temensis*), characiforms (*Boulengerella cuvieri*, *B. lucius*, and *Hydrolycus armatus*), and a pimelodid catfish (*Pseudoplatystoma fasciatum*). These species are relatively mobile predators that often forage on river sandbanks. Based on three years of sampling with a variety of techniques (e.g., gill netting, hook-and-line fishing), we estimate occurrence of these large piscivores typically ranges from 5 to 40 individuals per 75-m stretch of sandbank over a 24-h period (C. A. Layman, *unpublished manuscript*).

Four piranha species (*Serralsalmus* spp., *Pristobrycon* spp.) are abundant in the river, but are not considered here because they primarily inhabit deeper areas of the main river channel and floodplain lagoons. River dolphin, *Inia geoffrensis*, also feed in deeper areas, not on sandbanks, and are far less dense than piscivorous fishes (McGuire and Winemiller 1998). Spectacled caiman, *Caiman crocodilus*, and birds (e.g., Osprey, *Pandion haliaetus*; Cocoi Heron, *Ardea cocoi*) could feed in all experimental areas equally, but were never observed feeding in any treatment.

METHODS

We employed a randomized block design, with each block ($n = 6$) placed in a different location and different time during January–March 2001. Each block consisted of three treatments arranged in random order in the littoral region of a sandbank. Exclosure treatments were constructed with 60 m of poultry wire (mesh 2.5 cm) attached with plastic ties to 1.8-m metal posts spaced at 5-m intervals. The wire barrier was arranged in an elongated semicircle shape along $\sim$35 m of sandbank to enclose an area of $\sim$500 m² (Fig. 1).

The wire mesh was pushed ≥5 cm into the substrate along the entire enclosure length. This design excluded all large-bodied fishes from passing into exclosures, while allowing full movement of most prey of excluded large-bodied piscivores. Control treatments included 60 m of wire, but with two 5-m gaps (in deeper water at the exclosure back) that allowed fishes of all sizes to move in and out freely. We observed *Cichla* spp. and *Boulengerella* spp. feeding inside control treatments and just outside exclosures, suggesting presence of the wire did not substantially affect natural feeding behavior. Natural reference plots were comparable sandbank areas without wire or posts. The three experimental areas within a block were separated by 50 m of unmanipulated beach.

After approximately two weeks, experimental areas were sampled during the day and night using a seine (6.4 × 1.8 m, 4-mm mesh). During the day, one sample consisted of three hauls made parallel to the beach with one end of the seine pulled along the shoreline. Each seine haul was conducted along a different 10-m stretch of beach within the experimental area. Deepwater seine hauls ($n = 3$ in each experimental area) were initiated at the back of the enclosure, and the seine was hauled directly toward shore. Nighttime seine hauls were conducted only along the shoreline ($n = 3$ in each experimental area) due to safety concerns of sampling deeper water at night. Day and night samples were not pooled due to differences in sampling methodology (i.e., no deepwater seine hauls at night) and due to differences in assemblage composition between day and night samples (Arrington and Winemiller 2003). Specimens were preserved and transported to the Universidad de Los Llanos Occidentales (UNELLEZ) in Guanare, Venezuela. Individuals were identified to species and enumerated. Voucher specimens were archived in the Museo de Ciencias Naturales at UNELLEZ and the Texas Cooperative Wildlife Collection, College Station, Texas, USA.

Due to logistical constraints of measuring every individual fish ($n > 14\,000$), analyses were based on two size classes established a priori (small, <40 mm; medium, >40 mm), and not exact lengths of individuals. Size categories commonly are used to establish feeding relationships and examine outcomes of ecological interactions (Peterson and Andre 1980, Dial and Roughgarden 1995, Schoener and Spiller 1999, Greenberg et al. 2000, Spiller and Schoener 2001, Schoener et al. 2002). For example, Schoener et al. (2002) used size categories of arthropods (>4 mm and <4 mm) to describe food web differences on islands with and without the lizard predator *Leiocephalus carinatus*. Use of size categories reduces power to detect subtle size-based differences, but facilitates analysis of large samples.

