Body size, not other morphological traits, characterizes cascading effects in fish assemblage composition following commercial netting

C.A. Layman, R.B. Langerhans, and K.O. Winemiller

Abstract: Traits used to group species and generalize predator–prey interactions can aid in constructing models to assess human impacts on food webs, especially in complex, species-rich systems. Commercial netting has reduced populations of large-bodied piscivores in some lagoons of a Venezuelan floodplain river, and cascading effects result in distinct prey fish communities in netted and unnetted lagoons. In 2002 and 2003, we sampled assemblages of prey fishes in netted and unnetted lagoons and tested whether fish size and (or) other morphological characteristics were associated with differences in assemblage composition. In both years, prey fish assemblages in netted lagoons were dominated numerically by larger species. We used geometric morphometric methods to test for a relationship between species morphological characteristics and found that neither overall morphological ordination nor specific morphological traits could be used to distinguish among assemblages. Thus, size was the only variable that was useful in explaining differences in assemblage composition. Even in this species-rich river with a complex food web, size-structured predator–prey interactions apparently influence community-level patterns and can be used to characterize human impacts.

Résumé : Les caractéristiques utilisées pour regrouper les espèces et pour généraliser les interactions prédateurs–proies peuvent servir à construire des modèles d'évaluation des impacts anthropiques sur les réseaux alimentaires, particulièrement dans les systèmes complexes, riches en espèces. La pêche commerciale au filet a réduit les populations des piscivores de grande taille dans certains lagons de la plaine de débordement d'une rivière du Venezuela et les effets en cascade qui s'en sont suivis ont donné des communautés distinctes de poissons proies dans les lagons soumis à la pêche et dans ceux qui ne le sont pas. En 2002 et 2003, nous avons échantillonné des peuplements de poissons proies dans des lagons exploités et non exploités et vérifié s'il existe une association entre la taille et (ou) d'autres caractéristiques morphologiques des poissons et les différences de composition des peuplements. Durant les deux années, les peuplements de poissons proies dans les lagons exploités étaient dominés numériquement par des espèces plus grandes. Des méthodes morphométriques géométriques nous ont servi à chercher à découvrir une relation entre les caractéristiques morphologiques des espèces; nous n'avons trouvé ni d'ordination globale morphologique, ni de caractéristiques morphologiques spécifiques qui permettent de distinguer les peuplements. La taille est donc la seule variable utile pour expliquer les différences de composition des peuplements. Même dans cette rivière riche en espèces et à réseau alimentaire complexe, les interactions prédateurs–proies reliées à la taille semblent influencer les patrons au niveau de la communauté et peuvent servir à caractériser les impacts anthropiques.

[Traduit par la Rédaction]

Introduction

Predicting effects of human activity on ecological interactions and ecosystem function is one of the most important challenges facing ecologists. Species exploitation, species introductions, and habitat alteration all can lead to changes in food web structure, and understanding these changes is necessary to mitigate negative impacts of human activities. Perturbations propagate through multiple trophic and nontrophic pathways rendering it difficult to predict impacts, es-

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pecially in complex food webs (Yodzis 2000; Wootton 2001; Relyea and Yurewicz 2002). Yet, modeling effects of human-induced perturbations is essential to guide conservation and management efforts (Chapin et al. 2000; McCann 2000).

Grouping species according to traits, such as size, morphology, or behavior, is one means to simplify species-rich communities, and sometimes provides better predictive capabilities than analyses performed at higher levels of taxonomic resolution. For example, morphological traits are a primary component of "plant functional groups", classifications used to simplify complex plant communities, which have been especially useful for predicting ecosystem- and community-level responses to local and global environmental change (Lavorel et al. 1997; Smith et al. 1997; Dyer et al. 2001). Body size influences population and community responses to perturbations in species-rich arthropod food webs (Dial and Roughgarden 1995; Spiller and Schoener 2001; Schoener et al. 2002). If phenotypic traits can be used to assess ecological responses to perturbations in a broad range of communities, then trait classifications may be a primary tool for assessing anthropogenic impacts on food webs.

Net fishing is one of the most common human influences in tropical inland waters, and can cause major changes in fish communities (Goulding 1980; Bayley and Petrere 1989; Crisman et al. 2003). Piscivore introductions have been shown to substantially alter prey assemblages in tropical lentic systems (Zaret 1979; Kaufman 1992; Crisman et al. 2003), but there have been few studies that examine effects following piscivore removal. In the Río Cinaruco, Venezuela, netters substantially reduce population sizes of large-bodied piscivores in some lagoons of the floodplain landscape. We previously simulated commercial netting effects by excluding large-bodied piscivores on sandbank habitats of the river (exclusion areas ~500 m^2). Piscivore exclusion resulted in shifts in assemblage composition, indicating effects of large piscivores on medium-sized fishes at lower trophic levels (Layman and Winemiller 2004). Assemblage differences were best characterized by the body size of prey taxa, suggesting that phenotypic characteristics might be useful in predicting landscape-scale effects of commercial netting.

