THE ROLE OF PISCIVORES IN A SPECIES-RICH TROPICAL RIVER

A Dissertation

by

CRAIG ANTHONY LAYMAN

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2004

Major Subject: Wildlife and Fisheries Sciences

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ABSTRACT

The Role of Piscivores in a Species-Rich Tropical River. (August 2004)

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Much of the world’s species diversity is located in tropical and sub-tropical ecosystems, and a better understanding of the ecology of these systems is necessary to stem biodiversity loss and assess community- and ecosystem-level responses to anthropogenic impacts. In this dissertation, I endeavored to broaden our understanding of complex ecosystems through research conducted on the Cinaruco River, a floodplain river in Venezuela, with specific emphasis on how a human-induced perturbation, commercial netting activity, may affect food web structure and function. I employed two approaches in this work: (1) comparative analyses based on descriptive food web characteristics, and (2) experimental manipulations within important food web modules. Methodologies included monthly sampling of fish assemblages using a variety of techniques, large-scale field experiments, extensive stomach content and stable isotope analyses. Two themes unite the information presented: (1) substantial spatial and temporal variability in food web structure, and (2) how body-size can be used to generalize species-interactions across this complexity. Spatial variability occurred at various scales, from among small fish assemblages on seemingly homogeneous sand banks, to differences among landscape scale units (e.g. between lagoons and main river channel). Seasonal variability was apparent in predation patterns, with relative prey availability and body size primarily resulting in decreasing prey sizes with falling water levels. Body size was also related to functional outcomes of species interactions, for example, a size-based response of prey fishes to large-bodied piscivore exclusion. This pattern was further substantiated at the landscape-scale, as differences in assemblage structure among netted and un-netted lagoons were largely size-based. Trophic position of fish and body size was not found to be related, likely due to the diversity of prey available to consumers, and may signify that commercial netting activity will not decrease food chain lengths. In sum, by describing human impacts within a food web context, I endeavor to provide predictive power regarding a specific human-induced environmental problem, yet still allowing for generality that will broaden the theoretical foundations and applications of food web ecology.

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I want to thank the three people who were especially instrumental in helping me complete my work on the Cinaruco River. First, Kirk Winemiller proved to be the perfect advisor throughout my dissertation work. He provided the freedom I needed to excel, yet when I was on the wrong trajectory, he always knew the best way to guide me in a more fruitful direction. He helped me take my research to a level I could not have achieved on my own, always making the little (and sometimes big) suggestions necessary to significantly improve my work. His time commitment to graduate students is unmatched by any professor I have been associated with, and this never went unnoticed.

Second, my closest colleague and friend throughout my dissertation work has been Albrey Arrington. His dissertation research on the Cinaruco River provided the foundation from which I was able to build my current research program. We have shared ideas, problems, and opportunities, and I hope he has benefited as much from our relationship as I have.

Third, Alexis Medina, who has been an invaluable and tireless worker on the river. He began working with me on one of the initial experiments I conducted on the river (Chapter III), and has played a critical role in collecting data for every component of the work I present here. Equally important, he has made my time on the river much more enjoyable than it would have been otherwise. There is always something missing in my boat when he is not with me.

As with most dissertations, it is impossible to compile a complete list of people have contributed to the work. I apologize to any people I do not name explicitly. The Cinaruco Fishing Club and Tour Apure were instrumental in this work being completed. I especially thank Edgar Pelaéz and Glenn Webb who supported me 100% in all my endeavors, and who I now count among my close friends. Don Taphorn helped with logistics throughout my work. People who helped with field collections include Albrey Arrington, Candido Garcia, David Hoeinghaus, Todd Kennedy, Brian Langerhans, Pablo Medina, Aaron Kloch, Hernan Lopez, Carmen Montaña, and Jeremy Walther.

A number of people deserve acknowledgment for components of the data presented. Albrey Arrington and David Jepsen carried out a sub-set of the isotope and stomach content analyses. Brian Langerhans collaborated with the data analysis conducted in Chapter IV. Carmen Montaña helped identify, sort and measure fish samples, and David Hoeinghaus processed many of the isotope samples.

Finally, my family has been especially supportive throughout my graduate work. I hope they take pride that they helped me accomplish all the work that will culminate in my earning a Ph.D degree.

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CHAPTER I

INTRODUCTION: STUDY OF SPECIES-RICH FOOD WEBS

Much of the world's species diversity is located in tropical and sub-tropical ecosystems, and a better understanding of the ecology of these systems is necessary to help stem biodiversity loss and assess community- and ecosystem-level responses to anthropogenic impacts. Important discoveries regarding food webs typically have emerged from studies in relatively isolated temperate systems (e.g. lakes), or in ecosystems where interactions can be experimentally manipulated at small spatial scales (e.g. rocky intertidal). Most of the world's biodiversity, however, is embedded within complex, reticulate and spatially inter-connected food webs. Some classic ecological approaches, such as relatively small-scale experiments involving a few key species, are less useful in complex systems because it is difficult to isolate particular groups of species that drive overall community and ecosystem-level patterns. It is critical, however, to extend and test current ecological theory in complex food webs, especially in ecosystems where human threats are great and ongoing.

In one of the most influential papers in food web ecology over the past two decades, Winemiller (1990) established the context for study of food webs in diverse systems. He posited that general topological webs (i.e. lists of potential feeding links, without quantification or verification) do not provide adequate descriptions of food web interactions, and emphasized the central role that direct diet analyses (i.e. stomach

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The style followed in this dissertation is that of Ecology.

content analysis) should have in descriptions of food web structure. Further, he detailed great spatial and temporal variability in food webs. The difficulty in analyzing species-rich food webs is further complicated by the fact descriptive food webs, such as those compiled by Winemiller (1990), do not necessarily indicate the functional effects of species within the web (Paine 1988, Polis 1991, Paine 1992, Polis and Strong 1996). For example, keystone species (Mills et al. 1993, Menge et al. 1994, Paine 1995, Power and Mills 1995, Navarrete and Menge 1996, Power et al. 1996) may have disproportionate food web effects that cannot be elucidated from descriptive food webs alone.

Because of these considerations, the most useful food web studies are those that include both descriptive and functional analyses (Winemiller and Layman 2004). In this study, I combine comparative analyses based on descriptive food web characteristics with experimental manipulations within important food web modules (sensu Holt 1997), to describe food web structure in a species-rich tropical floodplain river. Tropical floodplain rivers are characterized by high degree of spatial and temporal heterogeneity (Hamilton and Lewis 1992, Forsberg et al. 1993, Winemiller 1996, Winemiller and Jepsen 1998, Lewis et al. 2000, Lewis et al. 2001, Arrington 2002, Bunn et al. 2003, Hoeinghaus et al. 2003), creating numerous challenges to adequately describe food web structure. Yet tropical floodplain rivers are increasingly threatened by human activities, especially direct faunal exploitation (Bayley and Petere 1989, Ribeiro and Petrere 1990, Rodríguez 2000), and a better understanding of food web structure in these systems is critical to assess and mediate human impacts.

I focused on the Cinaruco River, a floodplain river in southwestern Venezuela, that supports an extremely complex food web (e.g. >280 fish species). Previous work in this system has suggested the importance of large-bodied piscivorous fishes on community- and ecosystem-level processes (Jepsen et al. 1997, Winemiller et al. 1997, Winemiller and Jepsen 1998, 2003), and I explored the role of these fishes in much more detail. By combining descriptive and experimental approaches, I sought to provide insight into the structure and function of the components of the food web influenced directly by large-bodied piscivores. Further, I evaluated potential effects following removal of the large-bodied piscivores by commercial and recreational sport fisherman. By describing human impacts within a food web context, I endeavor to provide predictive power regarding a specific ecological problem (removal of piscivores), yet still allowing for generality that will broaden the theoretical foundations and applications of food web ecology.

In Chapter II, I describe the distribution of large-bodied fishes, as based on gill net sampling, using a large-scale comparative approach. This provides the context for remaining chapters, dealing with specific components of the piscivorous fish fauna. Chapter III describes an experiment within one “module” of the river food web, specifically that of predators and their prey on river sand banks. This manipulation suggested size could be used to generalize species’ response to piscivore exclusion, providing a general variable that can be used to assess functional effects of predators within the web. I extend these ideas in Chapter IV by examining if prey response to experimental piscivore exclusion is consistent with landscape-scale patterns produced following commercial netting of piscivores from floodplain lagoons, thereby increasing the spatial scale of experimental results. I also begin to explore the role that morphology may play in mediating predator-prey interactions, a topic that I return to in Chapters V and VI.

In Chapter V, I examine the relationship among body size, trophic position, and species diversity based on extensive stomach content and stable isotope ratios analyses. The patterns described emphasize short food chain lengths in the web, and the overall compressed food web structure (i.e. most secondary consumers feeding at relatively low trophic positions). In Chapter VI, I further detail predator-prey dynamics, focusing on the central role of size-structured interactions and physical drivers (i.e. seasonal hydrology) underlying these patterns. Analyses in both Chapter V and VI relate patterns of predation back to the underlying characteristics of this species-rich food web (e.g. prey availability, morphology, and size). In Chapter VII, I return to the issue of commercial netting, using a field experiment to examine if peacock bass, *Cichla temensis*, move into shoreline habitats in response to presence of piranhas, *Serrasalmus manueli*, perhaps rendering them more susceptible to commercial netting. In Chapter VIII, I summarize two themes that unite the previous chapters, and identify areas where further research is needed.

CHAPTER II

PATTERNS OF HABITAT SEGREGATION AMONG LARGE FISHES IN A NEOTROPICAL RIVER

Introduction

Neotropical freshwater fish communities may be stochastically assembled (Lowe-McConnell 1987, Goulding et al. 1988, Jepsen 1997, Saint-Paul et al. 2000) or non-randomly structured according to habitat selection and/or biological interactions (Winemiller 1996, Jepsen et al. 1997, Rodríguez and Lewis 1997, Arrington 2002, Layman and Winemiller 2004). These alternative views are largely derived from patterns viewed from different spatial and temporal scales (see Levin 1992). For example, there are five spatial scales at which fish communities may exhibit non-random structure: (1) among drainage basins, (2) among habitats (e.g., between river channel and floodplain lagoons), (3) among sites for a given habitat type (e.g., among lagoons that vary in transparency), (4) among micro-habitats within a habitat (e.g., sand bank vs. rocky structure in one lagoon), and (5) according to fine-scale abiotic variation (e.g., water velocity, water column position, or substrate composition) within a habitat.

Studies in tropical freshwaters typically examine fish assemblage structure among drainage basins (Agostinho et al. 2000, Saint-Paul et al. 2000), or at one of the latter three scales identified above (Winemiller 1989, 1990, Rodríguez and Lewis 1997, Tejerina-Garro et al. 1998, Winemiller and Jepsen 1998, Súarez et al. 2001, Arrington 2002, Layman et al. 2004, Arrington et al. submitted). In this study, I examine assemblages of large-bodied fishes in the Río Cinaruco, Venezuela, among four landscape-scale habitat types: sand banks, backwater creeks, floodplain lagoons, and the river channel. Peacock cichlids (*Cichla* spp.), among the most common large-bodied taxa in the river, have been shown to partition habitats, with *C. intermedia* restricted largely to the main river channel and *C. orinocensis* to floodplain lagoons (Jepsen et al. 1997, Winemiller et al. 1997). Here I further examine potential landscape-scale habitat associations of other large-bodied fish species in the Río Cinaruco, using data from >10,000 hours of gill net sampling over a three-year period.

Methods

The Río Cinaruco is a tropical floodplain tributary of the Orinoco River that drains the llanos (savanna) of southern Venezuela (6º 32’ N, 67º 24’ W). The Cinaruco is an oligotrophic, moderate blackwater river with high levels of dissolved organic carbon and low pH. Hydrology is strongly seasonal, with water levels fluctuating more than 5 m annually. In the wet season (May to October) the riparian forest is flooded, and dispersal of organisms is extensive (Welcomme 1979, Lowe-McConnell 1987). From November to January, rapidly falling water results in higher fish densities and intensification of many biotic interactions (e.g., predation) during the dry season (February-April) (Winemiller 1990, Rodríguez and Lewis 1994, 1997, Layman and Winemiller 2004). Maximum width of the main channel during the dry season is 50-200 m. The river supports a diverse fish community (>280 species), with taxa representing a wide range of ecological attributes and life history strategies (Winemiller 1990, Rodríguez and Lewis 1994, 1997). A detailed description of Cinaruco River can be found in Jepsen (1999).

Four habitats are common in the Río Cinaruco: sand banks, backwater creeks, floodplain lagoons, and the river channel. During the dry season (January to April), the main river channel contains long (up to 2 km), broad sand banks that constitute a large proportion of river shoreline. Sand banks slope gradually, with the majority of the bank area <1.5 m. Meandering creeks fringed by dense gallery forest drain the floodplain and flow into backwater areas of lagoons. During the dry and early rising water periods, creeks have low water velocity (0 – 0.2 m sec^{-1}), and have similar habitat characteristics to floodplain lagoons (more information in Hoeinghaus et al. 2003). Lagoons (~1-30 km^2) are connected to the river by varying degrees. In the dry season, most lagoons become partially isolated water bodies, as connections between lagoons and the river channel become restricted (width of connections at lagoon mouths ~1-100 m). Maximum lagoon depths are ~7 m in the dry season, but most areas of lagoons are <2.5 m in depth. Both creeks and lagoons have heterogeneous habitat features including sand, leaf litter, cut banks, partially submerged overhanging vegetation, submerged branches and tree falls, and reaches with accumulated detritus. The main river channel is 3-7 m deep in the dry season.

Sampling was conducted from January 2 to June 5 in three years (2001, 2002, 2003). My intention was to describe assemblage composition among the four habitat types, but not to compare micro-habitats within habitats. Thus, sampling locations were haphazardly chosen within habitats, and no location was sampled more than once. Multiple sites from 10 different sand banks, 4 creeks, 10 lagoons, and a 12-km stretch of the main river channel were sampled during the course of the study. Sampling dates were chosen at random in each year, but I ensured all habitat types were sampled throughout the hydrological cycle during each of the three years. Samples in January-April were considered to be dry season, and May and June rising water period.

Fishes were sampled with three monofilament gill nets (25 m x 2 m), each with a different mesh size (2.5, 3.75, and 5 cm). Nets of each mesh size were simultaneously deployed with ~5 m between nets. In creeks, lagoons, and river channel, nets were secured by the float-line to submerged or overhanging vegetation near the bank, and the nets stretched taut. Nets on sand banks were secured to 1.8 m metal posts that were driven into the sand. In most cases, nets were set so most of their length was in contact with the substrate. I standardized sampling effort by deploying nets for 24 hours at each site. Nets were checked at dawn, mid-day, and dusk, and all individuals were measured (standard length, SL, in millimeters and weight in grams) and identified to species. Problematic species were identified to genus and assigned a numeric species indentifier (Table 1). In gill net sampling, vagile piscivores that feed on fishes caught in nets (e.g., piranhas) may be over-estimated due to high net encounter rates, whereas sedentary species may be underestimated. Gill net samples do not provide an unbiased description of species relative abundance, but biases can be assumed to be the same across dates and locations in the system, thus allowing for comparisons among standardized samples (Hickford and Schiel 1995, Kurkilahti and Rask 1996, Miranda et al. 2000, Saint-Paul et

TABLE 1. Percentage of the total number of individuals representing each species and the frequency which with each was collected in the 150 samples.

	Percentage of All Fishes	Frequency of Occurrence
Hydrolycus armatus	12.7%	50.6%
Semaprochilodus kneri	10.3%	56.5%
Serrasalmus manueli	9.9%	64.3%
Boulengerella lucius	6.2%	44.8%
Leporinus sp. 1	5.7%	37.7%
Boulengerella cuvieri	4.0%	27.9%
Hassar ucayalensis	3.6%	20.8%
Triportheus albus	3.1%	24.0%
Myleus spp.	3.0%	24.0%
Laemolyta taeniatus	2.7%	24.7%
Hemiodus unimaculatus	2.3%	22.1%
Chalceus macrolepidotus	2.2%	14.3%
Geophagus spp.	2.1%	26.6%
Plagioscion squamosissimus	1.9%	19.5%
Cichla temensis	1.8%	26.0%
Curimata incompta	1.6%	15.6%
Metynnis hypsauchen	1.6%	13.6%
Pristobrycon striolatus	1.6%	18.8%
Cynodon gibbus	1.4%	9.1%
Myleus schombergki	1.4%	16.2%
Leporinus sp. 2	1.2%	11.0%
Loricariichthys brunneus	1.1%	13.6%
Serrasalmus rhombeus	1.1%	15.6%
Leporinus sp. 3	1.0%	15.6%
Hemiodus argenteus	1.0%	11.7%
Pellona castelnaeana	0.8%	12.3%
Pseudoplatystoma fasciatum	0.8%	13.6%
Holias malabaricus	0.8%	9.7%
Semaprochilodus laticeps	0.7%	5.2%
Serrasalmus altuvei	0.7%	13.6%
Curimata vittata	0.7%	6.5%
Acestrorhynchus falcirostris	0.6%	11.0%
Hemiodis immaculatus	0.6%	9.1%

TABLE 1. Continued.