A substantial proportion of species in the river mature at sizes <40 mm, including dozens of small characid species that are extremely common on sandy beach habitats (Arrington and Winemiller 2003). In the present study, "small" fishes refer to all fishes <40 mm, irrespective of maturation status. Depending on methodology (e.g., net dimensions, mesh size) and site, 79–100% of fishes on sandbanks have been estimated to be <40 mm in length (C. A. Layman and K. O. Winemiller, *unpublished manuscript*). The largest fish collected in experimental areas was 110 mm, so all fishes within 40 to 110 mm were categorized as "medium." Potential prey fishes on sandbanks are highly diverse, both taxonomically (81 genera, 24 families) and functionally (i.e., in terms of feeding strategy, habitat utilization).

We also analyzed stomach contents of the seven most common piscivore species. From January to April during both 2001 and 2002, piscivores were collected on sandbank habitats where the experiments were conducted and on other nearby sandbanks. Fishes were collected with gill nets, and by hook and line using artificial lures. Fishes were measured (standard length [SL], ±1.0 mm) and stomachs were analyzed using one of two methods. *Cichla temensis*, *C. orinocensis*, *C. intermedia*, and *Pseudoplatystoma fasciatum* stomachs were examined by pressing down the posterior region of the tongue and pushing gently on the fish's stomach while holding the fish in a head-down position. Subsequent dissection of a subset of individuals ($n = 71$) confirmed this method is 100% effective in recovering stomach contents, regardless of prey size. *Boulengerella cuvieri*, *B. lucius*, and *Hydrolycus armatus* were euthanized, and stomachs removed for examination. Data were pooled for the seven species to provide a composite view of size of prey consumed by large piscivores on sandbanks.

Statistical Analysis

The two aggregate response variables analyzed were fish abundance and species density. Abundance was total number of individuals collected by standardized seining of a fixed area within each treatment; species density (following Gotelli and Colwell [2001]) was expressed as number of species collected in the standardized seining area. Analyses were conducted (separately for day and night) using a randomized-block ANOVA on overall fish abundance and species density, as well as on medium and small size classes independently. Medium fish, but not small individuals, responded to piscivore exclusion (see *Results*), so additional analyses were conducted on the medium size class.

Specifically, we wanted to know if overall response of medium fishes (Fig. 2) was attributable to similar patterns of response by multiple taxa. To control for the effect of between-species differences in total abundance, we converted raw species abundance values to Z scores within each block of the experiment. The Z scores were calculated as follows:
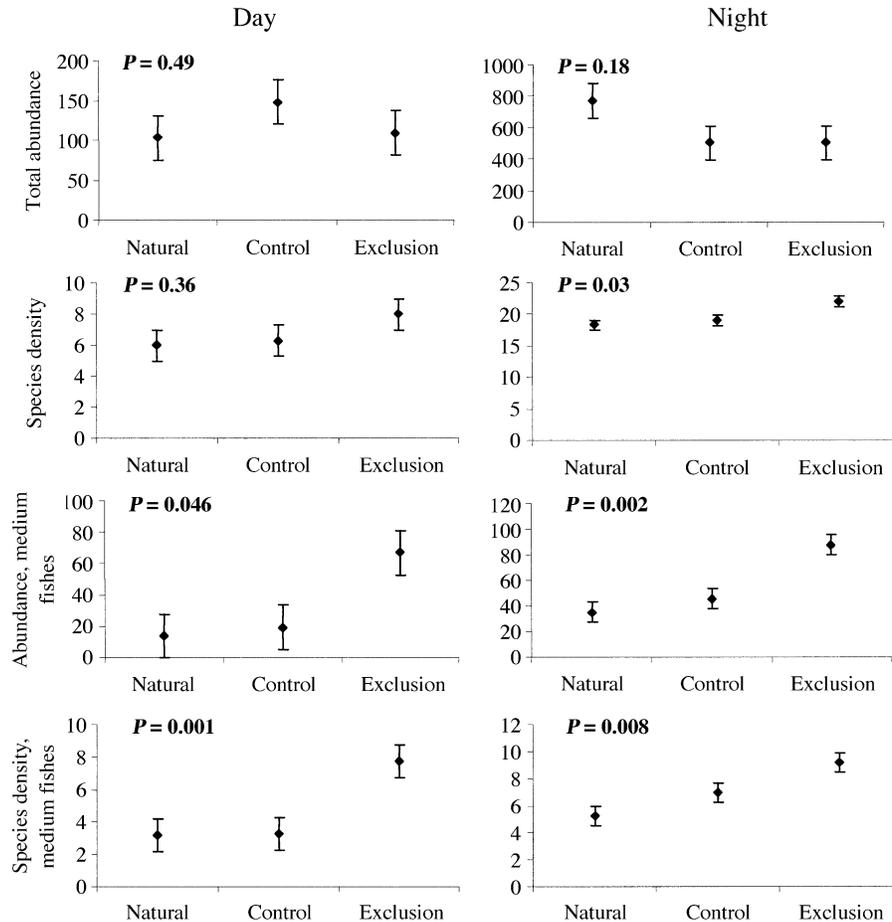
$$Z = (X_i - \mu)/\sigma$$