We tested the utility of phenotypic traits in characterizing differences in fish assemblages of netted and unnetted lagoons. We specifically assessed whether, as suggested by experimental manipulations, body size could be used to generalize assemblage differences following piscivore removal from lagoons. Second, because body morphology is related to ecological attributes (e.g., vulnerability to predators, swimming performance, feeding behavior) in many fish taxa (e.g., Keast and Webb 1966; Winemiller 1991; Wainwright and Richard 1995), we examined whether morphological traits of prey species could characterize netting effects at the landscape scale. We especially were interested in identifying traits (e.g., relative size of the caudal peduncle region) that may reflect the ability of prey to avoid or escape predators (e.g., Walker 1997; Langerhans et al. 2004, 2005). We examined a subset of the overall food web, i.e., a food web module (sensu Holt 1997), which includes the most important prey species of large-bodied piscivores. Our objectives were to (*i*) describe differences in fish assemblage structure between netted and unnetted lagoons within this food web module and (*ii*) investigate whether prey size and (or) other morphological characteristics can be used to generalize these differences.

Materials and methods

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 has a forested riparian zone with open grassland dominating the drainage basin. The river supports at least 280 fish species that span a wide range of ecological attributes and life history strategies (Langerhans et al. 2003; Arrington et al. 2005; Layman and Winemiller 2005). The river has a strongly seasonal hydrology with water levels typically fluctuating >5 m during an annual hydroperiod. Floodplain lagoons (~1–30 km^2) are connected to the river by varying degrees. During the wet season (June–October), lagoons are broadly connected to the main channel, and dispersal of organisms is extensive. During the dry season (January–April), most lagoons become partially isolated water bodies with restricted connections to the river channel (width of connections at lagoon mouths ~1–100 m). During the dry season, species interactions, predation in particular, intensify as densities of aquatic organisms increase with falling water levels (Jepsen et al. 1997; Rodríguez and Lewis 1997; Layman and Winemiller 2004).

During the dry season when water levels are low and fish densities high, some lagoons of the Cinaruco floodplain are exploited by commercial net fishers. Netters use long beach seines (~300 m in length, mesh size ~20 cm) to harvest large-bodied fishes. The seine is deployed in a broad semicircle using a small boat and then pulled onto shore. We classified lagoons a priori as either netted or unnetted based on visual monitoring throughout the dry seasons (January–April) of 2002 and 2003. Evidence of netting activity was direct observation of either netters or piles of discarded carcasses from the fish by-catch (e.g., *Hoplias malabaricus*, *Geophagus* spp.) on lagoon shorelines. Each lagoon was checked at least weekly for evidence of recent netting activity. Lagoons classified as "netted" had evidence of netting on at least five occasions during 2002 or 2003. Lagoons classified as "unnetted" were those in which we never observed any evidence of netting activity. Seven lagoons in 2002 (four unnetted, three netted) and eight in 2003 (five unnetted, three netted) met these criteria and were included in this study. None of the lagoons used was netted in one year and unnetted in the other. There were no differences between netted and unnetted lagoons in area (*t* test, $t = 0.66$, $p = 0.53$), average depth ($t = 0.58$, $p = 0.58$), maximum depth ($t = 1.6$, $p = 0.16$), or average transparency ($t = 1.7$, $p = 0.13$), suggesting that patterns reported in this study are not due to differences in lagoon physical characteristics. Lagoon accessibility largely determined netting status, i.e., netters primarily fished lagoons that were adjacent to roads.

Netters target high-value fish species, including the most common large-bodied piscivores (peacock cichlids (*Cichla orinocensis* and *Cichla temensis*) and a characiform (*Hydrolycus armatus*)). Lagoons are never depleted completely of piscivores because of net avoidance and immigration from the main river channel, but catch-per-unit-effort (CPUE) estimates of *Cichla* spp. and *H. armatus* in netted and unnetted lagoons suggest that population sizes may be reduced 50% or more by netters. Based on standardized hook-and-line fishing (the most effective methodology to capture *Cichla*), an average of 6.0 *Cichla* individuals were collected per 100 casts in unnetted lagoons compared with <2.4 in netted lagoons (CPUE data summed for 2002 and 2003, total casts = 4856). In standardized gillnet sampling (a more effective method of capturing *H. armatus*), an average of 6.2 *H. armatus* were collected in 24-h sampling periods in unnetted lagoons compared with 2.5 in netted lagoons (total gillnetting hours = 2736).