	Percentage of All Fishes	Frequency of Occurrence
Anodus orinocensis	0.5%	5.8%
Satanoperca daemon	0.5%	7.8%
Boulengerella maculata	0.4%	7.8%
Crenicichla cf lugubris	0.4%	7.8%
Oxydoras niger	0.4%	7.1%
Ageneiosus brevifilis	0.3%	5.8%
Mylossoma aureus	0.3%	5.8%
Platynematichthys notatus	0.3%	3.9%
Serrasalmus medinae	0.3%	5.8%
Argonectes longiceps	0.3%	4.5%
Cichla intermedia	0.3%	5.2%
Cichla orinocensis	0.2%	6.5%
Brycon falcatus	0.2%	6.5%
Bivibranchia fowleri	0.2%	5.8%
Hypostomus argus	0.2%	5.8%
Leporinus sp. 4	0.2%	2.6%
Brycon sp.	0.2%	4.5%
Heros sp.	0.2%	1.9%
Agoniates anchovia	0.1%	3.2%
Hoplarchus psitticus	0.1%	1.9%
Pachypops furcraeus	0.1%	3.2%
Platydoras costatus	0.1%	1.9%
Pristobrycon calmoni	0.1%	2.6%
Leiarus marmoratus	0.1%	3.2%
Piaractus brachypomum	0.1%	1.9%
Psectrogaster ciliata	0.1%	2.6%
Pygocentrus cariba	0.1%	1.9%
Catoprion mento	0.1%	1.3%
Serrasalmus elongatus	0.1%	0.6%
Cochliodon plecostomoides	0.1%	1.9%
Glyptoperichthys gibbiceps	0.1%	1.9%
Pseudoplatystoma tigrinum	0.1%	1.9%
Auchenipterichthys longimanus	0.0%	1.3%
Rhamdia sp.	0.0%	1.3%

al. 2000, Silvano et al. 2000, Tejerina-Garro and De Merona 2001, Hoeinghaus et al. 2003). Abundance was recorded as catch per unit effort (CPUE), the number of individuals collected from a gill net sample (3 gill nets at a given site over a 24 hour period). Species density was the number of species collected in each standardized sample (following Gotelli and Colwell 2001).

To best assess assemblage structure and dynamics, both aggregate (e.g., CPUE and species density) and composition measures should be used in analyses (Micheli et al. 1999). Comparisons among mean aggregate values were conducted using non-parametric Kruskal-Wallis ANOVA and the Mann-Whitney Rank Sum Test. Multi-dimensional scaling (MDS) was used to compare fish assemblage similarity/dissimilarity based on species relative abundances. MDS constructs a 2-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). Analysis of similarities (ANOSIM, Clarke and Warwick 1994), a non-parametric analog of MANOVA, was used to test for differences in species composition between habitat categories. When ANOSIM revealed significant differences, similarity percentage analysis (SIMPER) (Clarke and Warwick 1994) was performed to identify species accounting for differences.

Results

In 150 samples (10,800 gill net hours), I collected 4,140 individuals of 72 species from 13 families. The three most commonly collected species, accounting for 33% of all individuals, were the piscivores *Hydrolycus armatus* and *Serrasalmus manueli* and the algivore/detritivore *Semaprochilodus kneri*. Other common fish (>3.0% of all individuals collected) were ctenolucid piscivores *Boulengerella* spp., omnivorous *Leporinus* spp., omnivorous *Triportheus albus*, herbivorous *Myleus* spp., and the benthic insectivore *Hassar ucayalensis*. Average CPUE and species density were significantly different among habitat types (Figure 1; Kruskal-Wallis, both factors $P < 0.001$). Creeks had highest CPUE (mean ± SD, 46.9 ± 43.1) and species density (9.4 ± 5.2). Sand banks had lowest mean CPUE (17.8 ± 23.6), and river channel sites the lowest mean species density (5.1 ± 3.0). The range of individuals collected in a sample was 1-146, and the range of species density was 1-30.

Assemblage composition was significantly different among habitats (ANOSIM, $P < 0.001$; Figure 2). Pair-wise comparisons revealed significant differences between all habitat pairs (ANOSIM, all $P < 0.001$) except between creeks and lagoons ($P = 0.13$). *H. armatus* and *S. kneri* were more commonly collected in creeks and lagoons, and *S. manueli* and *S. rhombeus* most commonly in river channels. *Boulengerella* spp. revealed habitat partitioning, with *B. cuvieri* more common on main channel sand banks and *B. lucius* common in creeks and lagoons. Benthic invertivores, such as *H. ucayalensis* and

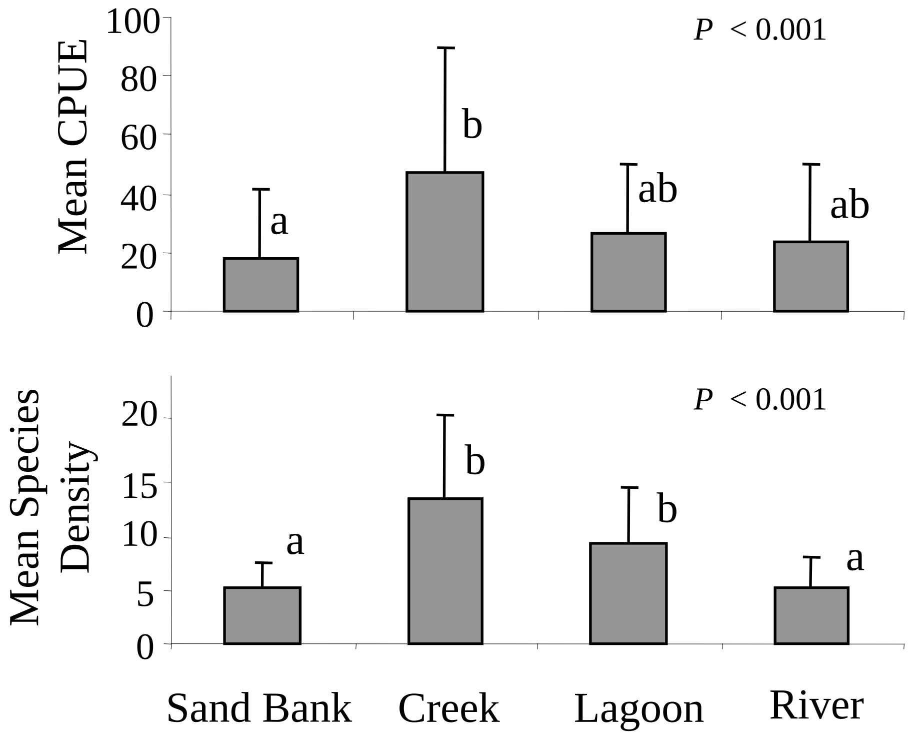


Figure 1. Mean CPUE (catch per unit effort) and species density in the four habitat types. Error bars are 1 S.D. Letters next to habitat types represent results of Dunn's post-hoc test for differences in mean values between each habitat pair.

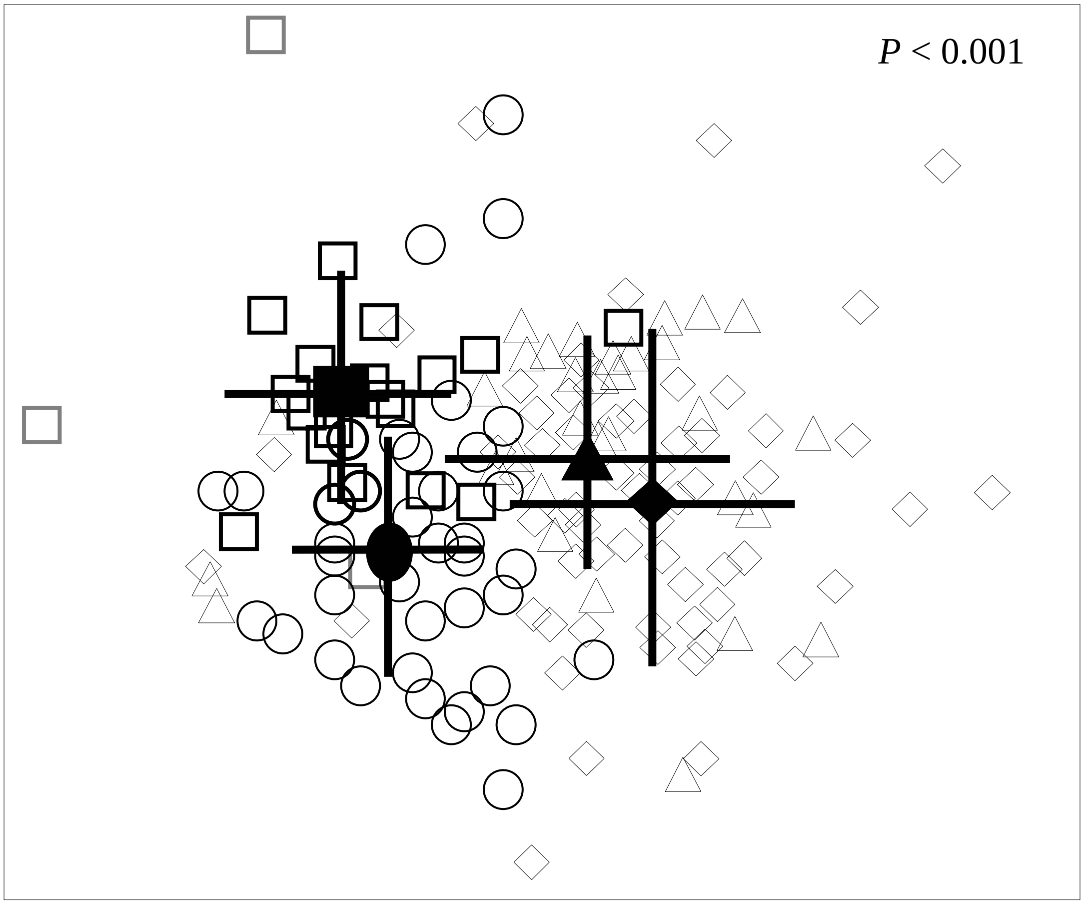


Figure 2. Multi-dimensional scaling (MDS) ordination depicting the relative similarity of assemblage composition. Each open symbol on the graph represents one sample (i.e., 3 gill nets set for 24 hours), and the closed symbols are sample means for each of the four habitat types. Error bars are 1 S.D. Channel = squares; sand bank = circles; creek = triangles; lagoon = diamonds.

Geophagus spp., were collected most often in lagoons. *Triportheus albus* and *Leporinus* sp. 1 were most commonly collected in creeks (except for *Leporinus* sp. 1 during one week in May, see below). There were no species collected on either sand banks or in the river channel that were not also collected in either a lagoon or creek sample. In contrast, 21 species were collected in both creeks and lagoons, but in neither of the other two habitats.

Average CPUE was higher during the dry season (33.1 ± 31.9) relative to the rising water period (22.3 ± 26.0; Mann-Whitney $P = 0.04$). CPUE of the four most commonly collected species (Table 1) was higher during the dry season than rising-water period. Assemblage composition was significantly different during dry- and rising-water periods (ANOSIM, dry $P < 0.001$, rising $P = 0.011$), with MDS ordinations suggesting slightly more structured communities (i.e., higher similarity in composition within habitat types) for the dry season samples. Assemblage composition did not differ among years (ANOSIM, $P = 0.57$), and, within habitats, there was no evidence for assemblage structure among replicate sites (ANOSIM, sand banks $P = 0.39$, creeks $P = 0.16$, lagoons $P = 0.17$).

Highest CPUE recorded for a lagoon sample ($n = 119$), highest for a channel sample ($n = 114$), and second highest for a sand bank sample ($n = 40$) occurred during a one week period, May 19-26, 2002. The mean CPUE of all samples taken during this week (44.5 ± 34.8) was significantly higher than the mean CPUE for the remaining samples (26.2 ± 28.0; Mann-Whitney, $P = 0.021$). These samples were characterized by higher CPUE of *Leporinus* sp 1 (CPUE all samples = 1.1, CPUE May 19-26 = 7.3), *Myleus* spp.(0.4, 2.7) and *Semaprochilodus kneri* (2.9, 4.2). The mean CPUE (13.4 ± 19.9) of samples taken after this week (May 27-June 5) was significantly lower than the average CPUE of remaining samples (28.6 ± 29.0, Mann-Whitney *P* = 0.021).

Discussion

Although fish assemblage composition was extremely variable among samples within each habitat type, assemblage structure tended to differ between habitat categories. In pair-wise comparisons, assemblage composition of habitat types (except creeks and lagoons) was found to be significantly different, suggesting some level of structure at the landscape scale. Two questions stem from these data: (1) what is the mechanism(s) producing assemblage structure at the landscape scale?, and (2) what factors contribute to high variability in fish assemblages within habitats?

Patterns observed are most likely driven by species-specific habitat affinities, manifest in the relative abundance of common species and the presence/absence of rarer species in certain habitat types. For example, *Serrasalmus* spp. had higher mean CPUE at deeper sites, and thus were more frequently collected in the main river channel; few were collected from sand banks. Alternatively, *Boulengerella* spp. rarely were collected in deep water sites, but dominated sand bank assemblages. Relative abundances of *Serrasalmus* and *Boulengerella* species accounted for much of the difference between assemblages on sand banks and the river channel. Relatively high mean CPUE of *Semaprochilodus kneri* and *Hydrolycus armatus* in creeks and lagoons was a factor differentiating assemblages in these two habitats from sand bank and the river channel assemblages. Detritivorous *S. kneri* may inhabit creeks and lagoons to exploit large deposits of particulate organic matter and relatively high benthic primary production (as indexed by chlorophyll *a* concentrations, Winemiller and others, *unpublished manuscript*) in these habitats.

Species collected exclusively in creeks and lagoons also distinguish assemblages in these habitats from those of sand banks and the main channel. Most of the 21 species collected exclusively from creeks and lagoons can be classified into one of three trophic categories: (1) piscivores (e.g., *Ageneiosus brevifilis, Cichla orinocensis, Hoplias malabaricus*), (2) species that consume allocthonous terrestrial plant material such as flowers and seeds (*Chalceus macrolepidotus*, *Mytennis hypsauchen*), and (3) algivore/detritivores (*Hypostomus argus*, *Psectrocaster ciliata*, *Semaprochilodus laticeps*). These species may prefer creeks and lagoons because these habitats contain submerged structure that attracts small prey fishes, abundant overhanging vegetation that supplies flowers and seeds, and benthic algal and detrital resources. During the dry season, creeks are essentially lentic extensions of lagoons, and it is not surprisingly that these habits had similar fish assemblages.

Fish assemblage structure at (and within) the landscape scale also could be influenced by species interactions. For example, some of the most common prey species (*Hemiodus immaculatus*, *Laemolyta taeniatus*, *Leporinus* sp.1, *Semaprochilodus kneri*) of large piscivores (e.g., *Cichla* spp.) had highest mean CPUE in creeks. These prey taxa were especially abundant in the upper, shallower portions of creeks where large piscivores are rare. This is consistent with prey distribution patterns driven by predator avoidance, as experimentally demonstrated for prey on sand bank habitats in the river channel (Layman and Winemiller 2004). Further experiments are needed to test if predator avoidance and/or the availability of food resources determines distribution of prey species among (and within) habitats.

Fish assemblage composition within habitat types was variable because of the high spatial and temporal heterogeneity characteristic of floodplain rivers. Physical habitat characteristics varied widely within each of the four habitat categories. Lagoons have backwater areas with substrates dominated by coarse particulate organic matter, as well as broad, sandy flats. Hence, a lagoon sample from a sandy area should more closely resemble a river sand bank sample than an average lagoon sample. Similarly, samples from deep-water lagoon locations may be similar to samples from the river channel. Sampling sites within habitats were chosen essentially at random. Significant differences in assemblage composition, despite heterogeneity of sites within habitat types, suggest characteristic fish assemblages in the four habitat types.

Floodplain rivers are dynamic (Welcomme 1979, Hamilton and Lewis 1987, Lewis et al. 2000), and fish assemblages may differ substantially among seasons (Saint-Paul et al. 2000, Arrington 2002). The peak in mean CPUE during a single week in May 2002 likely was the result of the "*ribazón*", an annual migration of fishes during rising- and falling-water periods (Goulding 1980, Lowe-McConnell 1987). Species with higher than average CPUE during this week (*Leporinus* spp. *Myleus* spp., and *Semaprochilodus kneri*) are major components of the *ribazón* in other floodplain rivers (Goulding 1980, Lowe-McConnell 1987). For example, *S. kneri* undergoes long distance migrations to spawn in the productive Orinoco floodplain (Winemiller and Jepsen 1998, 2003), and the high CPUE in late May may reflect this seasonal movement. Mean CPUE of samples was significantly lower following this week, likely the result of rapidly increasing water levels (thus flooding the riparian forest, providing additional aquatic habitat for fish dispersal) and emmigration of certain species in the *ribazón*.