FIG. 2. Least-squares means of total abundance and species density of all fishes (top two rows) and medium fishes (40–110 mm; bottom two rows) within experimental areas. Total abundance is the number of individuals collected by standardized seine sampling; species density is the number of species collected in this same area. The left column reports day sampling; the right column reports night sampling. *P* values are from ANOVA on response variables with significant values in boldface. Error bars represent ±1 SE.

where X_i is the abundance of the ith species in one treatment of an experimental block and μ and σ are the mean and standard deviation, respectively, of the three abundance values for the ith species in that block (Fig. 3; Zar 1996). A multivariate analysis of variance (MANOVA) was conducted separately for day and night samples, with experimental treatment as the independent variable and species standardized abundance (i.e., Z score) as the dependent variable. Rare species were excluded from the analysis (species with <10 individuals collected), because there were not enough degrees of freedom to conduct MANOVA with all species included. Significant MANOVA results are followed by univariate tests (i.e., one-way ANOVA) for each species examining abundance differences among treatments (Scheiner and Gurevitch 2001).

For those species in which individuals <40 mm and >40 mm were collected in more than half of the blocks, we also tested for a size-based intraspecific response. Contingency tables were inappropriate for these anal-

yses, as expected cell values were low due to high variability in presence of individuals among blocks. Abundance of individuals <40 mm and >40 mm were standardized to Z scores within each block as described. Standardized abundance (Z score) then was analyzed using ANOVA and Tukey's post hoc test. Analyses were conducted using JMP software (Version 4.04, SAS Institute, Inc, Cary, North Carolina, USA).