Fish sampling

Fish communities were sampled by cast-netting at the end of the dry season (April) in 2002 and 2003. Prey taxa most commonly consumed by large-bodied piscivores (Jepsen et al. 1997; Winemiller et al. 1997) are collected efficiently by cast-netting, and this methodology (relative to seining, gillnetting, etc.) was likely to reflect differences in prey fish assemblage structure among netted and unnetted lagoons. In doing so, we were targeting a specific food web module, a subset of interacting species from a larger food web (sensu Holt 1997). Samples were obtained using a 244-cm cast net (mesh size 6.3 mm) thrown from a small boat. All sites were adjacent to woody debris along lagoon shorelines at depths of 40–125 cm. Sites were chosen haphazardly in each lagoon, a sampling design intended to reflect lagoon-scale patterns and not site-specific characteristics (sites per lagoon 3.4 ± 0.8). Three consecutive throws were made with the cast net at each site (sampling an area of ~4.5 m^2) and all fishes were identified to species, enumerated, measured to the nearest 1.0 mm standard length (SL), and released into the lagoon. Voucher specimens of each species were archived in the Museo de Ciencias Naturales at UNELLEZ, Guanare, Venezuela, and the Texas Cooperative Wildlife Collection, College Station, Texas.

Data analysis

For univariate comparisons, *t* tests were employed when assumptions of normality and homogeneity of variance were met and the Mann–Whitney *U* test when they were not. Nonmetric multidimensional scaling (MDS), using the Primer v5.0 statistical package (Clarke and Gorley 2001), was used to compare fish assemblage similarity or dissimilarity based on relative abundances of individual taxa. MDS constructs a two-dimensional ordination in a manner that best represents relationships among samples in a similarity matrix (Field et al. 1982; Clarke and Warwick 2001). In ordination plots, the relative distance between points reflects the dissimilarity of species composition in those samples. Similarity matrices were calculated with the Bray–Curtis similarity index (Bray and Curtis 1957). We conducted a nested multivariate analysis of variance (MANOVA) using the two MDS axes as dependent variables to test for effects of netting regime (netted versus unnetted) and lagoons nested within netting regime on species composition of samples. To compare size structure of assemblages based on all individuals collected, data were pooled for netted and unnetted lagoons for 2002 and 2003 (each year separately). A Mann–Whitney rank sum tested for differences in overall length–frequency distributions for both 2002 and 2003.

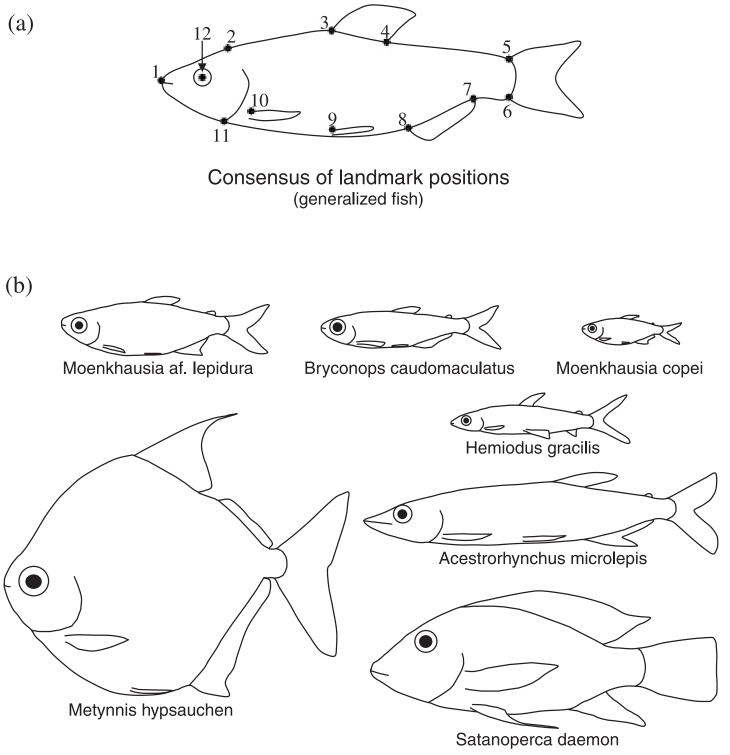
To obtain morphometric data, we captured a lateral image of the left side of three adult individuals for each species using a digital camera (Sony DSC-S30) mounted on a tripod. The size of individuals used for each species was ±1 SD of the mean size of all individuals of that species collected over 2 years of the study. Individuals used in the analysis were collected previously from the Río Cinaruco, fixed in 10% formalin, preserved in 70% alcohol, and catalogued at the Texas Cooperative Wildlife Collection, College Station, Texas. We digitized 12 landmarks on each image using tpsDig software (Rohlf 2003) for geometric morphometric analysis. Location of landmarks and examples illustrating the range of interspecific variation among fish species in body size and shape are depicted in Fig. 1.