Some large-bodied species which are common in the river were not effectively sampled by the gill netting methodology. For example, data from hook-and-line sampling suggests that *Cichla* spp. are among the most common large-bodied fishes in the river (Jepsen et al. 1997, Winemiller et al. 1997, Chapter VI). *Cichla* are diurnally active, visually orienting predators and probably avoid gill nets. At night cichlids rest near structure in shallow waters, and thus are captured infrequently. Sedentary species, such as loricariid catfishes, also are less likely to encounter gill nets. In speciose aquatic systems, multiple sampling methodologies are needed to assess overall fish abundance and distribution. Nevertheless, standardized CPUE information provided by gill net sampling allows comparisons among sites, especially for susceptible species, and also provides baseline data that can be used to assess shifts in assemblage composition over time.

In recent years, illegal commercial netting has increased in the Río Cinaruco. Netters target large-bodied taxa, including the two most common species in my samples, *H. armatus* and *S. kneri*. These species have important ecological functions (Layman and Winemiller 2004, Layman et al. 2004), and population reductions could result in altered ecological dynamics. For example, the algivorous/detritivorous *S. kneri* is a major prey of large piscivores (Layman et al. 2004), and by feeding low in the food web, piscivores increase efficiency of energy conversion. Compressed food webs are characteristic of Neotropical floodplain rivers (Lewis et al. 2001, Chapter V), and may explain why fish production is so high. Consequently, declining *S. kneri* populations could result in reduced piscivore populations. My gill net survey data provide a baseline for monitoring long-term changes in fish stocks in response to commercial fishing and to implement future conservation initiatives.

CHAPTER III

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

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 may 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, Klebanoff 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. 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 (Wootton 1993, Marquis and Whelan 1994, Dial and Roughgarden 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 I test for a behavioral response of multiple prey species ($n > 50$) to multiple piscivore species ($n > 7$) using large experimental exclosures (ca. ~ 500 m^2). I 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, I *a priori* divided potential prey fish into size categories and evaluated results based on these groupings. I tested the null hypothesis that there would be no difference in fish abundance or species density among experimental treatments, regardless of fish size.

Methods

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 more than five meters in an annual hydroperiod. During the dry season (January to April), the main river channel contains long (up to 2 km), broad sand banks that constitute a large proportion of river shoreline. River width in the dry season is 40-200 m, water temperatures typically range from 28-36 °C, Secchi depths are approximately 1 m in the main river channel adjacent to beaches, and dissolved oxygen is always near saturation in the main channel.

The river supports at least 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 on-going research, seven species have been identified as the most common large-bodied (total length > 350 mm) piscivores of sand bank 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), I estimate occurrence of these large piscivores typically ranges from 5-40 individuals per 75m stretch of sandbank over a 24 hour period (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 sand banks, 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.

I 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 sand bank. 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 elongate semi-circle shape along ~35 m of sand bank to enclose an area of ca. 500 m^2. The wire mesh was pushed at least 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. I 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 sand bank 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 at day and night using a seine (6.4 m x 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. Deep-water 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 deep water 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 < 40mm; medium > 40mm), 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 (> 4mm and < 4mm) 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 less than 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 sand banks have been estimated to be < 40 mm in length (Layman and Winemiller, *unpublished manuscript*). The largest fish collected in experimental areas was 110 mm, so all fishes between 40 and 110 mm were categorized as "medium". Potential prey fishes on sand banks are highly diverse, both taxonomically (81 genera, 24 families) and functionally (i.e., in terms of feeding strategy, habitat utilization).

I also analyzed stomach contents of the seven most common piscivore species. From January to April during both 2001 and 2002, piscivores were collected on sand bank habitats where the experiments were conducted and on other nearby sand banks. Fishes were collected with gill nets, and by hook and line using artificial lures. Fishes were measured (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 sand banks.

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, but not small individuals, responded to piscivore exclusion (see Results), so additional analyses were conducted on the medium size class.

Specifically, I wanted to know if overall response of medium fishes was attributable to similar patterns of response by multiple taxa. To control for the effect of between-species differences in total abundance, I converted raw species abundance values to Z-scores within each block of the experiment. Z-scores were calculated according to

$$Z = (X_i - \mu) / \sigma$$

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 *i*th species in that block (Zar 1996). A MANOVA was conducted separately for day and night samples with experimental treatment as the independent variable and species standardized abundance (i.e., Z-scores) 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, I also tested for an size-based intraspecific response. Contingency tables were inappropriate for these analyses, 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 above. Standardized abundance (*Z*-scores) then was analyzed using ANOVA and Tukey's post-hoc test. Analyses were conducted using JMP software (Version 4.04, SAS Institute Inc.).

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. CA is an indirect analysis technique used to detect gradients in species composition from observed species abundance (Hill and Gauch 1980, Peet et al. 1988).

CA was conducted using CANOCO 4 (ter Braak & Šmilauer, 1998). Canonical ordination scores were analyzed to assess whether assemblages differed significantly according to treatment or experimental block. I used multivariate analysis of variance (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 (day samples Figure 3; night samples not shown). 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, 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, I performed a MANOVA on standardized species abundance (Z-scores). There was a significant effect of treatment in both day (Wilks' lamda = 0.022, $F_{16,16} = 5.77$, $P = 0.0005$) and night (Wilks' lamda = 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 (Figure 4; all $P \leq 0.05$).

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 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* $F_{2,15} = 0.01$, $P = 0.99$).

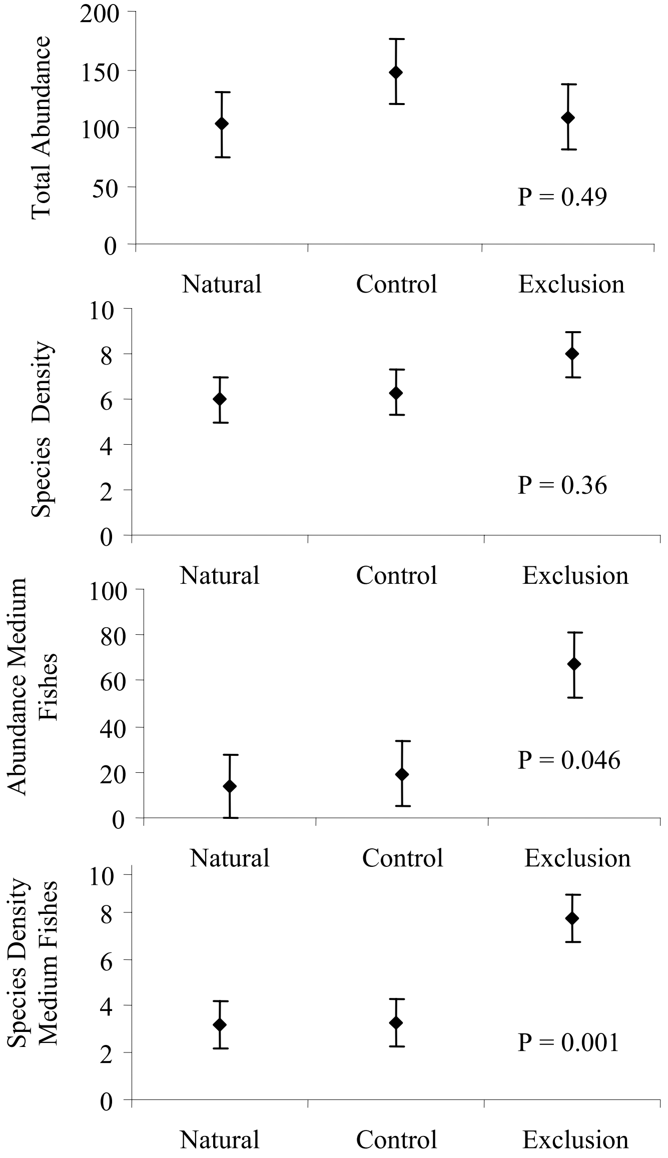


Figure 3. Least-squares means of total abundance and species density of all fishes and medium fishes (40-110 mm) within experimental areas. Total abundance is the number of individuals collected by standardized seine sampling; species density is the number of species collected in this same area. *P* values are from ANOVA on response variables with significant values in boldface. Error bars represent ± one standard error.

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. CA revealed no significant grouping of treatments in ordination space. MANOVA using canonical ordination scores revealed no significant effect of treatment (day: Wilks' lamda = 0.78, $F_{8,14} = 0.64$, $P = 0.73$; night: Wilk's lamda = 0.37, $F_{8,14} = 1.1$, $P = 0.40$). There was a significant experimental block (i.e., location) effect for night (Wilks lamda = 0.005, $F_{20, 24.2} = 4.9$, $P < 0.001$) and marginally significant effect for day (Wilks' lamda = 0.21, $F_{20,24.2} = 1.97$, $P = 0.057$) samples.

I recovered 68 measurable prey fish (by volume, >99% of identifiable stomach contents were fishes) from 449 large-bodied piscivores captured on sand banks (Table 2). Prey sizes in stomach contents coincided with the size class that responded to predator exclusion (Figure 5). Despite high abundance of small fishes on beaches (see Methods section), 90.0% of prey in stomachs were between 40 and 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. Extensive stomach content analyses of the same seven piscivore species collected from lagoons in the Río Cinaruco floodplain revealed significantly smaller prey sizes compared to piscivores from sand banks (Mann-Whitney, T = 19,654.0, $P < 0.001$; sand bank prey standard length = 71.8 ± 24.8; lagoon prey standard length = 34.0 ± 31.2).

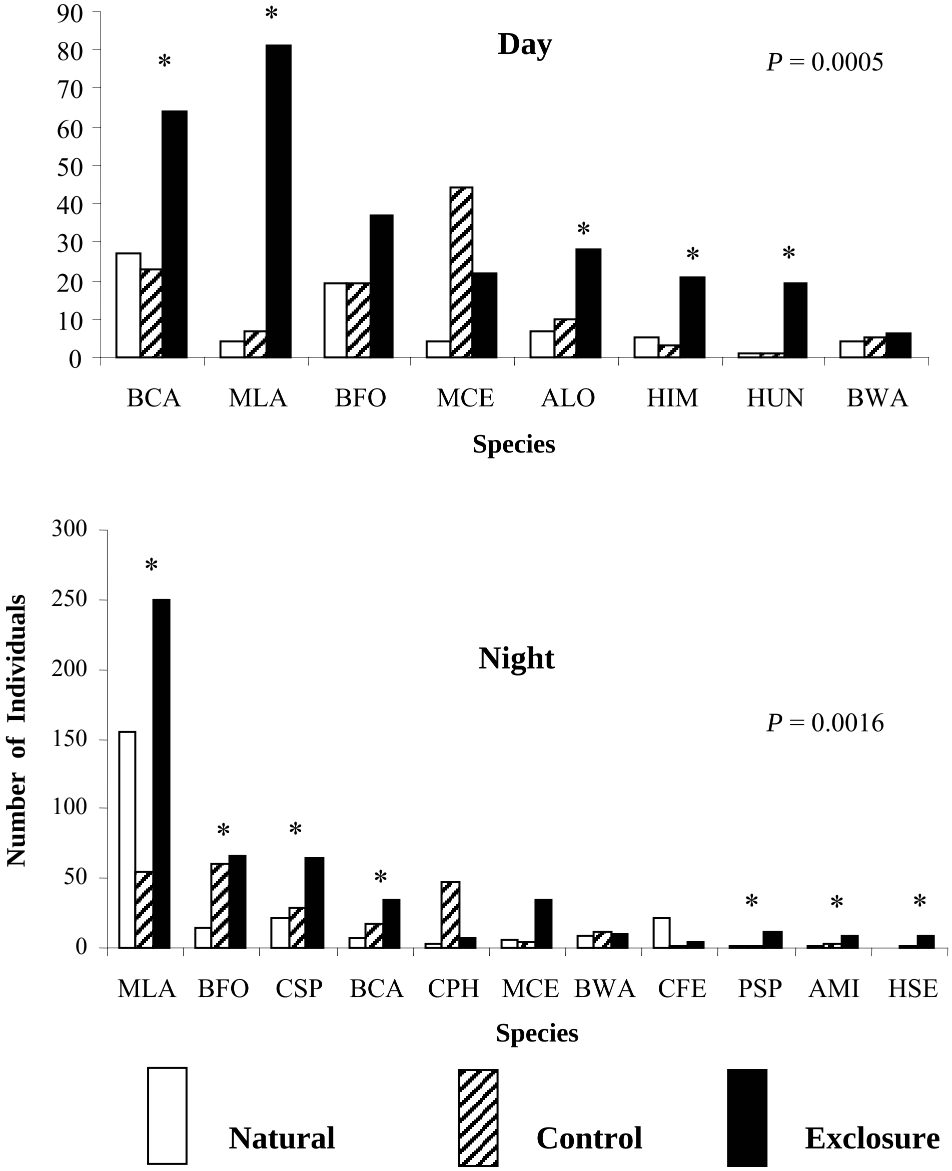


Figure 4. Plots of abundance of individual species among treatments (summed across blocks) in day and night sampling. Rare species (i.e., <10 individuals collected) are not depicted in the figure. Significant univariate tests (i.e., one-way ANOVA, $P < 0.05$) for individual species are indicated with an asterisk. Species codes are: BCA, *Bryconops caudomaculatus*; MLA, *Moenkhausia af. lepidura.*; BFO, *Bivibranchia fowleri*; MCE, *Moenkhausia* cf. *ceros*; ALO, *Argonectes longiceps*; HIM, *Hemiodus immaculatus*; HUN, *Hemiodus unimaculatus*; BWA, *Biotodoa wavrini*; CSP, *Cyphocarax spilurus*; CPH, *Creagrutus phasma*; CFE, *Cyphocarax festivus*; PSP, *Pimelodella* sp.; AMI, *Acestrorhyncus minimus*; HSE, *Hemiodus semitaeniatus*.

TABLE 2. Stomach contents summary of the seven most common piscivores captured on river sand banks in the Rio Cinaruco.

Species	Number Examined	Empty Stomachs (%)	Number of Measured Prey	Prey Length(mm) x (± sd)
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)

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 non-lethal responses in predator-prey interactions (Lima and Dill 1990, Abrams et al. 1996, Lima 1998, Sih et al. 1998, Lima 2002), and highlights the need to incorporate behavioral traits into models of community dynamics (Abrams 1995, Luttbeg and Schmitz 2000, Schmitz 2000).

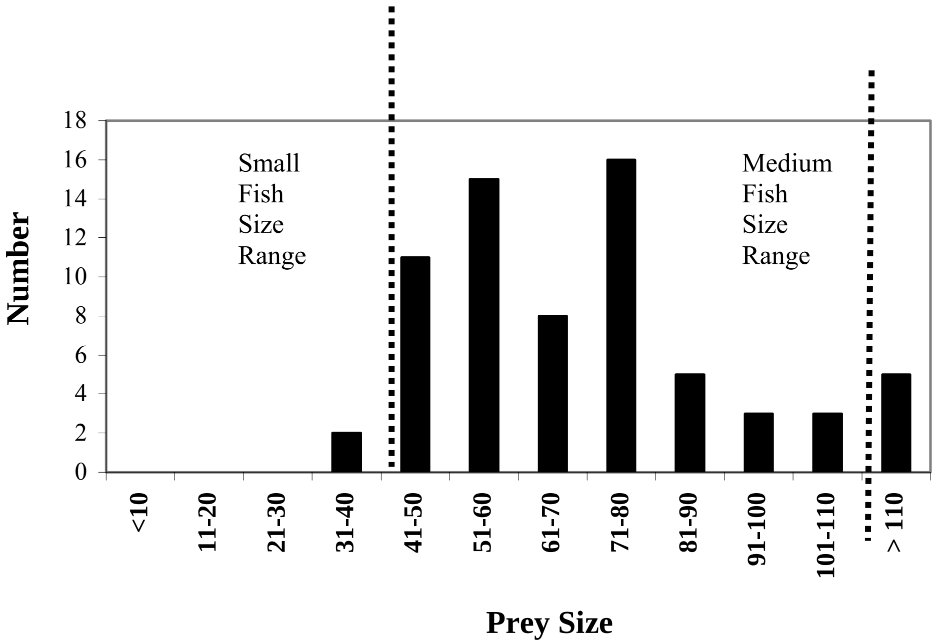


Figure 5. Frequency histogram of prey fishes as determined by stomach content analyses of the seven most common large-bodied piscivores. These data are restricted to those individuals captured on main river sand banks, and data are pooled across piscivore taxa.

Adaptive behavioral responses to predation threat can have significant implications at both community and ecosystem levels. Habitat shifts induced by predators may 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. I am 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 species-specific characteristics can be powerful predictors of the outcome of multi-species 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 can 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 sand banks may select fishes in the medium size range, thereby maximizing profitability (sensu Scharf et al. 2002). In my 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, my 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, Flecker 1996, Pringle and Hamazaki 1997, Pringle et al. 1999, 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 (Layman and 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 mid-water. 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. My 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 may provide a means to aggregate food web elements and facilitate study of complex food webs.

CHAPTER IV

DO SPECIES TRAITS CHARACTERIZE CHANGES IN FISH ASSEMBLAGE COMPOSITION FOLLOWING COMMERCIAL NETTING?