To best assess assemblage structure and dynamics, both aggregate (e.g., abundance and species density) and composition measures should be used in analyses (Micheli et al. 1999). Correspondence analysis (CA), a composition-based technique, was used to determine if particular assemblages of fish were representative of given treatments. Correspondence analysis is an indirect technique used to detect gradients in species composition from observed species abundance (Hill and Gauch 1980, Peet et al. 1988). Here, CA was conducted using CANOCO 4 (ter Braak and Šmilauer 1998). Canonical ordination scores were analyzed to assess
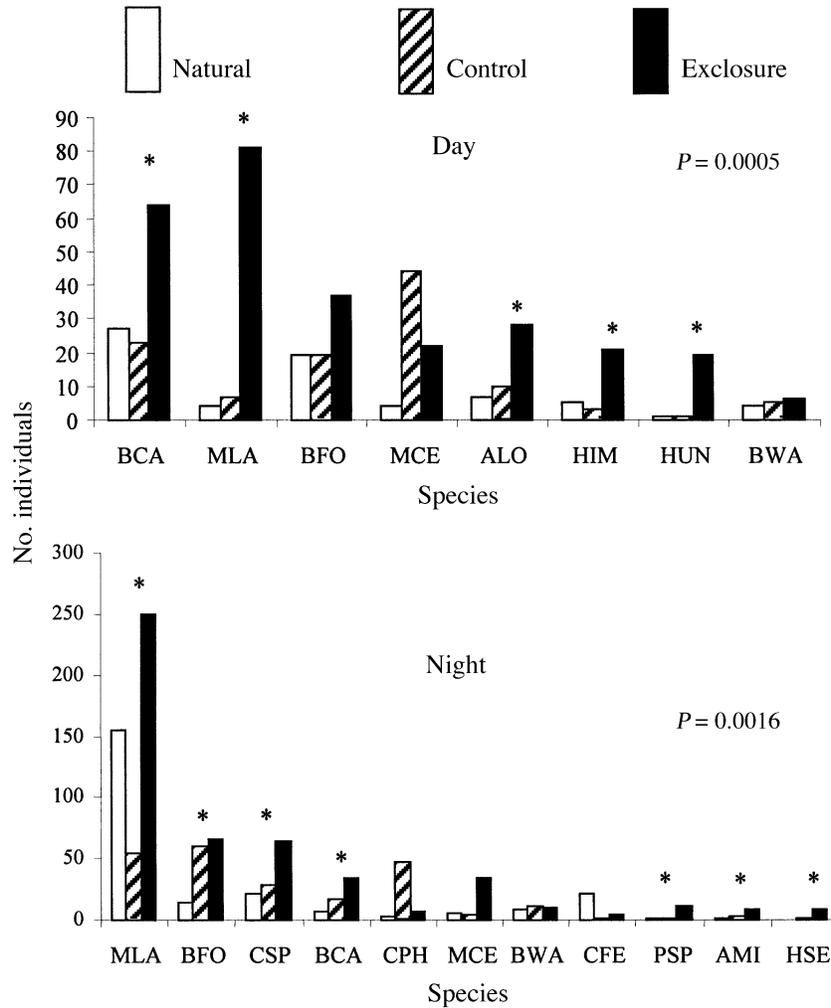
Fig. 3. Plots of abundance of individual species among treatments (summed across blocks) in day and night sampling, revealing response of multiple species to piscivore exclusion. Rare species (i.e., <10 individuals collected) are not depicted in the figure. *P* values represent results of MANOVA with experimental treatment as the independent variable and species standardized abundance as the dependent variable. Significant univariate tests (i.e., one-way ANOVA, *P* < 0.05) for individual species are indicated with an asterisk. Species codes: BCA, *Bryconops caudomaculatus*; MLA, *Moenkhausia af. lepidura*; BFO, *Bivibranchia fowleri*; MCE, *Moenkhausia* cf. *ceros*; ALO, *Argonectes longiceps*; HIM, *Hemiodus immaculatus*; HUN, *Hemiodus unimaculatus*; BWA, *Biotodoma wavrini*; CSP, *Cyphocharax spilurus*; CPH, *Creagrutus phasma*; CFE, *Cyphocharax festivus*; PSP, *Pimelodella* sp.; AMI, *Acestrorhynchus minimus*; HSE, *Hemiodus semitaeniatus*.

whether assemblages differed significantly according to treatment or experimental block. We used MANOVA to test for significance of these two factors, with the first four canonical axes serving as dependent variables.

RESULTS

There were no significant treatment effects on total abundance of fishes in either day ($F_{2,10} = 0.76$, $P = 0.49$) or night ($F_{2,10} = 2.04$, $P = 0.18$) samples (Fig. 2). Abundance of medium fishes for both day ($F_{2,10} = 4.26$, $P = 0.046$) and night ($F_{2,10} = 12.06$, $P = 0.002$) was significantly different among treatments. In day samples, abundance of medium fishes was 383% greater in experimental than in natural plots, and 248% greater than in control treatments. For night samples,

abundance of medium fishes was 148% and 91% greater in experimental treatments relative to natural plots and control treatments, respectively. Total species density was not significantly different among treatments in day samples ($F_{2,10} = 1.14$, $P = 0.36$), but treatments were significant for night samples ($F_{2,10} = 5.41$, $P = 0.03$). Exclosures averaged an increase of 3.7 species over natural plots and 3.0 over control treatments in night samples. This greater overall species density in enclosures is largely attributable to a response by medium fishes (increases of 4.0 and 2.2 species relative to natural and control areas, respectively). For both day ($F_{2,10} = 14$, $P < 0.001$) and night ($F_{2,10} = 8.05$, $P = 0.008$) samples, species density of medium fishes differed significantly among treatments. For small fishes,

TABLE 1. Stomach contents summary of the seven most common piscivores captured on river sandbanks in the Río Cinaruco.