We conducted a relative warp analysis of superimposed landmark coordinates using tpsRelw software (Rohlf 2003). For more information on relative warp analysis and other geometric morphometric techniques, see Bookstein (1991), Rohlf and Marcus (1993), Marcus et al. (1996), and Zelditch et al. (2004). Essentially, relative warp analysis is a principal components analysis of the covariance matrix of the aligned specimens (i.e., rotated, translated, and scaled landmark coordinates). This procedure produces multiple morphological axes (i.e., orthogonal multivariate shape dimensions) in a manner that best explains variance in body shape among specimens. Each relative warp axis represents a set of specific morphological characteristics, allowing particular morphological attributes of species to be analyzed directly. We calculated the average score on each relative warp (n = 20) for each species. Because superimposition methods of geometric morphometrics scale specimens to a common centroid size, size differences among species are removed from the analysis, permitting an evaluation of morphology largely independent of size.

We evaluated three questions. (*i*) Do morphologically similar species exhibit similar patterns of abundance in netted or unnetted lagoons? (*ii*) Can any particular morphological axis (i.e., multivariate description of shape variation) be used to differentiate abundance of species in netted or unnetted lagoons? (*iii*) Considered simultaneously, does body size or shape better characterize assemblage differences? To answer these questions, we quantified CPUE (i.e., mean abundance of individuals per sample) differences among netted and unnetted lagoons ($\mathrm{CPUE} = \mathrm{CPUE}_{\mathrm{netted}} - \mathrm{CPUE}_{\mathrm{unnetted}}$) for each species and evaluated body shape variation among species using relative warp analysis and MDS. Because CPUE values for each species were repeatable across years (r = 0.71, p = 0.0003), we pooled data across years to estimate CPUE.

For the first question, we constructed a two-dimensional morphospace representing similarity or dissimilarity in body morphology of all species using MDS. These two axes were generated based on a Bray–Curtis similarity index of relative warp scores. Using these two axes, we conducted a canonical correlation analysis to test for a multivariate relationship between body shape and CPUE. This analysis addressed

Fig. 1. Landmarks used for morphometric analyses and illustration of variation in size and morphology of fish assemblages. (*a*) Consensus landmark configuration depicting average position of the 12 digitized landmarks; (*b*) seven fish species illustrating variability of body forms observed within this food web module. The relative size of species (mean size of individuals of each species collected in this study) is drawn to scale.



whether morphologically similar species exhibited similar patterns of abundance.

To answer our second question, we tested for a correlation between CPUE and each of the 20 relative warps. We used Bonferroni-adjusted p values for multiple comparisons to test for significance.

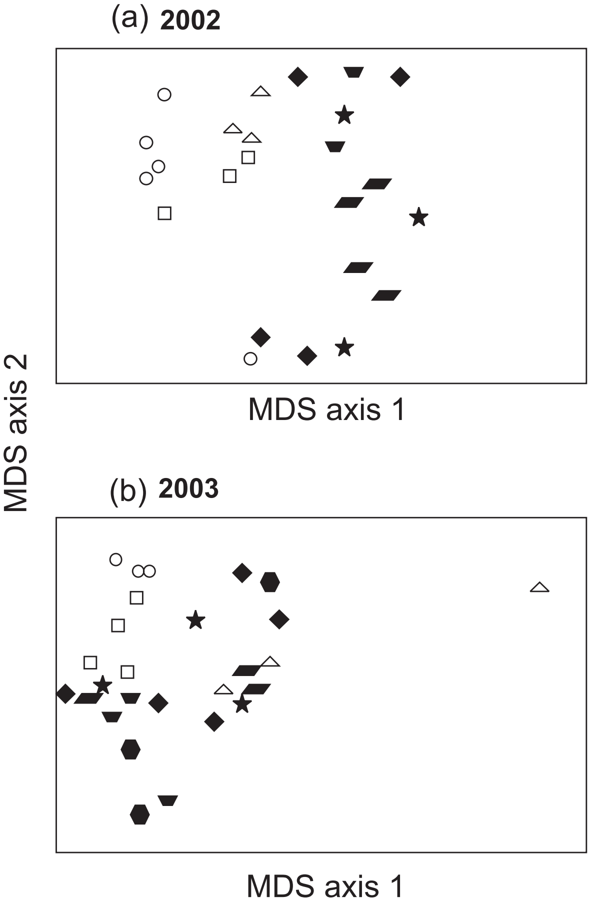
Our third question addressed the utility of using body size and body morphology to characterize species abundance patterns associated with commercial netting. Based on results of a previous study (Layman and Winemiller 2004), as well as results from the assemblage analysis of this study (see Results section), we placed each species into one of two size classes (<40 and >40 mm SL). We performed a general linear model evaluating differences in species abundances between netted and unnetted lagoons (CPUE, the response variable) as predicted by size class and the two morphological axes generated by MDS. We tested for interactions among effects and found no significant interaction and thus excluded all interactions in the final model.