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 impacts of human activities. Perturbations propagate through multiple trophic and non-trophic pathways rendering it difficult to predict impacts, especially 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 (Box 1981, Keddy 1992, 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 (Peterson and Andre 1980, 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 natural and anthropogenic impacts to food webs.

Net fishing is one of the most common human influences in tropical inland waters, and it 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, Gophen et al. 1995, Crisman et al. 2003), but there have been few studies in tropical freshwater systems that examine effects following piscivore removal (ICES-SCOR 2000). In the Río Cinaruco, Venezuela, netters substantially reduce population sizes of large-bodied piscivores in some lagoons of the floodplain landscape. I previously simulated commercial netting effects by excluding large-bodied piscivores on sand bank habitats of the river (exclusion areas ca. 500 m^2). Piscivore exclusion resulted in significant changes in assemblage composition, indicating effects of large piscivores on both small piscivores and medium-sized fishes at lower trophic levels (Layman and Winemiller 2004). Assemblage differences were best characterized by the body size of prey taxa, suggesting phenotypic characteristics might be useful in predicting landscape-scale effects of commercial netting.

In this study, I tested the utility of phenotypic traits in characterizing differences in fish assemblages of netted and un-netted lagoons. I specifically assessed whether, as suggested by experimental manipulations, body size could be used to generalize assemblage differences following piscivore removal from lagoons. Since body shape is related to ecological attributes (e.g., predator vulnerability, swimming performance, feeding behavior) in many fish taxa (Keast and Webb, 1966; Winemiller 1991; Wainwright and Richard, 1995), I additionally examined whether morphology of prey species could characterize netting effects at the landscape-scale. I examined a sub-set of the overall food web, i.e., a food web module (sensu Holt 1997), that includes the most important prey species of large-bodied piscivores. My objectives were: (1) to describe differences in fish assemblage structure between netted and un-netted lagoons within this food web module, and (2) investigate whether prey size and/or other morphological characteristics can be used to generalize these differences.

Methods

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 (Jepsen et al. 1997, Winemiller et al. 1997, Arrington and Winemiller 2003, Winemiller and Jepsen 2003). The river has a strongly seasonal hydrology with water levels typically fluctuating > 5m 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 in floodplain and channel habitats (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 semi-circle using a small boat, and then pulled onto shore. I classified lagoons *a priori* as either netted or un-netted based on visual monitoring throughout two dry seasons (January-April) of 2002 and 2003. Evidence of netting activity was either direct observation of netters, or piles of discarded carcasses from the fish by-catch (e.g., *Hoplias malabaricus*, *Geophagus* spp.) on lagoon shorelines following netting. 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 “un-netted” were those in which I never observed any evidence of netting activity. Seven lagoons in 2002 (4 un-netted and 3 netted) and 8 in 2003 (5 un-netted and 3 netted) met these criteria and were included in this study. None of the lagoons used were netted in one year and un-netted in the other. Lagoon accessibility largely determined netting status, and thus there were no systematic differences between netted and un-netted 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 ($t = 1.7$, $p = 0.13$) .

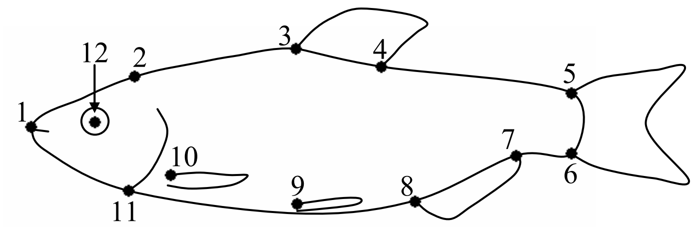
Netters target high-value fish species, including the most common large-bodied piscivores (peacock cichlids *Cichla orinocensis* and *C. temensis*, and a characiform *Hydrolycus armatus*). Lagoons are never depleted completely of piscivores due to net avoidance/ escapement and immigration from the main river channel, but catch-per-unit-effort (CPUE) estimates of *Cichla* spp. and *H. armatus* in netted and un-netted lagoons suggest population sizes may be reduced 50% or more by netters. Based on standardized hook and line fishing (the most effective methodology to capture *Cichla*), 6.0 *Cichla* individuals were collected per 100 casts in un-netted lagoons, compared to less than 2.4 in netted lagoons (CPUE data summed for 2002 and 2003; total casts = 4856). In standardized gill net sampling (a more effective method of capturing *H. armatus*), an average of 6.2 *H. armatus* were collected in 24-hour sampling periods in un-netted lagoons, compared with 2.5 in netted lagoons (total gill netting hours = 2,736).

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 efficiently collected by cast netting, and this methodology (relative to seining, gill netting, etc.) was likely to reflect differences in prey fish assemblage structure among netted and un-netted lagoons. In doing so, I was 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 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 ca. ~ 4.5 m^2) and all fishes were identified to species, enumerated, and measured to the nearest 1.0 mm standard length (SL). Voucher specimens are archived in the Museo de Ciencias Naturales at UNELLEZ, Guanare, Venezuela, and the Texas Cooperative Wildlife Collection, College Station, Texas, USA.

Non-metric multidimensional scaling (MDS) was used to compare fish assemblage similarity/dissimilarity based on relative abundances of individual taxa. MDS constructs a 2-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). I conducted a nested multivariate analysis of variance (MANOVA) using the two MDS axes as dependent variables to test for effects of netting regime (netted vs. un-netted) 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 un-netted 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, I 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 two 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, USA. I digitized 12 landmarks on each image using tpsDig (Rohlf 2002) for geometric morphometric analysis. Location of landmarks and examples illustrating the range of inter-specific variation among fish species in body size and shape are depicted in Figure 6.

I conducted a relative warp analysis (RWA) of superimposed landmark coordinates using tpsRelw (Rohlf 2002). For more information on RWA and other geometric morphometric techniques, see Bookstein (1991), Rohlf and Marcus (1993), and Marcus et al. (1996). Essentially, RWA 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 RW axis represents a set of specific morphological characteristics, allowing particular morphological attributes of species to be analyzed directly. Since RWA scales specimens to a common centroid size, size differences among species are removed from the analysis permitting an evaluation of morphology



Consensus of Landmark Positions
(generalized fish)

a)

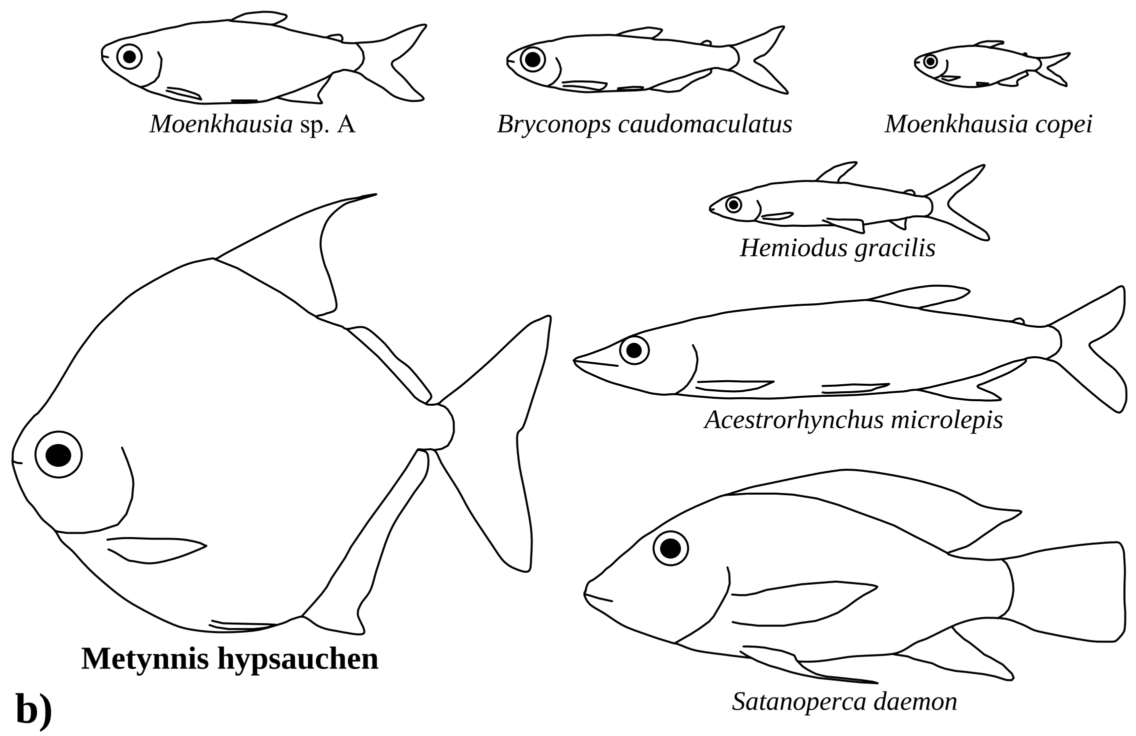


Figure 6. Landmarks used for morphometric analyses and illustration of variation in size and morphology of fish assemblages. a) Consensus landmark configuration depicting average position of the 12 digitized landmarks. b) Seven fish species illustrating variability of body forms observed within this food web module. Size of species (mean size of individuals of each species collected in this study) is drawn to scale.

largely independent of size. I calculated the average score on each relative warp ($n = 20$) for each species.

I evaluated three questions: (1) Do morphologically similar species exhibit similar patterns of abundance in netted/un-netted lagoons?; (2) Can any particular morphological axis (i.e., multivariate description of shape variation) be used to differentiate abundance of species in netted/un-netted lagoons?; (3) Considered simultaneously, does body size or shape better characterize assemblage differences? To answer these questions, I quantified catch per unit effort (CPUE, i.e., mean abundance of individuals per sample) differences among netted and un-netted lagoons ($\Delta\text{CPUE} = \text{CPUE}_{\text{netted}} - \text{CPUE}_{\text{un-netted}}$; data pooled across years) for each species and evaluated body shape variation among species using RWA and MDS.

For the first question, I constructed a 2-dimensional morphospace representing similarity/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 ANOSIM, I tested whether ordination in morphospace differed among four categories of response to netting: much more abundant in netted lagoons ($\Delta\text{CPUE} > 0.5$), moderately more abundant in netted lagoons ($0.0 < \Delta\text{CPUE} < 0.5$), moderately more abundant in un-netted lagoons ($-0.5 < \Delta\text{CPUE} < 0.0$), and much more abundant in un-netted lagoons ($\Delta\text{CPUE} < -0.5$). These classifications were used because ANOSIM evaluates differences based on categorical variables. Using these two axes, I conducted a canonical variates analysis (CVA) to test for a multivariate relationship between body shape and

ΔCPUE. This analysis explicitly addressed whether morphologically similar species exhibited similar patterns of abundance.

To answer my second question, I tested for a correlation between ΔCPUE, and each of the 20 relative warps. I used Bonferroni adjusted *P*-values for multiple comparisons to test for significance. My 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 length frequency analysis, Figure 3), I placed each species into one of two size classes (SL < 40 mm, SL > 40 mm). I performed a general linear model evaluating differences in species abundances between netted and un-netted lagoons (ΔCPUE, the response variable) as predicted by size class and the two morphological axes generated by MDS. I tested for interactions among effects and found no significant interaction, and thus excluded all interactions in the final model.

Results

A total of 2,633 individual fishes representing 40 species were collected using the standardized cast-netting protocol. Twenty of the 40 taxa were collected rarely (5 or less 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; un-netted = 17 ± 15), but not in 2002 (Mann-Whitney U, $P = 0.34$; netted = 85

± 54; un-netted = 76 ± 85). Species density (sensu Gotelli and Colwell 2001) per sample also was significantly higher in netted lagoons in 2003 (t-test, $p = 0.042$; netted = 5.8 ± 3.5; un-netted = 3.6 ± 1.8), but not in 2002 (t-test, $p = 0.14$; netted 6.8 ± 1.6; un-netted = 5.6 ± 2.1). Taxa were variable in size (11-257 mm SL) and morphology (see Figure 6). Taxa collected included pelagic characids and hemiodids (e.g., *Moenkhausia* sp. A, *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 un-netted 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 ($F_{10,32} = 1.26$, $p = 0.29$) (Figure 7). Thus, although differences in composition of netted and un-netted 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 Figure 7). During both years, netted lagoon sites were dominated numerically by *Moenkhausia* sp. af. *lepidura* (2002, 44% of individuals collected; 70%, 2003). In un-netted lagoons, *Moenkhausia* sp. 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 un-netted lagoons, 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. There

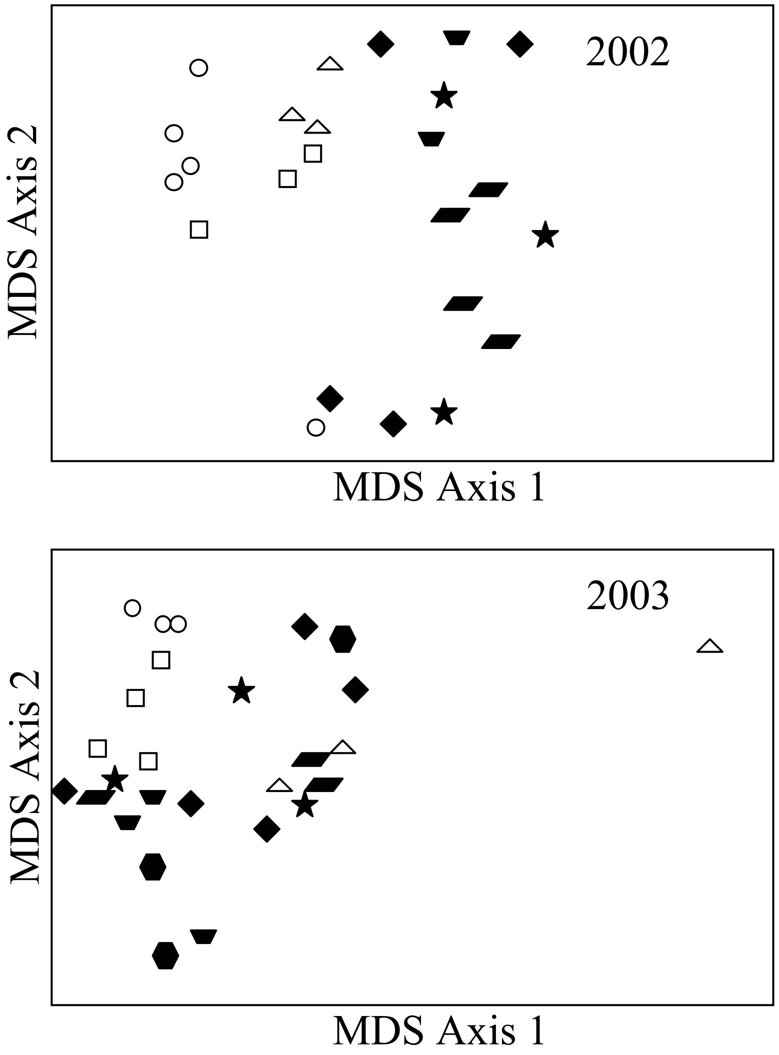


Figure 7. Differences in species assemblage composition as reflected by nonmetric multidimensional scaling. MANOVA revealed significant differences in assemblage composition between netted and un-netted lagoons in both years. Each symbol represents a different lagoon; open symbols are sites in netted lagoons and filled symbols sites in un-netted lagoons.

also was a significant effect of lagoon during both 2002 (ANOSIM, $p = 0.003$) and 2003 ($p = 0.001$).

I found significant differences in overall size distribution of fishes, regardless of species (i.e., individual-level analysis), between netted and un-netted lagoons for both years (Mann-Whitney U Test, $p < 0.001$, both years; Figure 8). Un-netted lagoons were dominated by fishes < 40 mm SL. This was largely accounted for by the two most common species in un-netted lagoon samples, *M. copei* (SL ± SD, 35.5 ± 3.7) and *Hemigrammus* sp. (16.8 ± 1.0). In netted lagoons, there was a peak both years in fishes 61-70 mm, accounted for largely by *Moenkhausia* sp. af. *lepidura* (66.9 ± 5.1). Other larger species, including *Bryconops caudomaculatus*, *Acestrorhynchus microlepis*, and *A. 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 attributable to apparent reduced netting activity during January-February 2003 which could have removed fewer piscivores and resulted in less distinct divergence in faunal composition.