Species	Number examined	Empty stomachs (%)	No. measured prey	Prey length† (mm)
Boulengerella cuvieri	203	78	46	68.8 (21.5)
Boulengerella lucius	71	85	10	69.9 (20.9)
Cichla intermedia	47	97	1	41 (—)
Cichla orinocensis	41	95	1	80 (—)
Cichla temensis	34	91	2	127.0 (82.0)
Hydrolycus armatus	48	83	4	69.0 (41.0)
Pseudoplatystoma fasciatum	5	20	4	99.5 (31.8)

† Values are means (1 SD).

there were no consistent trends in abundance or species density among treatments in day or night samples ($P > 0.16$ for each test). Abundance and species density of fishes were consistently higher in night samples, consistent with results of previous day–night faunal comparisons (Arrington and Winemiller 2003).

To test whether the overall response of medium fishes was due to multiple taxa, we performed a MANOVA on standardized species abundance (*Z* scores). There was a significant effect of treatment in both day (Wilks' lambda = 0.022, $F_{16,16} = 5.77$, $P = 0.0005$) and night (Wilks' lambda = 0.0038, $F_{22,10} = 6.92$, $P = 0.0016$) samples, with a consistent trend of highest abundance of species in exclusion treatments. Subsequent univariate analyses revealed that 5 of 8 species in day samples, and 7 of 11 species in night samples, were significantly more abundant in exclusion treatments ($P \leq 0.05$ in all cases).

Three species were collected in sufficient numbers in night samples to evaluate potential size-dependent intraspecific responses. Medium individuals of all three species displayed highly significant differences in abundance among treatments (*Moenkhausia* af. *lepidura*, $F_{2,15} = 24.21$, $P < 0.001$; *Bryconops caudomaculatus*, $F_{2,15} = 12.00$, $P < 0.001$; *Bivibranchia fowleri*, $F_{2,15} = 17.53$, $P < 0.001$). For all three species, Tukey's post hoc test indicated medium individuals were most
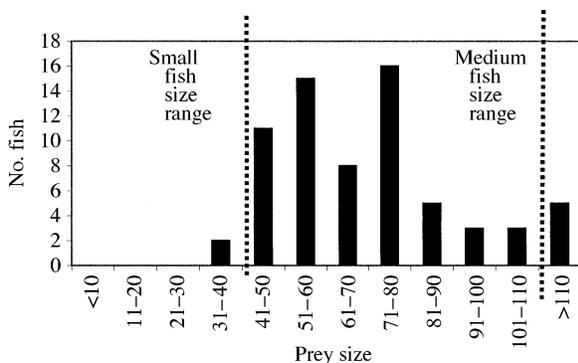

FIG 4. Frequency histogram of prey fishes as determined by stomach content analyses of the seven most common large-bodied piscivores in Río Cinaruco. These data are restricted to those individuals captured on main river sandbanks, and data are pooled across piscivore taxa.

abundant in exclusion treatments. In contrast, for the small size class, none of the three species showed significant differences in abundance among treatments (*Moenkhausia* af. *lepidura*, $F_{2,15} = 1.75$, $P = 0.21$; *Bryconops caudomaculatus*, $F_{2,15} = 2.60$, $P = 0.11$; *Bivibranchia fowleri* $F_{2,15} = 0.01$, $P = 0.99$).

Although there were significant differences in measures of abundance and species density among treatments for medium fishes, consistent assemblage-level patterns of medium fishes were not observed among treatments. Correspondence analysis revealed no significant grouping of treatments in ordination space. A MANOVA using canonical ordination scores revealed no significant effect of treatment (day, Wilks' lambda = 0.78, $F_{8,14} = 0.64$, $P = 0.73$; night, Wilks' lambda = 0.37, $F_{8,14} = 1.1$, $P = 0.40$). There was a significant experimental block (i.e., location) effect for night (Wilks' lambda = 0.005, $F_{20,24.2} = 4.9$, $P < 0.001$) and marginally significant effect for day (Wilks' lambda = 0.21, $F_{20,24.2} = 1.97$, $P = 0.057$) samples. Experimental block predicted assemblage composition better than treatment because species composition was more similar within a block of the experiment than across blocks for a given treatment.