Results

A total of 2633 individual fishes representing 40 species were collected using the standardized cast-netting protocol. Twenty of the 40 taxa were collected rarely (five or fewer individuals collected in all samples from both years) and were excluded from assemblage and morphological analyses. Abundance of fishes collected per site was significantly higher in netted lagoons in 2003 (t test, $p = 0.011$; mean ± 1 SD: netted = 44 ± 35, unnetted = 17 ± 15) but not in 2002 (Mann–Whitney U test, $p = 0.34$; netted = 85 ± 54, unnetted = 76 ± 85). Species density (i.e., number of species collected in a standardized sample (sensu Gotelli and Colwell 2001)) also was significantly higher in netted lagoons in 2003 (t test, $p = 0.042$; netted = 5.8 ± 3.5, unnetted = 3.6 ± 1.8) but not in 2002 (t test, $p = 0.14$; netted = 6.8 ± 1.6, unnetted = 5.6 ± 2.1). Taxa were variable in size (11–257 mm SL) and morphology (see Fig. 1). Taxa collected included pelagic characids and hemiodids (e.g., *Moenkhausia* af. *lepidura*, *Hemiodus gracilis*), benthic cichlids (e.g., *Satanoperca daemon*), other demersal species (e.g., *Cyphocharax oenas*), a loracariid algivore (*Rineloricaria* spp.), and deep-bodied pelagic granivores (e.g., *Metynnis hypsauchen*).

MANOVA revealed that species composition significantly differed between netted and unnetted lagoons in 2002 ($F_{[2,16]} = 32.23$, $p < 0.0001$) and 2003 ($F_{[2,18]} = 4.28$, $p = 0.03$) and among lagoons nested within netting regime in 2003 ($F_{[12,36]} = 2.25$, $p = 0.03$) but not in 2002 ($F_{[10,32]} = 1.26$, $p = 0.29$) (Fig. 2). Thus, although differences in composition of netted and unnetted lagoon sites were significant during both years, they were more distinct in 2002 (i.e., clearer separation in ordination space, less variation within netting regimes; see Fig. 2). During both years, netted lagoon sites were dominated numerically by *M.* af. *lepidura* (2002, 44% of individuals collected; 2003, 70%). In unnetted lagoons, *M.* af. *lepidura* accounted for only 3% (2002) and <1% (2003) of individuals collected. *Moenkhausia copei* accounted for 71% (2002) and 40% (2003) of fishes collected in unnetted la-

Fig. 2. Differences in species assemblage composition as reflected by nonmetric MDS: (*a*) 2002; (*b*) 2003. MANOVA revealed significant differences in assemblage composition between netted and unnetted lagoons in both years. Each symbol represents a different lagoon; open symbols are sites in netted lagoons and solid symbols are sites in unnetted lagoons.



goons and 10% in both 2002 and 2003 in netted lagoons. Abundance of these two species largely accounted for relative positions of the sites in the MDS ordination in both years.

We found significant differences in overall size distribution of fishes, regardless of species (i.e., individual-level analysis), between netted and unnetted lagoons for both years (Mann–Whitney *U* test, $p < 0.001$, both years) (Fig. 3). Unnetted lagoons were dominated by fishes <40 mm SL. This was largely accounted for by the two most common species in unnetted lagoon samples, *M. copei* (SL ± SD = 35.5 ± 3.7 mm) and *Hemigrammus* sp. (SL = 16.8 ± 1.0 mm). In netted lagoons, there was a peak in both years in fishes 61–70 mm, accounted for largely by *M.* af. *lepidura* (66.9 ± 5.1 mm). Other larger species, including *Bryconops caudomaculatus*, *Acestrorhynchus microlepis*, and *Acestrorhynchus minimus*, were also more commonly collected in netted lagoons. Differences in assemblage composition and size structure were more distinct in 2002 than in 2003; this could be attributed to apparent reduced netting activity during January–February 2003, which could have resulted in less distinct divergence in faunal composition.