In morphological analyses, CVA found no significant association between body morphology and ΔCPUE ($F_{2,17} = 0.13$, $p = 0.88$). Although species exhibited distinct differences in morphological features, these differences/similarities were not correlated with abundance patterns in netted/un-netted lagoons. After Bonferroni adjustment (i.e., using significance level of $p= 0.0025$), no correlations among RWs ($n = 20$) and ΔCPUE were significant (Table 3; the first two RWs accounting for 72.6% of the total

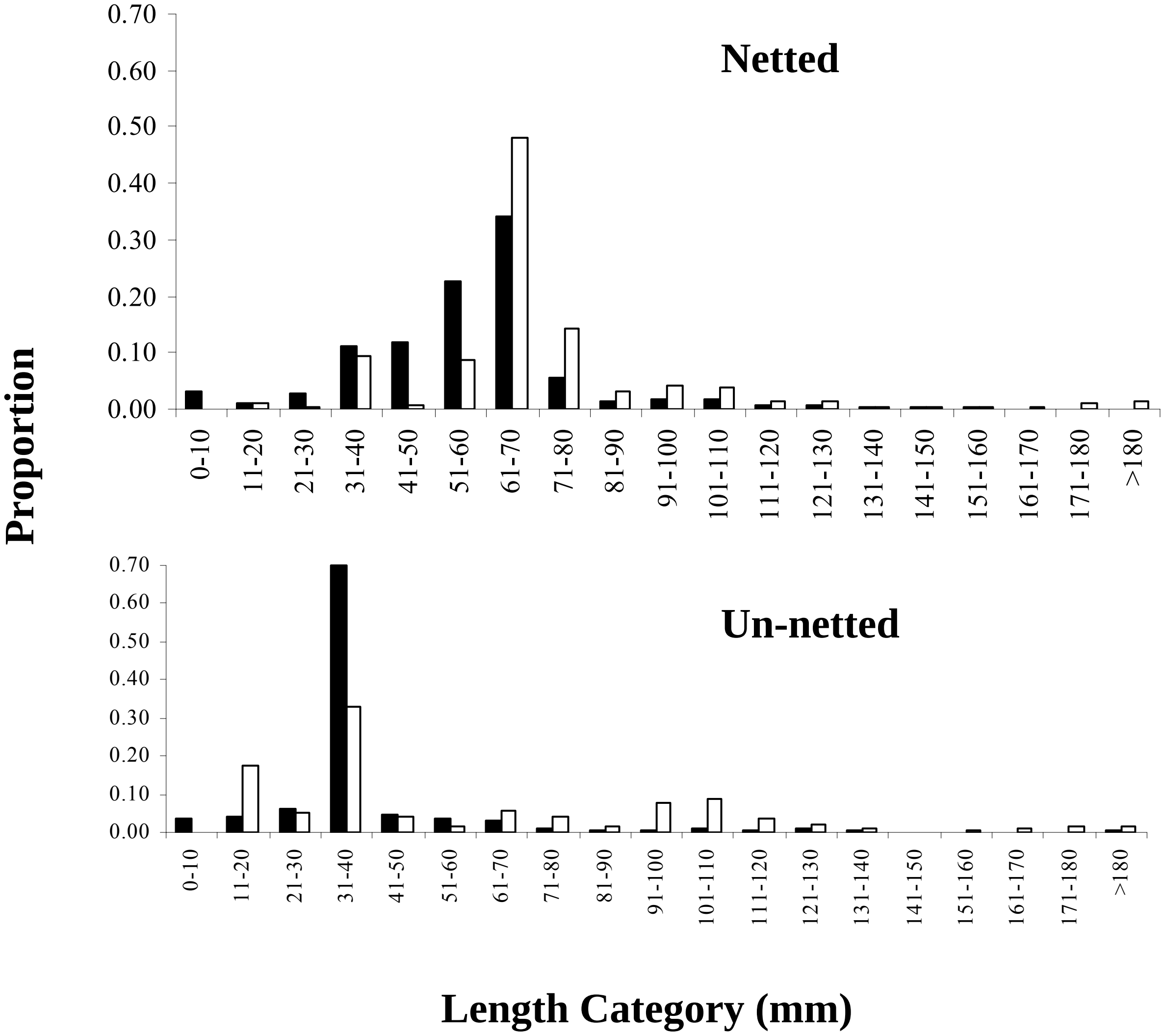


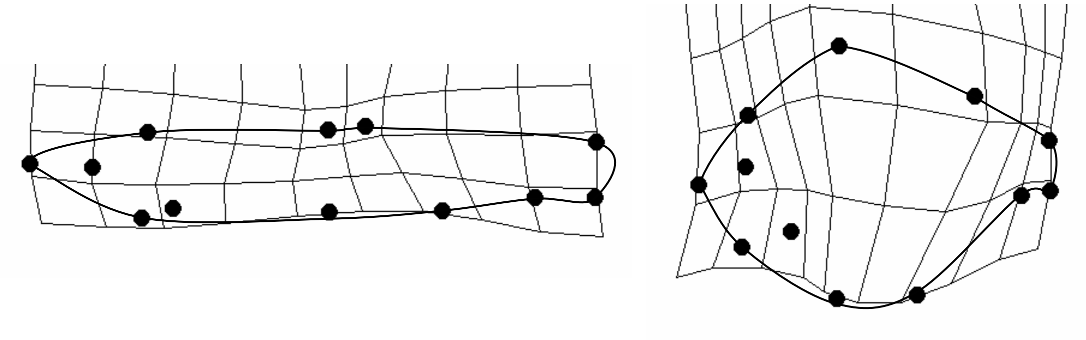
Figure 8. Length frequency histograms showing different size structures of assemblages in netted and un-netted lagoons. Bars represent proportion of total fishes collected in each size category. Filled bars 2002; Open bars 2003.

TABLE 3. Descriptive information and correlation statistics for the first ten relative warps (explaining approximately 99% of morphological variance). None of the correlations between relative warps (*n* = 20) and ΔCPUE were significant using Bonferroni correction for multiple comparisons. With Bonferroni adjustment, I used a significance level of P = 0.0025.

Warp	Relative % variance explained	Cumulative % variance explained	Correlation with ΔCPUE	
			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

morphological variance, are depicted in Figure 9). One relative warp (RW 20, explaining only 0.03% of morphological variance) was highly correlated with ΔCPUE before Bonferroni correction (R = 0.56, *p* = 0.011). Visual inspection suggested this relative warp described subtle morphological differences between species < 40 mm and > 40 mm SL. I tested this hypothesis using a *t*-test and found significant differences in RW 20 values between the two size classes of fish ($R^2 = 0.30$, *p* = 0.013). Thus, the only morphological attribute that characterized ecological patterns between netted and un-netted lagoons primarily described differences between these two size classes of fish.

RW 1 (51.5% of variance)



RW 2 (21.1% of variance)

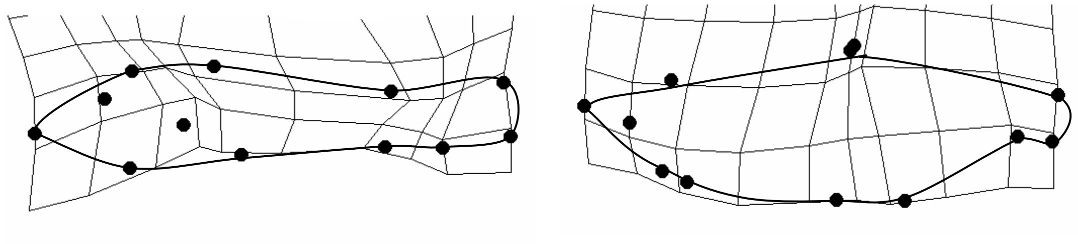


Figure 9. Thin-plate spline transformations of landmark coordinates depicting morphological characteristics described by the first two relative warps (accounting for 72.6% of the morphological variance). Low values of relative warps are on the left, high values on the right.

In a general linear model examining effects of size class and morphology on ΔCPUE, I 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, I found no evidence that morphological features could be used to characterize differences in netted and un-netted lagoons, whereas a simple size class categorization could be used to assess effects of commercial netting. This species-level analysis indicated that species > 40 mm SL exhibited greater abundance in commercially netted lagoons, and species < 40 mm SL were more abundant in un-netted lagoons. Thus, differences in length distributions revealed by individual-level analysis (Figure 8) were not solely due to differences exhibited by a few species.

Discussion

Prey size, but not other morphological traits, was associated with differences in assemblage composition in lagoons exploited by commercial netters. 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 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 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 my results suggest that size can be used to assess fishing effects even in this complex food web.

Following other studies of lake/lagoon-scale patterns of community structure (Tonn and Magnuson 1982, Rahel 1984, Robinson and Tonn 1989, Tonn et al. 1990, Rodríguez and Lewis 1994, Rodríguez and Lewis 1997), I employed a comparative-based approach, and analyzed patterns based on an underlying variable. Rodríguez and Lewis (1997) demonstrated how 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 I based my comparison *a priori* on a single categorical variable (netting history). Together, these studies demonstrate piscivory is an important factor structuring fish assemblages in floodplain lagoons of the Orinoco basin. Similar to the study of Rodríguez and Lewis (1994), I suggest that species-specific differences in vulnerability to piscivores strongly influences assemblage composition during the dry season. However, my results suggest that, at least within this food web module, predator vulnerability is largely determined by body size and not shape.

In large-scale comparative studies, mechanisms (sensu Dunham and Beaupre 1998) determining relative abundance of organisms may not be demonstrated directly, but additional data can be used to strengthen inferences about underlying causes of observed patterns. In netted lagoons, the most abundant prey were 51-70 mm SL, corresponding to the size range of fishes that responded to piscivore exclusion in experimental manipulations (Layman and Winemiller 2004). *Moenkhausia* sp. af.

lepidura and *Bryconops caudomaculatus* displayed the most significant response to piscivore exclusion, and also displayed the largest ΔCPUE in the present study. Moreover, stomach content analyses indicate that large-bodied piscivores target fish > 40 mm in length (Jepsen et al. 1997, Winemiller et al. 1997, Layman et al. 2004). Together, experimental manipulations, stomach content analyses, and large-scale patterns based on *a priori* designations, strongly suggest that reduced densities of piscivores from harvesting results in major differences in fish assemblage structure in netted lagoons.

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 (Werner 1974, Mittelbach 1981, Magnhagen 1985, Blaxter 1986, Hoyle and Keast 1987, Sih and Moore 1990, Juanes and Conover 1994, Christensen 1996, Mittelbach and Persson 1998, Sih and Christensen 2001, Scharf et al. 2002). Large-bodied piscivores in the Río Cinaruco likely maximize profitability by feeding primarily on larger fishes, especially abundant algivores/detritivores that allow them to exploit short, productive food chains (Layman et al. 2004). Gape limitation may influence size of prey consumed (Webb 1986, Hambright 1991, Nilsson et al. 1995, Persson et al. 1996, Nilsson and Brönmark 2000), but body depths of >97% of individuals sampled in this study are unlikely to exceed gape limits of adult large-bodied piscivores, and thus should not significantly limit prey choice. Thus, by preferentially consuming larger prey species, piscivores may allow smaller prey to dominate fish assemblages. Commercial netting reduces densities of large-bodied piscivores, allowing larger prey fishes to 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, He et al. 1994, Post et al. 1997).

Why is morphology less useful in describing differences in assemblage composition? In general, 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. Taxa with defensive spines (*Pimelodella* spp.), armour (*Scorpiodoras* spp., *Leptodoras* sp.), and cryptic morphologies (*Microglanis* sp.) have been recovered in stomach contents analyses of Cianruco piscivores (Layman et al., *unpublished data*). Diet breadths of these fishes indicate relatively low dietary electivity, perhaps mediated by predator and prey behavior and prey densities. 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 (Sih and Christensen 2001) may be relatively more important than constraints imposed by prey morphologies (Webb 1986, Wahl and Stein 1988, Hambright 1991, Einfalt and Wahl 1997). Foraging opportunism has been inferred by other studies conducted in tropical floodplain rivers (Jepsen et al. 1997, Jepsen and Winemiller 2002), and my results provide further evidence that interspecific morphological differences, at least within this food web module, are not strong determinants of predator-prey interactions.

There is continuing discussion as to whether lumping or grouping species into “kinds of organisms”, trophospecies, or functional groups is useful when modeling food webs (Cohen 1978, Sugihara et al. 1997, Chapin et al. 1998, Solow and Beet 1998, Wilson 1999, Yodzis and Winemiller 1999, Schmitz and Sokol-Hessner 2002, Chalcraft and Resetarits 2003). My study revealed that fish size, but not other morphological characteristics, could be used to group diverse prey taxa in order to predict assemblage changes following a specific perturbation, i.e., size selective predation. 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.

CHAPTER V

BODY SIZE, TROPHIC POSITION, AND SPECIES DIVERSITY IN A SPECIES-RICH FOOD WEB

Introduction

A better understanding of species-rich, tropical, food webs, including those of some of the most threatened ecosystems on the planet (e.g., rain forests, coral reefs, and freshwater lotic systems), is critical to stem biodiversity loss and assess community- and ecosystem-level responses to human-induced habitat change. Body size-based descriptions of trophic structure have long been acknowledged as a primary tool in food web ecology (Elton 1927), and increasingly they are being applied to analyze structure of complex food webs (Warren and Lawton 1987, Cohen et al. 1993, Memmott et al. 2000, Williams and Martinez 2000, Kerr and Dickie 2001, Cohen et al. 2003). Trophic position (i.e., the average level, relative to primary producers, at which an organism feeds) often increases with body-size (Cohen et al. 1993, France et al. 1998, Jennings et al. 2001, Woodward and Hildrew 2002, Jennings and Mackinson 2003), and this relationship results in predictable consequences of human-induced perturbations to food web structure. For example, in marine systems, commercial fisheries generally results in an overall reduction in food chain length (Rice and Gislason 1996, Pauly et al. 1998).

Similar analytical approaches may be especially useful in reticulate food webs of species-rich tropical ecosystems where traditional ecological approaches (e.g., pair-wise species manipulations) often do not provide robust predictive ability, largely because of complex, indirect, and diffuse effects of perturbations (McCann et al. 1998, Yodzis 2000). In the present study, I examine the relationship between predator and prey mean body size, and between predator body size and trophic position, within a guild of predatory fish in the species-rich Cinaruco River (Venezuela). By combining stable isotope ratio and stomach content analyses, I was able to evaluate explicitly the relationship between trophic position and predator body size. Mean body size of predatory fish taxa and mean body size of their prey were significantly correlated, but trophic position of predator taxa was not correlated with body size. This is attributed to the lack of relationship between body size and trophic position of prey taxa on which the predatory fish feed, as the diversity of primary consumers allows all predators to exploit short, productive food chains.

Methods

The Cinaruco River is a tropical tributary of the Orinoco River that drains the llanos (savanna) of southern Venezuela (6º 32' N, 67º 24' W). The Cinaruco is an oligotrophic, moderate blackwater floodplain river with high levels of dissolved organic carbon and low pH. Hydrology is strongly seasonal, with water levels fluctuating more than 5 m annually (Arrington and Winemiller 2003). Maximum width of the main channel during the dry season is 50-200 m. The river supports a diverse fish community (>280 species), with taxa representing a wide range of ecological attributes and life history strategies (Layman and Winemiller 2004, Layman et al. 2004)

Predatory fish were collected with gill nets, cast nets, and by hook and line using artificial lures, from 1993-2003, and data for all years are pooled for these analyses. *Cichla* spp. 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 (Layman and Winemiller 2004). All other species were euthanized, and stomachs removed for examination. All stomach contents were quantified volumetrically. The majority of identifiable prey items were fish (Table 1), so I restrict size-based analysis of prey to fish taxa. Often prey items were partially digested and could only be identified to genus, particularly among closely related and morphologically similar taxa. Thus, fish prey were lumped at the generic level, and only those identified to genus were included in prey trophic position estimates. Body mass and length produce similar predator-prey size-based patterns (Jennings et al. 2001, Cohen et al. 2003), and I present data based on the latter. All predator and prey individuals were measured (SL, ±1.0 mm) in the field.

Collection, preservation, and preparation of tissues for stable isotope analyses follow Arrington and Winemiller (2002), and estimation of trophic position follows Layman et al. (2004). Primary consumers provide the best baseline for estimation of trophic position using $\delta^{15}N$ values, because they integrate temporal and spatial variation in isotopic signatures of basal resources (Post 2002). I identified two fish species, *Semaprochilodus kneri* (Characiformes: Prochilodontidae) and *Metynnis hypsauchen* (Characiformes: Characidae) that integrate the dominant source pools of primary production in the system: (1) *S. kneri* for autochthonous algal/detrital resources, and (2) *M. hypsauchen* for allocthonous C_3 plant material. I used a standard 2-source mixing model (Post 2002) to estimate trophic position of predators using these baseline taxa. I employ a mean $\delta^{15}N$ enrichment of 2.54 ‰ to estimate trophic position, following Vanderklift and Ponsard (2003). This is a lower enrichment value than is commonly used (Post 2002), and thus my estimates of predator trophic position may represent upper estimates. Samples were not available for some rare taxa, and these taxa are not included in trophic position analyses.

Results

I analyzed 5,439 stomachs of 31 predator species representing 8 fish families (Table 1). Mean predator size ranged from 69.2±5.9 to 458.2±89.7 mm (mean ± 1 SD) among species. Identifiable prey in fish stomachs included individuals from 35 fish genera, with measurable individuals varying from 5 to 225 mm. There was no correlation between mean predator size and the percentage (by volume) of total identifiable stomach contents that were fish (Table 4, $F_{1,30} = 0.13$, $P = 0.72$, $R^2 = 0.005$). The number of predator species in which each prey genus was identified (an estimate of prey "vulnerability", see Schoener 1989) decreased with increasing mean prey size (Figure 10, $F_{1,33} = 10.5$, $P = 0.003$, $R^2 = 0.24$), as based on measurable prey recovered in stomachs. Eighteen predator species had multiple identifiable and measurable fish in their stomach, and were included in size-based analyses. The mean size of prey individuals recovered from each predatory fish species was significantly correlated to the mean size of the predator (Figure 11A, $F_{1,17} = 19.4$, $P < 0.001$, $R^2 = 0.55$).