We recovered 68 measurable prey fish (by volume, >99% of identifiable stomach contents were fishes) from 449 large-bodied piscivores captured on sandbanks (Table 1). Prey sizes in stomach contents coincided with the size class that responded to predator exclusion (Fig. 4). Despite high abundance of small fishes on beaches (see *Methods*), 90.0% of prey in stomachs were within 40–110 mm. The most common identified prey were *Moenkahusia* af. *lepidura*, *B. caudomaculatus*, and hemiodid species. These species were also the most common medium fishes collected from experimental areas, and those that showed the strongest responses to predator exclusion. Importantly, medium prey found in piscivore stomachs was not an artifact of sampling methodology or digestive rates of different-sized prey. Extensive stomach contents analyses of the same seven piscivore species collected from lagoons in the Río Cinaruco floodplain revealed significantly smaller prey sizes compared to piscivores from sandbanks (Mann-Whitney, $T = 19,654.0$, $P < 0.001$; sandbank prey SL, 71.8 ± 24.8; lagoon prey

SL, 34.0 ± 31.2). On sandbanks, 97% of piscivore prey were >40 mm (*n* = 68), compared to 24% in lagoons (*n* = 308).

DISCUSSION

This study extends findings from temperate systems concerning size-dependent responses of fish prey to predators (Werner et al. 1983, Werner and Hall 1988, Harvey and Stewart 1991) and suggests a behavioral response that occurred in multiple species (*n* > 13) in a highly connected food web. Only by partitioning the prey fish assemblage into size categories was an effect of piscivore exclusion apparent, with medium fish (i.e., >40 mm) responding to piscivore exclusion. Predation effects in tropical fish communities has been inferred from stomach contents analysis (Goulding 1980, Winemiller 1989, 1990, Jepsen et al. 1997), comparisons of species assemblages among sites (Rodríguez and Lewis 1994, 1997), isotopic analyses (Jepsen and Winemiller 2002), and life history strategies (Reznick and Bryga 1987, Reznick et al. 2001). In the present study, the effect of predators on prey distribution was demonstrated experimentally using large field exclosures.

In ''open'' ecological experiments, organisms are allowed to pass in and out of experimental areas (Cooper et al. 1990). When the area over which organisms move is greater than size of experimental units, effects are primarily due to behavioral responses (Cooper et al. 1990, Englund 1997). In the present study, exclosures were large, but probably were smaller than the area covered by daily movements of most predator and prey species. In this system, some species apparently can perceive relative risk of predation and select littoral habitats accordingly. This adds to growing evidence of the importance of nonlethal responses in predator–prey interactions (Lima and Dill 1990, Abrams et al. 1996, Lima 1998, 2002, Sih et al. 1998) and highlights the need to incorporate behavioral traits into models of community dynamics (Abrams 1995, Luttbeg and Schmitz 2000, Schmitz 2000).

Adaptive behavioral responses to predation threat can have significant implications at both community and ecosystem levels. Habitat shifts induced by predators can affect feeding and/or growth rates of prey (e.g., Werner 1991, Fraser and Gilliam 1992, Turner 1997, Schmitz and Suttle 2001, Peacor 2002). Some of the medium fish that responded to predator exclusion (e.g., hemiodid species) are algivores/detritivores, and the habitat shifts displayed by these species may have important implications for the distribution of basal food resources. Behavior-mediated interactions have been found to have cascading effects on lower trophic levels in both terrestrial (Beckerman et al. 1997, Schmitz et al. 1997, Gastreich 1999) and aquatic (e.g., Power et al. 1985, Peckarsky and McIntosh 1998, Diehl et al. 2000, Turner et al. 2000, Bernot and Turner 2001) ecosystems. We are currently conducting experiments in

the Río Cinaruco to examine cascading effects of algivore/detritivore species on benthic productivity.