In morphological analyses, canonical correlation analysis revealed no significant association between body morphology and CPUE ($F_{[2,17]} = 0.13$, $p = 0.88$). Although species exhibited distinct differences in morphological features, these differences or similarities were not correlated with abundance patterns in netted or unnetted lagoons. After Bonferroni adjustment (i.e., using a significance level of $p = 0.0025$), no correlations among relative warps ($n = 20$) and CPUE were significant (Table 1) (the first two relative warps accounting for 72.6% of the total morphological variance are depicted in Fig. 4). One relative warp (relative warp 20, explaining only 0.03% of morphological variance) was highly correlated with CPUE before Bonferroni correction ($R = 0.56$, $p = 0.011$). Visual inspection suggested that this relative warp described subtle morphological differences between species <40 and >40 mm SL. We tested this hypothesis using a *t* test and found significant differences in relative warp 20 values between the two size classes of fish ($p = 0.0015$). Thus, the only morphological attribute that characterized ecological patterns between netted and unnetted lagoons primarily described differences between these two size classes of fish.

In a general linear model examining effects of size class and morphology (i.e., the MDS axes) on CPUE, we found that size class significantly characterized species abundance patterns ($F_{[1,16]} = 4.85$, $p = 0.043$) but that neither morphological axis was associated with abundance patterns (axis 1, $F_{[1,16]} = 0.009$, $p = 0.925$; axis 2, $F_{[1,16]} = 1.65$, $p = 0.218$). Again, we found no evidence that morphological features could be used to characterize differences in netted and unnetted lagoons, whereas a simple size-class categorization could be used to assess effects of commercial netting. Further, the analysis had adequate statistical power to detect putative effects of morphology on CPUE (statistical power of 0.97 assuming an effect size equivalent to that of the size-class factor). This species-level analysis indicated that species >40 mm SL exhibited greater abundance in netted lagoons and that species <40 mm SL were more abundant in unnetted lagoons. Thus, differences in length distributions revealed by individual-level analysis (Fig. 3) were not solely due to differences exhibited by numerically dominant species.

Discussion

Body size, but not other morphological traits, was associated with differences in prey assemblage composition among netted and unnetted lagoons. These results are consistent with experimental manipulations demonstrating a size-based prey response to piscivore exclusion in this system (Layman and Winemiller 2004) and suggest that experimental results “scale up” to characterize landscape-level patterns. Body size has been used similarly to model human impacts on marine fishing stocks (Rice and Gislason 1996; Pauly et al. 1998; Shin and Cury 2001) and to predict phytoplankton community shifts in response to nutrient and food web manipulations (Cottingham 1999; Klug and Cottingham 2001). Size-structured predator–prey interactions are fundamental for understanding aquatic food web structure, and our results suggest that size can be used to assess fishing effects even within highly diverse, reticulate food webs.

Fig. 3. Length–frequency histograms showing different size structures of assemblages in (*a*) netted and (*b*) unnetted lagoons. Bars represent proportion of total fishes collected in each size category: solid bars, 2002; open bars, 2003.