Predator trophic position, estimated using stable isotopes, was independent of predator size (Figure 11B, $F_{1,20} = 0.19$, $P = 0.68$, $R^2 = 0.001$, total isotope samples analyzed = 403). To examine this pattern further, I used stable isotope ratios to estimate mean trophic position of all prey genera recovered from piscivore stomachs.

Table 4. Species on which stomach content analyses were conducted. N represents the total number of individual predators (i.e., stomachs) examined, and % fish the volumetric proportion of stomach contents identifiable as fish remains.

Species	Mean SL (mm)	N	% Fish
Pseudoplaystoma fasciatum	458.2 (±89.7)	77	98.1
Platynematichthys notatus	428.2 (±74.5)	30	100.0
Raphiodon vulpinnis	397.5 (±21.2)	11	40.0
Pseudoplaystoma tigrinum	382.7 (±100.0)	3	100.0
Boulengerella cuvieri	361.5 (±59.1)	292	100.0
Pellona castellnaeana	356.6 (±86.5)	52	61.9
Cichla temensis	356.3 (±87.1)	1365	100.0
Boulengerella lucius	343.1 (±50.5)	411	100.0
Ageniosis brevifilis	340.5 (±97.9)	4	33.3
Cichla intermedia	333.6 (±50.9)	307	97.6
Leiarius marmoratus	312.2 (±46.8)	5	100.0
Plagioscion squamossissimus	310.2 (±53.1)	115	94.7
Hydrolycus armatus	304.9 (±64.3)	510	100.0
Hoplias malabaricus	302.0 (±56.9)	39	100.0
Cichla orinocensis	301.5 (±49.7)	755	99.8
Brycon sp. A	297.5 (±116.7)	4	16.7
Boulengerella maculata	283.7 (±36.0)	22	100.0
Serrasalmus manueli	236.8 (±65.2)	597	93.1
Crenicichla af. *legubris*	228.6 (±31.8)	24	90.5
Serrasalmus rhombeus	217.5 (±37.6)	67	91.8
Pygocentris caribe	193.1 (±36.4)	17	91.6
Cynodon gibbus	191.2 (±34.7)	44	50.0
Acestrorhynchus falcirostris	189.2 (±73.2)	12	100.0
Brycon falcatus	178.1 (±34.5)	11	80.0
Agoniates anchovia	170.0 (±17.7)	14	100.0
Serrasalmus medinai	161.7 (±33.6)	16	38.3
Serrasalmus altuvei	161.0 (±35.4)	29	84.6
Pristobrycon striolatus	145.9 (±26.6)	58	61.6
Acestrorhynchus microlepis	107.9 (±19)	464	96.9
Acestrorhynchus grandoculis	90.0 (±8.9)	19	100.0
Acestrorhynchus minimus	69.2 (±5.9)	65	100.0

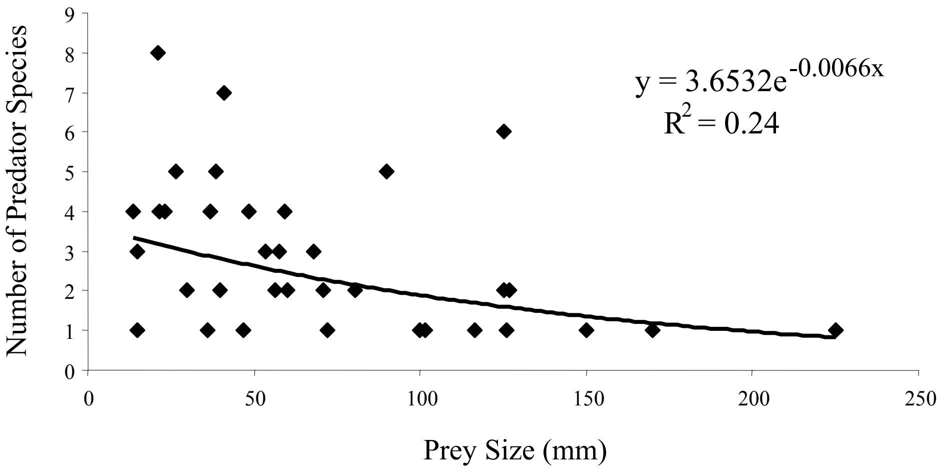


Figure 10. Relationship between mean prey size (SL of prey recovered from predator stomachs) and the number of predator species in which each prey taxa (i.e., genus) was identified.

Taxa analyzed for isotopes were collected independently (i.e., individuals analyzed were not from predator estimate mean trophic position of all prey genera recovered from piscivore stomachs), and generally were in the same size range as individuals recovered from stomachs. Mean body size and estimated trophic position were not correlated for prey genera (Figure 11C, $F_{1,30} = 0.006$, $P = 0.94$, $R^2 = 0.0002$; total isotope samples analyzed = 617). A genus of detritivorous fishes (*Curimata* spp., estimated trophic position = 2.08 ± 0.38) had the third largest mean body size in piscivore stomachs (150 mm), whereas the second smallest prey genera (*Apistogramma* sp., 15 mm) had the second highest estimated trophic position (3.5), both examples of the lack of positive relationship between prey body size and trophic position.

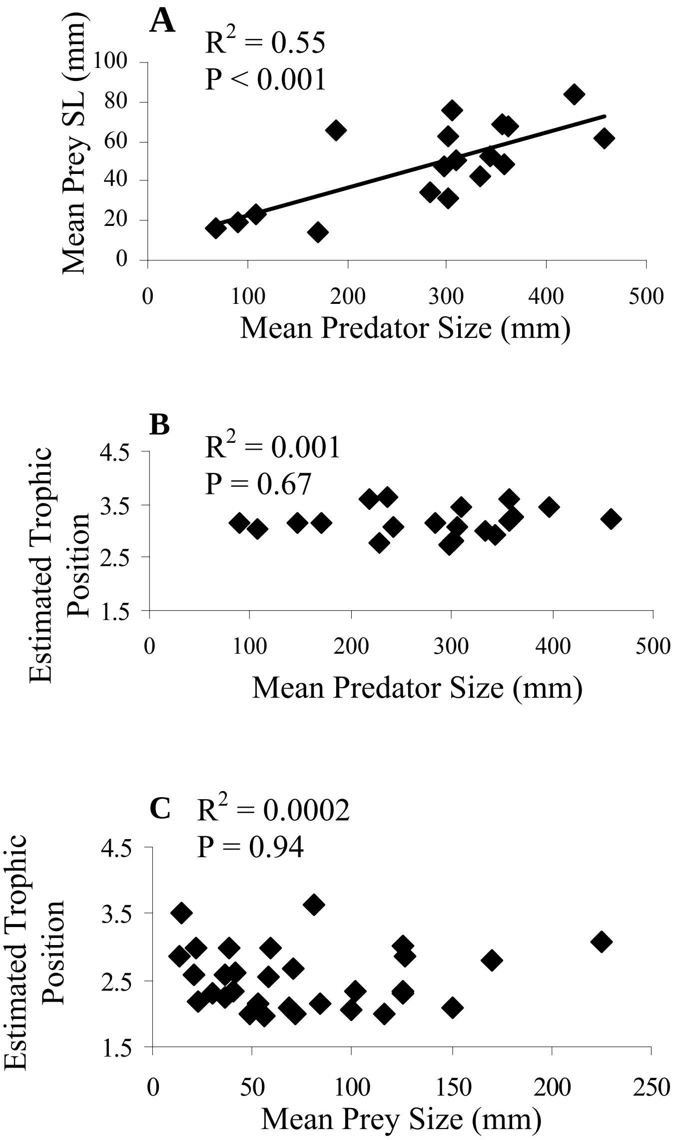


Figure 11. Relationship between (A) mean predator and prey body size (SL), (B) estimated trophic position of predators (based on stable isotope analysis) and body size, and (C) estimated trophic position of prey and their body size.

Discussion

I found no relationship between body size and trophic position of predators, a pattern that reflects the underlying species diversity of this food web. In tropical rivers, primary consumers (i.e., algivore/detritivores) are abundant and diverse in terms of size, morphology, and habitat affinity (Winemiller 1990, Flecker 1992). In the Cinaruco River, they exhibit a range of body sizes from some of the smallest (e.g., loricariid catfishes) to among the largest (*Semaprochilodus laticeps*) individuals in the fish community. There is also substantial morphological and behavioral diversity within the predatory fish guild. All predators in this system thus can maximize profitability (sensu Scharf et al. 2002) both by feeding on optimally-sized prey and, importantly, by exploiting short, productive, food chains. This compressed food web structure appears to be one of the primary reasons tropical floodplain rivers support such high levels of secondary production (Lewis et al. 2001, Layman et al. 2004). Ontogenetic changes in diet composition by individuals (Winemiller 1990, Woodward and Hildrew 2002) may have little effect on trophic position, because fish consumed by piscivores may feed at or below the trophic level of invertebrates (primary food resource of juvenile predators). It has long been recognized that most food chains are short (Elton 1927), but the Cinuraco River supports an especially compressed food web structure in which all predators seem to feed low in the food web.

This web structure seems to distinguish tropical lotic food webs from other systems where weak relationships between fish body size and trophic position have been described (Jennings et al. 2001, Jennings et al. 2002). Jennings et al. (2001) describe webs in which secondary consumer $\delta^{15}N$ values are more variable, and predators are apparently are not concentrated around a trophic position of 3. Since in both systems predatory fishes were examined, and approximately the same range in mean body lengths is included (~1 order of magnitude), the differences likely reflect distinct underlying food web structure. This intrinsic difference between trophic structure suggests that trophic level will not increase continuously with body mass in the whole Cinaruco food web, further distinguishing tropical lotic webs (France et al. 1998, Jennings et al. 2001, Jennings et al. 2002).

Although size alone may have limited value in predicting trophic position in diverse food webs, a combined approach which incorporates size and morphology may be more powerful. Morphology is often an indication of feeding strategy of fishes (Winemiller 1991), and thus may be used to predict trophic position. Multivariate ordination techniques (controlling for effects of body size) reveal distinct groupings of morphologically similar taxa within a module (sensu Holt 1997) of the Cinaruco River food web, and stable isotope ratios suggest these morphologically-related fish also occupy similar trophic positions (Layman, *unpublished work*). *Semaprochilodus* spp. and *Curimata* spp. are two of the most abundant detritivore genera in the river and, despite being distantly related (i.e., two separate families), have very similar morphology and estimated trophic position (2.0 and 2.08, respectively).

Food web structure largely determines system response to human exploitation. Human fishing pressure has been shown to reduce food chain length in marine fish communities, thereby “fishing down the food web” (Pauly et al. 1998). My data suggest a different effect of commercial fishing in the Cinaruco River. Commercial netters target large-bodied fishes, including both large-bodied predators and algivore-detritivores (Layman and Winemiller 2004, Layman et al. 2004). Removal of large-bodied predatory fishes will not decrease food chain length, because smaller predators (that are not removed by netters) feed at a similar trophic position as the large species. Removal of abundant algivore/detritivores (e.g., *S. kneri*), however, may result in a net *increase* in food chain length, as generalist predators shift their diets and consume taxa that occupy higher trophic positions (e.g., small-bodied predators). Food web structure thus is affected directly by removal of species, as well as indirectly by an overall decrease in secondary productivity as predators shift to feeding at trophic levels further removed from primary producers (Elton 1927). The relationship among body size, trophic position, and species diversity, and its implications for food web structure, warrants further attention, especially in species-rich systems where human-initiated threats to food web structure and ecosystem function are great and on-going.

CHAPTER VI

BODY SIZE AND PREY AVAILABILITY DRIVE PREDATION PATTERNS IN A SPECIES-RICH TROPICAL RIVER FOOD WEB

Introduction

Factors that determine the composition of predator diets are important because of the critical role predators play in determining community structure and ecosystem function (Brooks and Dodson 1965, Paine 1976, Sih et al. 1985, Stephens and Krebs 1986, Carpenter and Kitchell 1993). Body size is a critical constraint on the size of prey on which predators can feed (Cohen et al. 1993), though actual prey choice is a function of prey availability, environmental conditions, prey and predator behavior, and capture and handling efficiency (Werner 1974, Mittelbach 1981, Blaxter 1986, Hoyle and Keast 1987, Sih and Moore 1990a, Juanes and Conover 1994, Christensen 1996, Mittelbach and Persson 1998, Sih and Christensen 2001, Scharf et al. 2002). Factors determining prey selection are especially difficult to deduce in species-rich food webs, where both predators and prey can vary substantially in terms of size, morphology, mobility, and life-history strategy (Goulding 1980, Lowe-McConnell 1987, Winemiller 1989a, 1990). Experimental manipulations are extremely difficult in species-rich systems (e.g. optimal diet experiments, MacArthur and Pianka 1966, Schoener 1971, Werner and Hall 1974, Charnov 1976), because estimates of predator choice and prey profitability, within heterogeneous habitats for all potential predator-prey combinations, are logistically impossible.

A more tractable approach to the study complex food webs is to use large-scale patterns to infer underlying factors affecting predator-prey dynamics. For example, prey/predator body size ratios can be used to infer general predation patterns (Scharf et al. 2002, Jennings and Warr 2003), an approach that may be especially useful to generalize trends when predators consume multiple prey species (Woodward and Hildrew 2002). The relationship between body size and trophic position is being used increasingly to describe the structure of complex food webs (Cohen et al. 1993, France et al. 1998, Jennings et al. 2001, Woodward and Hildrew 2002, Jennings and Mackinson 2003). Furthermore, large-scale comparative approaches can provide robust predictions with regard to human-induced perturbations on food webs, for example, assessing effects following human exploitation of marine fisheries (Rice and Gislason 1996, Pauly et al. 1998).

Environmental conditions are a primary determinant of predator-prey dynamics (Menge 1976, Peckarsky 1983, Menge and Sutherland 1987, Power et al. 1996, Leonard et al. 1998), and can control the relative importance of body-size based mechanisms in determining predation patterns (Jennings and Warr 2003). In tropical floodplain rivers, a distinct seasonal hydrological cycle provides the context in which predator-prey dynamics are set (Goulding et al. 1988, Winemiller 1996, Rodríguez and Lewis 1997, Lewis et al. 2000). During high water, dispersal of organisms is extensive (Welcomme 1979, Lowe-McConnell 1987), but as water levels fall, prey densities increase, biotic interactions become more intense, and predation may drive many community- and ecosystem-level processes (Winemiller 1990, Rodríguez and Lewis 1994, 1997, Layman and Winemiller 2004). Changing water levels are also associated with spawning migrations of species, some of which provide important nutritional subsidies to predators in relatively nutrient-poor systems (Jepsen et al. 1997, Winemiller and Jepsen 1998, 2003). Reproductive cycles of many species are timed to coincide with the onset of rising waters, which allows juveniles to exploit extensive flooded areas as sources of refugia and food (Winemiller 1989b, 1990, 1996). All of these factors affect prey availability, and thus likely influence predator diets.

In this study, I evaluated how body size and prey availability may affect diets of piscivorous fish in the Cinaruco River, a species-rich floodplain system in Venezuela. I asked the following questions: (1) are size-structured predator-prey patterns detectable within the complex food web?, and (2) is prey selection related to patterns of prey abundance that vary with the seasonal hydrological cycle? Using data pooled over a 10-year study period, I characterize general trends in predator-prey relationships, and do not evaluate finer-scale temporal or spatial patterns. To evaluate apparent seasonal dietary patterns of common large-bodied piscivore taxa, I estimated species abundance within the prey-fish assemblage through the falling-water and dry seasons of 2002-2003.

Methods

The study was conducted in the Río Cinaruco, a blackwater, floodplain river in southwestern Venezuela (6° 32’ N, 67° 24’ W). The Cinaruco is an oligotrophic, moderate blackwater river with high levels of dissolved organic carbon and low pH. The river has a forested riparian zone with open grassland dominating the drainage basin, and is characterized by a strongly seasonal hydrology with water levels typically fluctuating >5 m during an annual hydrological cycle (Arrington and Winemiller 2003). Maximum width of the main channel during the dry season is 40-200 m. The river supports at least 280 fish species that span a wide range of ecological attributes and life history strategies (Jepsen 1997, Winemiller et al. 1997, Arrington and Winemiller 2003, Hoeinghaus et al. 2003, Winemiller and Jepsen 2003, Layman and Winemiller 2004).

Taxa expected to be piscivorous were collected with gill nets, cast nets, and by angling with artificial lures from 1993-2003, and data for all years were pooled. *Cichla* spp. (large piscivorous cichlids) and *Pseudoplatystoma fasciatum* (a large piscivorous catfish) 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 (Layman and Winemiller 2004). All other species were euthanized, and stomachs were removed for examination. Stomach contents were quantified volumetrically, and both predator and prey fishes were measured to the nearest 1.0 mm standard length.