Although aggregate measures in this study (abundance and species density) revealed significant effects to piscivore exclusion by medium fishes, multivariate analysis (the composition measure, CA) revealed no differences in assemblage composition among treatments. Significant variability in species composition existed among assemblages at different sites, but the size-specific response reflected in aggregate assemblage measures occurred at all sites. Other studies have emphasized predation effects on the composition of fish assemblages (Tonn and Magnuson 1982, He and Kitchell 1990, Rodríguez and Lewis 1997, MacRae and Jackson 2001), but in the current study variability among local assemblages masked detection of consistent shifts in composition. Yet regardless of the assemblage at a given site, a general response within the local assemblage could be predicted based on body size. This demonstrates that general species characteristics can be powerful predictors of the outcome of multispecies interactions in complex food webs.

Can the results of the present study, conducted at a relatively small scale, be used to predict population- and ecosystem-level patterns (see Lima 1998)? For example, results of small-scale behavioral experiments predict watershed-level distributions of a killifish in Trinidad (Fraser et al. 1995), and He and Kitchell (1990) showed how laboratory and field experiments could be used to predict fish emigration following introduction of a large piscivore (northern pike, *Esox lucius*) in a whole-lake experiment. In the Río Cinaruco, lagoons in which piscivore populations have been greatly reduced by commercial netters are dominated numerically by the prey species that responded strongly to piscivore exclusion (e.g., *Moenkahusia* af. *lepidura*, *B. caudomaculatus*). In lagoons that still support large numbers of piscivorous fishes, assemblages are dominated numerically by species that attain lengths <40 mm (Layman and Winemiller, *unpublished manuscript*). Similarly, body size has been used to predict phytoplankton community shifts in response to nutrient and food web manipulations (Cottingham 1999, Klug and Cottingham 2001) and model human impacts on fishing stocks (Rice and Gislason 1996, Shin and Cury 2001).

Juanes and Conover (1994) suggested that prey selection by many piscivores is relatively passive, driven by size-related differences in prey encounter and capture probabilities. During the dry season in the Río Cinaruco, larger prey (>110 mm) are less abundant than earlier in the year, apparently due to intense predation during gradual recession of floodwaters (Jepsen et al. 1997). Thus, piscivores on sandbanks may select fishes in the medium size range, thereby maximizing profitability (sensu Scharf et al. 2002). In our experiment, prey within this size range responded to predation risk, suggesting a ''trait-compensation'' response,

an adaptive behavioral response to compensate for vulnerability to predation (Dewitt et al. 1999, Rundle and Brönmark 2001).

In addition to large piscivores, our exclusion treatment also excluded other large fishes, including common algivore/detritivores (e.g., *Semaprochilodus kneri*). Algivore/detritivores have strong effects on sediments, primary production, and invertebrates in other tropical systems (Power 1984, Pringle et al. 1993, 1999, Flecker 1996, Pringle and Hamazaki 1997, Flecker et al. 2002), and increased abundance of medium fishes could have been a response to increased benthic primary production in exclusion areas. Four pieces of evidence suggest this was unlikely. First, correspondence between size of fishes that responded to experimental manipulations and those found in stomach contents of piscivores strongly suggests a response to piscivore exclusion. Second, additional experiments have demonstrated that when piscivores are enclosed within similar experimental arenas, medium fishes avoid these areas (C. A. Layman and K. O. Winemiller, *unpublished manuscript*). Third, the two most commonly collected medium fishes (*Moenkhausia* af. *lepidura*, *Bryconops caudomaculatus*) are primarily insectivores that feed at the surface or midwater. These species would not be expected to respond directly to enhanced benthic primary production. Finally, many small fishes collected in samples were algivore/detrivores, but these small species did not respond to large-fish exclusion. Lack of detectable response by small fishes, however, might also be attributable to the fact that small piscivores were able to pass through the large mesh of exclosures.

Manipulation of entire "guilds" of organisms has been criticized as being "mechanism-free" (sensu Dunham and Beaupre 1998), despite notable predictive success in some instances (e.g., Marquis and Whelan 1994, Schmitz and Sokol-Hessner 2002). In species-rich ecosystems, however, experimental manipulation of every pair of interacting species is impossible. An alternative approach is to examine multiple interacting species as a group and to rely on additional factors to infer mechanisms. Our study demonstrated how body size can be used to predict responses of multiple prey species to multiple predators. Use of size, and other traits, to predict outcomes of multiple species interactions might provide a means to aggregate food web elements and facilitate study of complex food webs.

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