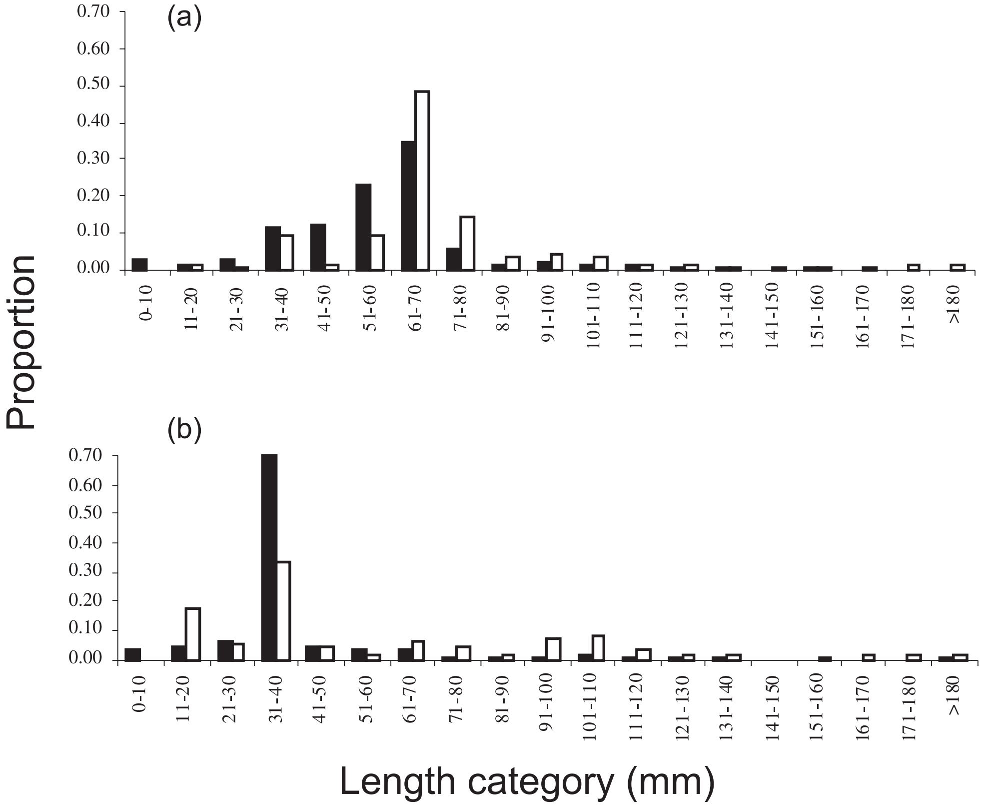


Table 1. Descriptive information and correlation statistics for the first 10 relative warps (explaining ~99% of the morphological variance).

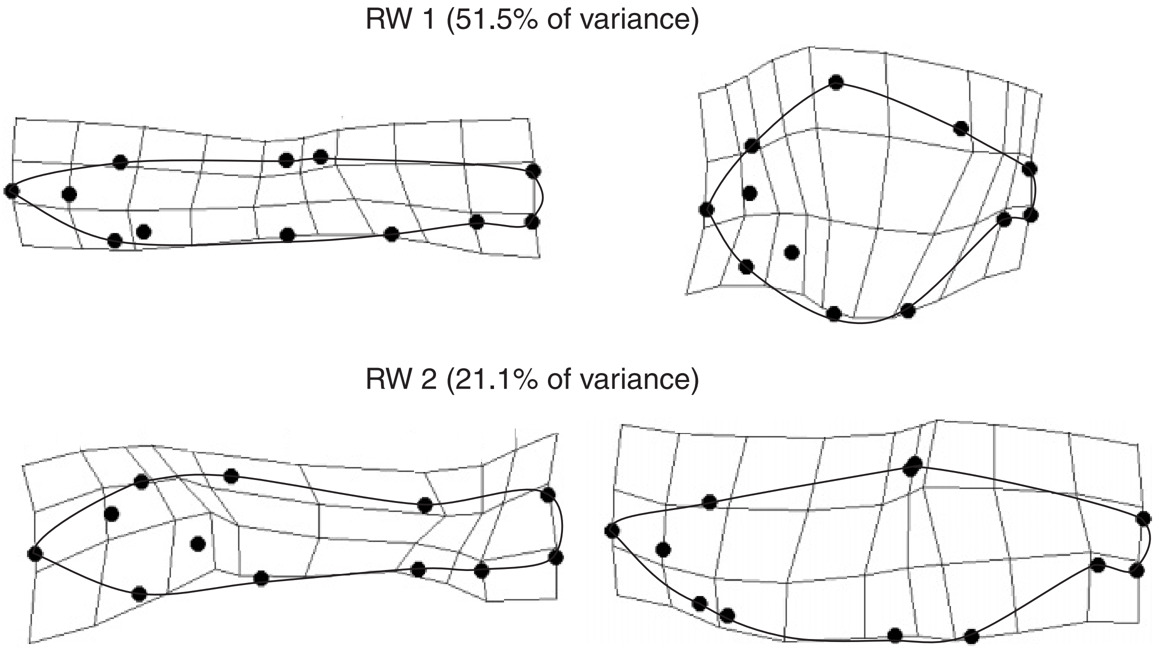
Relative warp	Percent variance explained	Cumulative percent variance explained	Correlation with CPUE	
			r	*p*
1	51.49	51.49	0.01	0.971
2	21.09	72.58	0.04	0.874
3	12.14	84.72	0.06	0.812
4	7.59	92.31	0.04	0.859
5	2.19	94.50	0.15	0.539
6	1.61	96.11	0.10	0.679
7	1.15	97.26	0.21	0.384
8	0.72	97.98	0.00	0.993
9	0.46	98.44	0.24	0.303
10	0.37	98.81	0.02	0.949

Note: None of the correlations between relative warps (n = 20) and ΔCPUE (i.e., the difference in CPUE) was significant using Bonferroni correction for multiple comparisons. With Bonferroni adjustment, we used a significance level of p = 0.0025.