Stable isotope ratios are commonly used as a means to estimate trophic position, as they provide a time- and space-integrated measure of consumer diets (Vander Zanden et al. 1999, Post 2002b, a, Jennings and Warr 2003, Jennings and Mackinson 2003, Layman et al. 2004). Collection, preservation, and preparation of isotope samples in this study follow Arrington and Winemiller (2002). Briefly, fishes were collected to represent a random sub-sample from the community. Immediately following capture, fishes were euthanized, and ~2 g of dorsal muscle was removed and covered with 20 g of non-iodized table salt. In the laboratory, salt-preserved samples were rinsed in distilled water, soaked in distilled water for 4 h, rinsed again, and dried at 60°C for 48 h. Once dry, samples were ground to a fine powder using a mortar and pestle and loaded into tin capsules. Samples were analyzed at the Stable Isotope Laboratory at the University of Georgia's Institute of Ecology for determination of percent carbon, percent nitrogen, and stable isotope ratios. Stable isotope values are reported using δ (delta) notation where:

$$(1)\qquad \delta^{15}C \text{ or } \delta^{15}N = ([R_{sample} / R_{standard}] - 1) \times 1000$$

where R is $^{13}C{:}^{12}C$ or $^{15}N{:}^{14}N$. Working standards were bovine (*n* = 49, $\delta^{13}C$ = -22.11‰, SD = 0.06‰, 48.8% C, $\delta^{15}N$ = 7.47, SD = 0.07‰, 10.0% N) and poplar (*n* = 81, $\delta^{13}C$ = -27.34‰, SD = 0.10‰, 48.1% C, $\delta^{15}N$ = -2.47, SD = 0.16‰, 2.7% N).

It is now widely acknowledged that primary consumers provide the best baseline to estimate trophic position using $\delta^{15}N$ because they integrate temporal and spatial variation in isotopic signatures of basal resources (Cabana and Rasmussen 1996, Vander Zanden and Rasmussen 1999, Post 2002b). When consumers acquire nitrogen from more than one module (*sensu* Holt 1997) of a food web (e.g. the littoral and pelagic food webs in a lake), the following model is typically used to assess trophic position of a secondary consumer (S):

$$(2)\quad \text{Trophic position} = \lambda + (\delta^{15}N_{S} - [\delta^{15}N_{B1} \times \alpha + \delta^{15}N_{B2} \times (1-\alpha)])/\Delta$$

where λ is the trophic position of the organism(s) used to estimate baseline values (in this study λ = 2, the trophic position of primary consumer taxa), S is the consumer in question, B1 and B2 are the two baseline taxa, α the proportion of nitrogen in the consumer derived from the food web module which B1 represents, and Δ is the enrichment in $\delta^{15}N$ per trophic level. Two species integrate dominant source pools of primary production in the Cinaruco River: (1) *S. kneri* for autochthonous algal/detrital resources, and (2) *M. hypsauchen* for allochthonous C_3 plant material. These two taxa were used as baselines to estimate the trophic position of other consumers (Layman et al. 2004). I assumed that nitrogen and carbon move through food webs in similar fashion, which permits estimation of α (see equation 2) by:

$$(3) \qquad \alpha = (\delta^{13}C_S - \delta^{13}C_{B2})/(\delta^{13}C_{B1} - \delta^{13}C_{B2})$$

where the consumer taxa of interest is designated by S and baseline taxa are designated by B. I employ a mean $\delta^{15}N$ enrichment of 2.54 to estimate trophic position, following the meta-analysis of Vanderklift and Ponsard (2003). This is a lower enrichment value than is commonly used (Post 2002b), and thus my values of predator trophic position may represent upper estimates.

In heterogeneous ecosystems such as floodplain rivers (Hamilton and Lewis 1992, Winemiller 1996, Winemiller and Jepsen 1998, Lewis et al. 2000, Lewis et al. 2001, Arrington 2002), multiple sampling techniques are necessary to fully document fish relative abundance. In this study, I employed seine hauls along shoreline areas of the main river channel and floodplain lagoons. This methodology was unlikely to capture all species (e.g. large-bodied species such as *Semaprochilodus kneri* are effectively captured by gill netting, see Hoeinghaus et al. 2003), yet seining provided data sufficient to evaluate general trends within a sub-set of the potential prey fish community. Monthly seine hauls were conducted from November 2002 (falling water period) to April 2003 (end of dry season) on 7 sandbanks in the main-channel and along the shoreline in 5-8 lagoons. For each collection, a seine (6.4 m x 1.8 m with 4 mm mesh) was oriented parallel to shore at 1 m depth. The seine was hauled directly toward shore and all fishes were collected on the bank. At each site, three non-overlapping samples were taken for one composite site sample. All fishes were identified to species, enumerated, and measured to the nearest 1.0 mm standard length (SL). Voucher specimens are archived in the Museo de Ciencias Naturales at UNELLEZ, Guanare, Venezuela, and the Texas Cooperative Wildlife Collection, College Station, Texas, USA.

Piscivore stomach contents frequently contained partially digested fish remains that could only be identified to genus, particularly among closely related and morphologically similar taxa. In order to evaluate the number of predator species that feed on a given prey taxa (i.e., “prey vulnerability”, Schoener 1989), I grouped prey fish at the generic level. I recovered >15 measurable prey fish from the stomachs of each of five taxa (*Cichla temensis*, *C. orinocensis*, *C. intermedia, Boulengerella cuvieri*, and *B. lucius*), and used these five taxa to examine seasonal patterns of prey/predator body size ratios and prey composition. In this study, I report data on estimated trophic position (based on stable isotope ratios, see above) of two abundant piscivores, *C. temensis* (peacock cichlid) and *S. manueli* (piranha) during the falling-water (transition to dry season) and low-water (dry) periods. In all analyses, the interval October-December was considered the falling-water period, and January-April was the dry season.

Parametric statistics were used when data satisfied key assumptions related to distribution; otherwise, I employed non-parametric tests (e.g. Mann-Whitney Rank Sum test for bivariate comparisons). Statistical analyses were conducted with SigmaStat (1997) and SPSS. Multi-dimensional scaling (MDS) was used to compare fish assemblage similarity/dissimilarity based on relative abundance of individual taxa in seine hauls. MDS constructs a 2-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). Analysis of similarities (ANOSIM, Clarke and Warwick 1994), a non-parametric analog of MANOVA, was used to test for differences in species composition among months. When ANOSIM revealed significant differences, similarity percentage analysis (SIMPER, Clarke and Warwick 1994) was performed to identify species accounting for differences.

Results

I analyzed 5,439 stomachs of 31 taxa representing 8 fish families (Table 5). As expected, fish prey dominated stomach contents, ranging from 33.3% (*Ageniosis brevifilis*, an auchenipterid catfish) to 100% (multiple taxa) of identifiable stomach contents. Eighteen species had >50% empty stomachs, a common characteristic of piscivorous fishes (Arrington et al. 2002). At least 8 orders, 23 families, 49 genera, and 61 species of fish were identified in piscivore stomachs. Mean body depth of prey taxa negatively correlated with the number of piscivore species from which prey taxa were recovered (Figure 12, $R^2 = 0.20$, $F = 4.0$, $P = 0.029$). Stomach contents for individual piscivore taxa were dominated either by whole fish prey (for *Cichla* spp., *Boulengerella* spp.) or fragments, such as bones or muscle/skin tissue, of relatively large prey taxa (for *Serrasalmus* spp.), a pattern that reflects engulfing versus biting modes of feeding, respectively (Arrington and Winemiller 2002). No measurable whole fish were found in any stomachs of piranhas (*Pristobrycon* spp., *Pygocentris caribe, Serrasalmus* spp.) suggesting these piscivores feed exclusively on parts of relatively large fish in this system. Estimated mean trophic positions for piscivores were relatively low, with the highest estimated mean value (3.6) obtained for *Serralsalmus manueli* and the piscivorous clupeid *Pellona castellnaeana* (Table 5). Stomach contents analyses on five of the most abundant large-bodied piscivores in the river further suggest relatively short food chains, as algivore/detritivores (*Semaprochilodus kneri* and curimatid and hemiodontid characiforms) compromised a relatively large proportion (>60%) of

Table 5. Sample sizes for stomach content and stable isotope ratio analyses. Estimated trophic positions are based on stable isotope analyses (see Methods). Taxa are ordered from largest to smallest mean size (SL) of individuals examined.

Species	Total Stomachs Examined	Number of Individuals for Stable Isotope Ratios	Estimated Mean Trophic Position
Pseudoplaystoma fasciatum	77	3	3.2
Platynematichthys notatus	30	-	-
Raphiodon vulpinnis	11	6	3.5
Pseudoplaystoma tigrinum	3	-	-
Boulengerella cuvieri	292	4	3.3
Pellona castellnaeana	52	1	3.6
Cichla temensis	1365	184	3.2
Boulengerella lucius	411	4	2.9
Ageniosis brevifilis	4	9	3.1
Cichla intermedia	307	4	3
Leiarius marmoratus	5	-	-
Plagioscion squamossissimus	115	9	3.5
Hydrolycus armatus	510	13	3.1
Hoplias malabaricus	39	1	2.8
Cichla orinocensis	755	6	2.8
Brycon sp.	4	4	2.7
Boulengerella maculata	22	1	3.2
Serrasalmus manueli	597	148	3.6
Crenicichla cf *lugubris*	24	2	2.8
Serrasalmus rhombeus	67	2	3.6
Pygocentris cariba	17	-	-
Cynodon gibbus	44	-	-
Acestrorhynchus falcirostris	12	-	-
Brycon falcatus	11	-	-
Agoniates anchovia	14	3	3.1
Serrasalmus medinai	16	-	-
Serrasalmus altuvei	29	-	-
Pristobrycon striolatus	58	2	3.1
Acestrorhynchus microlepis	464	3	3.1

identifiable stomach contents for the cichlids *Cichla temensis* and *C. intermedia* and pike characins *Boulengerella cuvieri* and *B. lucius*.

Stomach contents of *Cichla* spp. and *Boulengerella* spp. showed a general trend of decreasing prey/predator body size ratios from high- to low-water periods (Figure 13). Body sizes (SL) of four piscivore taxa (i.e. those with measurable prey) did not reveal significant between-month variation (ANOVA, all $P > 0.19$). Only *C. intermedia* showed significant between-month variation in body size (Kruskal-Wallis ANOVA, $H = 14.8$, $P = 0.04$), and differences did not reveal any temporal trend (regression of date vs.

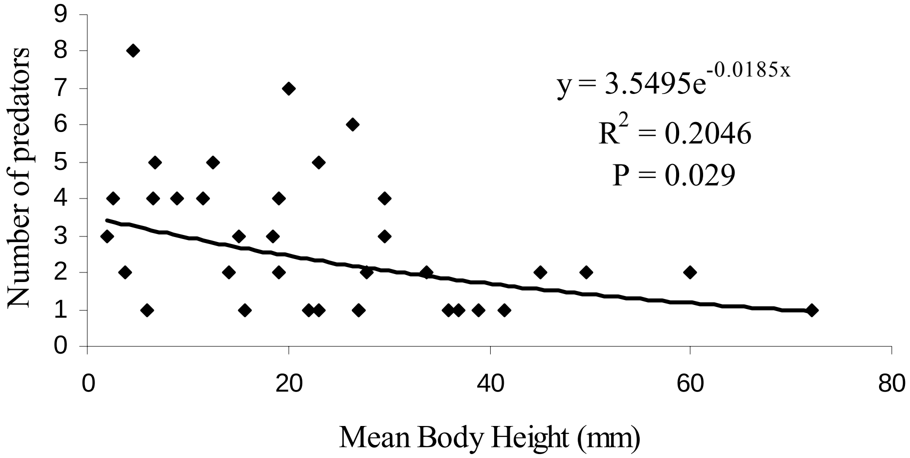


Figure 12. Number of predator species in which each prey genera was identified in stomach content analyses.

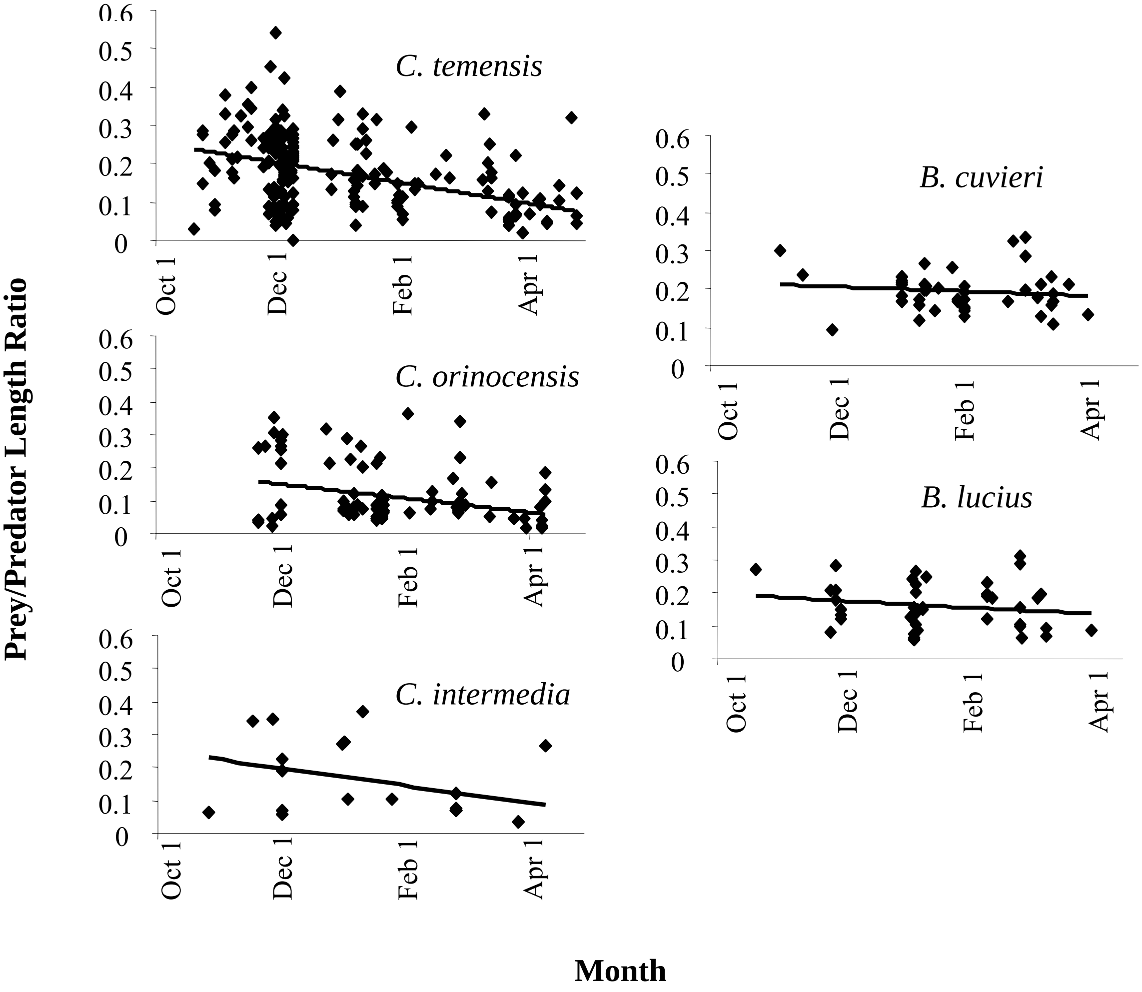


Figure 13. Declining prey/predator body length ratios from high to low water for 5 predator taxa.

predator size, $P = 0.90$). Thus, declining prey/predator ratios are attributed to shifts in the size of prey consumed by predators. Slopes of prey/predator ratios were not significantly different among the five piscivore taxa (F-test, F = 1.99, $P = 0.10$). Slopes were significantly negative for *C. temensis* and *C. orinocensis*, but not for the other species (Table 6). Compared with *Cichla* spp., *Boulengerella* spp. have much smaller mouth and throat diameters relative to body length, and the prey/predator ratios of *Boulengerella* spp. changed less by season (i.e. shallower slope) than those of *Cichla* spp. Mean predator/prey ratios varied from 0.11 for *C. orinocensis* to 0.20 for *B. cuvieri.*

Table 6. Statistical results from least-squares linear regression of prey/predator body size ratios and date. The mean ratio given is for measurable prey items from the entire dataset for each species.