Following other studies of lake- or lagoon-scale patterns of community structure (Rahel 1984; Tonn et al. 1990; Rodríguez and Lewis 1997), we employed a comparative-based approach and analyzed patterns based on an underlying variable. Rodríguez and Lewis (1997) demonstrated that a suite of abiotic (e.g., lagoon morphology, water transparency) and biotic (e.g., piscivore abundance) variables determined community structure in lagoons of the Río Orinoco, whereas we based our comparison a priori on a single categorical variable (netting history). Together, these studies demonstrate that piscivory is an important factor structuring fish assemblages in floodplain lagoons. Similar to the study of Rodríguez and Lewis (1994), we suggest that species-specific differences in vulnerability to piscivores strongly influence assemblage composition during the dry season in tropical floodplain lagoons.

The Río Cinaruco is characterized by a compressed food web in which all piscivores seem to exploit prey that both feed low in the food web (i.e., on algivores and detritivores) and are optimally sized (Layman et al. 2005*a*). At the end of the dry season (April), algivores and detritivores are largely depleted from the potential prey fish community (Jepsen et al. 1997; Layman et al. 2005*b*), but the present study suggests that piscivores continue to exploit optimally sized prey even as they are forced to feed on prey positioned higher in the food web (e.g., on omnivorous *Moenkhausia* and *Bryconops* spp.). Profitability (energy or biomass ingested in relation to capture and handling efficiencies) of a prey resource is typically greatest at intermediate to large prey sizes, although consumption of specific prey is a function of prey density, behavior, sensory ability, and predator capture and handling efficiency (Sih and Moore 1990; Sih and Christensen 2001; Scharf et al. 2002). By preferentially consuming larger individuals to maximize profitability, piscivores may allow smaller prey to dominate fish assemblages in Cinaruco lagoons. When commercial netting re-

Fig. 4. Thin-plate spline transformations of landmark coordinates depicting morphological characteristics described by the first two relative warps (RW) (accounting for 72.6% of the morphological variance). Low values of relative warps are on the left and high values are on the right.



duces densities of large-bodied piscivores, larger prey fishes dominate this module of the food web. Such size-based differences in fish assemblages are consistent with well-documented size-structured patterns in planktivore–zooplankton–phytoplankton interactions in lotic systems (Brooks and Dodson 1965; Carpenter and Kitchell 1993; Rodríguez et al. 1993).

Morphological traits could prove useful for describing differences in assemblage composition resulting from the influence of prey selection by predators and (or) the ability of prey to escape or avoid predators; we did not find evidence for either of these possibilities. First, if prey selection by predators is relatively unhindered by prey morphological traits, morphology would not be expected to be useful in predicting assemblage-level differences. Large-bodied piscivores in the Río Cinaruco feed on a variety of prey items with greatly varying morphologies, including taxa with defensive spines (*Pimelodella* spp.), armour (*Scorpiodoras* spp., *Leptodoras* sp.), and cryptic morphologies (*Microglanis* sp.) (C.A. Layman, unpublished data). But even with increases in "effective" body size because of spines and other morphological characteristics, body depths of >97% of individuals sampled in this study would not exceed gape limits of most adult large-bodied piscivores, and thus, morphology should not significantly limit prey choice. Prey choice of aquatic predators is often passive (Sih and Moore 1990; Juanes and Conover 1994), especially for species feeding on mobile taxa such as fishes (Sih and Christensen 2001). For large piscivores of Cinaruco lagoons, encounter frequency and prey density may be relatively more important than constraints imposed by prey morphologies for prey selection, especially in the peak dry season when large algivore and detrivores are greatly reduced in abundance.

Additionally, we found no morphological traits related to predator avoidance or escape ability that were correlated with assemblage-level differences. This is likely due to the phylogenetically and morphologically diverse group of prey species included in this study. Behavioral avoidance and escape mechanisms likely vary substantially among the suite of taxa studied, with the underlying morphologies supporting these mechanisms being equally diverse. For example, we have identified within-species morphological differences that consistently differ among individuals in netted and unnetted lagoons, but these morphological differences are unique for separate species (C.A. Layman and R.B. Langerhans, unpublished data). There have likely been multiple evolutionary solutions to predator avoidance and escape in this system, and we could identify no general morphological pattern across all species examined.

Discussion continues as to whether lumping or grouping species into "kinds of organisms", trophospecies, or functional groups is useful when modeling food webs (Yodzis and Winemiller 1999; Schmitz and Sokol-Hessner 2002; Chalcraft and Resetarits 2003). Our study revealed that fish size, but not other morphological characteristics, could be used to group diverse prey taxa to predict assemblage changes following a specific perturbation, i.e., netting of large-bodied piscivores. Consistent results from experimental manipulations and landscape-scale patterns provide strong evidence of the impacts of piscivore removal. Even in this species-rich, tropical food web, size-structured interactions yield large-scale fish assemblage patterns that can be used to assess human impacts.

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