Species	Regression	r^2	p	Mean Ratio
C. temensis	$y = -0.0009x + 32.779$	0.20	<0.001	0.17
C. orinocensis	$y = -0.0006x + 23.308$	0.10	0.001	0.11
C. intermedia	$y = -0.0009x + 32.816$	0.13	0.08	0.15
B. lucius	$y = -0.0003x + 11.356$	0.03	0.2	0.15
B. cuvieri	$y = -0.0002x + 6.7356$	0.02	0.5	0.20

Stable isotope analyses for *C. temensis* and *Serrasalmus manueli* also suggested seasonal diet trends. Trophic position estimates increased from 3.0 during the falling-water period to 3.3 ($t = 9.7$, $p < 0.001$) during the low-water period for *C. temensis*, and from 3.6 to 3.8 ($t = 5.3$, $p < 0.001$) during the same periods for *S. manueli*. This pattern was consistent with stomach contents analyses for *C. temensis* (the species with most stomachs examined, $n = 1,365$). During the early stages of floodwater recession in November, *S. kneri* (algivore/detritivore) comprised 59.8% of the identifiable prey items of *C. temensis*, with a guild of small omnivorous characid species (e.g. *Bryconops caudomaculatus*, *Moenkhausia* spp., *Hemigrammus* spp.) compromising 5.8% of their diet. At the end of the dry season (April), no *S. kneri* were identified in *C. temensis* stomachs, and 26.7% of *C. temensis* stomach contents were characids (Layman et al. 2004). The relatively low percentage of prey identifiable to genus level precluded detailed seasonal analysis of *S. manueli* stomach contents.

To compare diet patterns with prey availability, I conducted monthly seine hauls on sand banks of the main channel and along lagoon shorelines. A total of 13,846 fishes of 58 species were collected with mean length of all fishes (i.e. calculated across all species) generally declining from high to low water (Figure 14) with a significant trend for lagoon ($F_{1,5} = 17.0$, $p = 0.015$, $r^2 = 0.81$) but not main channel ($F_{1,4} = 2.6$, $p = 0.20$, $r^2 = 0.46$). This trend was primarily due to fewer large individuals during low water (Figure 15), which stemmed from a shift in assemblage composition (Figure 16). Assemblage composition on main-channel sand banks differed significantly among months (ANOSIM, $R = 0.29$, $P < 0.001$) due to both lower abundance of relatively large taxa

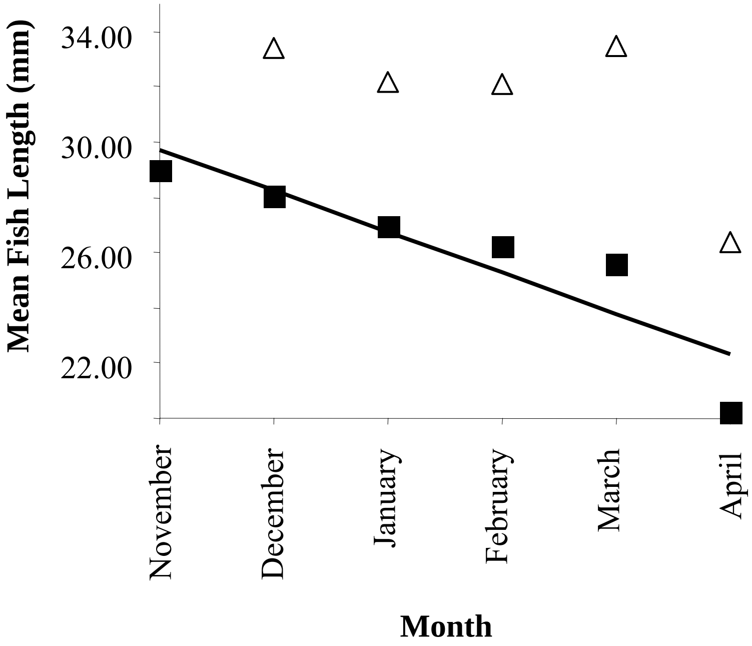


Figure 14. Mean SL of all prey fishes collected each month in seine samples from main channel (open triangles) and lagoon (filled squares) shorelines. The regression line indicates a significant relationship (*p* = 0.015).

(e.g. *Bryconops* spp, *Hemiodus* spp) during the dry season as well as increased abundance of juvenile individuals among those taxa that spawn just before the onset of the wet season (e.g. *Bivibranchia fowleri*). Lagoon assemblages were characterized by the same general, although non-significant, trend (ANOSIM, R = 0.02, P = 0.37). *Bryconops* spp. were more common in lagoons during the high-water period, with smaller species dominating assemblages during the dry season (*Hemigrammus* spp., *Moenkhausia copei*). The pattern of decreasing mean prey length with declining water level could have been a function of decline in the mean sizes of abundant taxa, so I compared mean length of

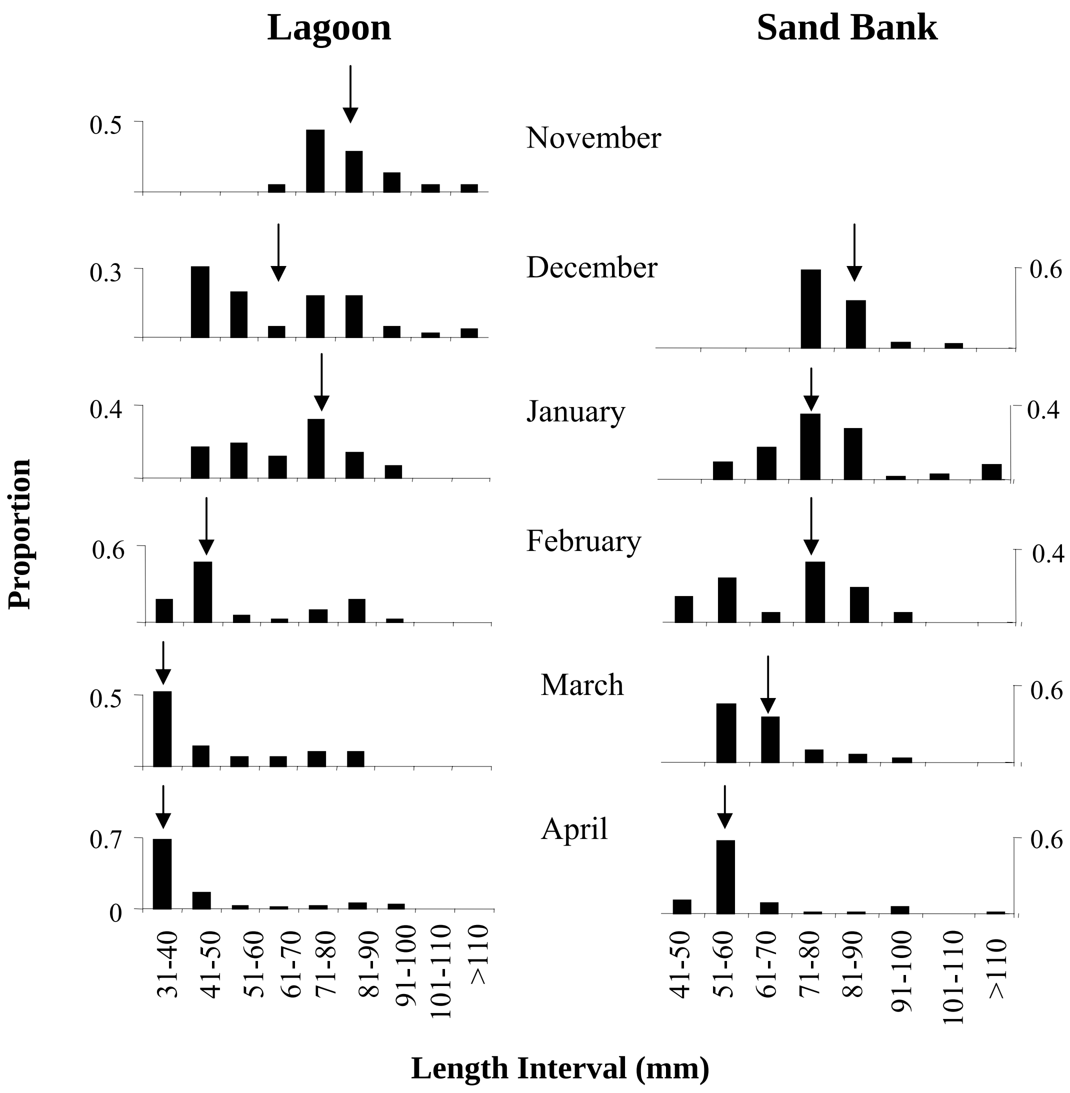


Figure 15. Frequency histograms of the largest (SL) 5% of individuals collected each month in seine hauls. Larger individuals become increasingly rare from November to April as water levels fall. Arrows indicate the median size for each month.

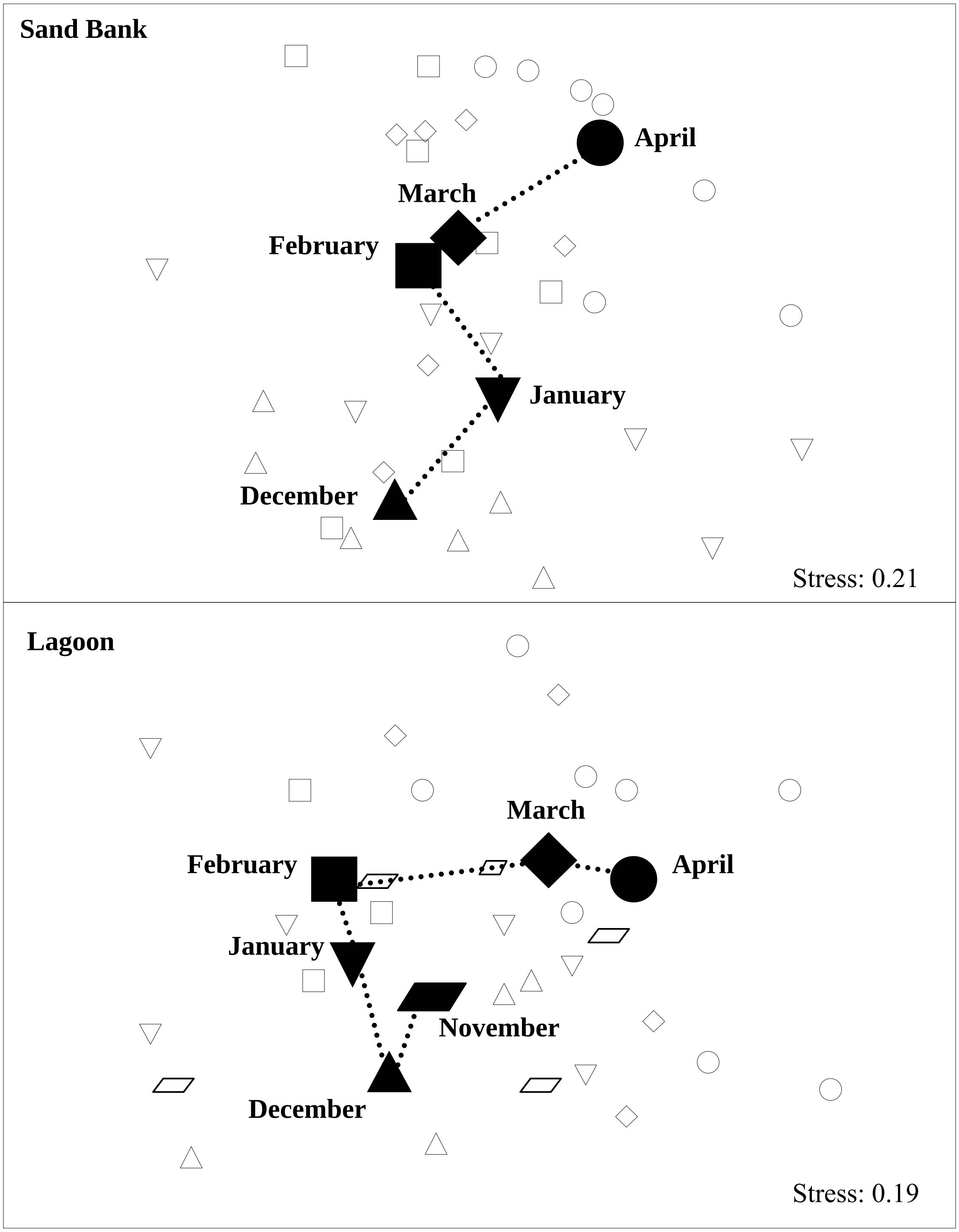


Figure 16. Assemblage composition of seine hauls as reflected by non-parametric multi-dimensional scaling. Open symbols represent individual samples and filled symbols are mean ordination positions for all samples in each month.

the five most common taxa between April and November (lagoons, 69% of all individuals collected) or December (main channel, 56%). The results were ambiguous as 4 of 5 taxa in lagoons, and 3 of 5 in the main channel, were significantly smaller in April (Mann-Whitney Rank Sum Test, all $p < 0.02$), with the remaining taxa from lagoons and 2 taxa from the main channel significantly larger in April (Mann-Whitney Rank Sum Test, $p < 0.001$).

Discussion

Piscivores examined in this study were found to consume phylogenetically and morphologically diverse fish taxa that reflect the overall diversity of fishes in this floodplain river (>280 species). Even for individual piscivore species, prey varied considerably in terms of body size and morphology. For example, at least 40 different prey species were identified in stomachs of the peacock cichlid *C. temensis*. Despite the potential complexity of predator-prey dynamics in this species-rich fish assemblage, size-structured interactions still largely determined predation patterns, as predicted by ecological theory (Cohen et al. 1993). There was nested hierarchy of predator-interactions (Woodward and Hildrew 2002, Sinclair et al. 2003) in which less deep-bodied prey tended to have more predators. Body depth strongly influences prey selection for gape-limited predators, thus providing ultimate constraints on the prey on which predators can feed (Keast and Webb 1966, Brönmark and Miner 1992, Persson et al. 1996, Karpouzi and Stergiou 2003).

Prey/predator body size ratios were extremely variable, but showed an overall decreasing trend from high- to low-water conditions. Profitability (a function of mass ingested in relation to capture and handling efficiencies, e.g. (Scharf et al. 1998, Scharf et al. 2002) typically has been shown to peak at prey/predator length ratios of 0.25-0.30 (Rice et al. 1993, Ellis and Gibson 1997, Scharf et al. 1998). Mean prey/predator ratios of the five taxa examined in this study were less than these reported values, likely reflecting specific properties of the food web. For example, small prey species often reach extremely high densities in habitats with high structural complexity such as woody debris along lagoon shorelines (Layman, Texas A&M, unpublished data). Relatively high abundance of small prey may result in higher encounter and capture frequencies for small prey, and large differences in encounter frequency may override all other factors determining predator feeding patterns (Scharf et al. 2002). This is consistent with the observation that *C. orinocensis* primarily occurs in structural complex lagoon habitats (Jepsen et al. 1997, Winemiller et al. 1997), and this piscivorous cichlid was characterized by the lowest mean prey/predator ratio. Further, the most profitable prey size may be reduced when larger prey have anti-predator morphological adaptations, such as the armour and spines of many Neotropical catfishes (Lowe-McConnell 1987), that decrease handling and capture efficiency and may provide a deterrent when piscivores have the option of prey choice (Sih and Moore 1990b, Juanes and Conover 1994, Christensen 1996).

Seasonal shifts in prey availability appear to drive the seasonal decline in the size of prey consumed by piscivores. Larger prey were more abundant as waters began to fall but, likely due to predator-induced mortality, they became less abundant throughout the dry season. Piscivores thus encountered smaller prey relatively more frequently during the low-water period, resulting in the seasonal trend in prey/predator body size ratios. *Cichla* spp. are less gape-limited and able to exploit large prey during the falling-water period, explaining why the decline in prey/predator size ratio with season is greater for *Cichla* than for *Boulengerella*. Stable isotope analysis of *C. temensis* and *S. manueli* also indicated a seasonal diet pattern with higher realized trophic positions (sensu Post 2002a) during the dry season. Piscivores thus may be optimizing food intake during the high-water period by feeding on relatively large algivores/detritivores (*S. kneri* for *Cichla* and *Serrasalmus*, hemiodontids for *Boulengerella*), thereby exploiting short, efficient food chains. Piscivores are more likely to feed on prey at trophic levels further removed from primary producers during the dry season.

Although the general patterns provide significant insight into general structure of predator-prey interactions, the mechanisms producing these patterns remain unclear. For example, prey selection may arise through either active or passive processes (Sih and Christensen 2001, Turesson et al. 2002). Predators that primarily feed on mobile prey may show little or no active choice among prey taxa (Juanes and Conover 1994, Christensen 1996, Scharf et al. 1998, Sih and Christensen 2001), and thus prey selection may be driven largely by differences in prey encounter rates (partially a function of prey availability) and capture probabilities. Piscivores often attack all prey within a given size range, with subsequent ingestion of prey being a function of prey density, behavior, ease of capture and handling constraints (Juanes and Conover 1994, Scharf et al. 2002). The range of prey taxa consumed by piscivores in this study suggests that selection may be largely passive in this system. Alternatively, I have observed on numerous occasions *Cichla* spp. actively pursuing and feeding on schools of *S. kneri*. Since >50% of *C. temensis* diet is composed of *S. kneri* during the falling-water period, and this prey taxa is unlikely to account for this proportion of the overall biomass in the system, these prey may be actively selected for. Controlled experiments could further evaluate the relative importance of passive and active prey selection by piscivores in this system.

Even in this species-rich, tropical food web, size-structured interactions yield large-scale patterns in relation to the annual flood-pulse regime. At the start of the falling-water period, predators seem to target relatively large, abundant prey. Predation mortality is very high in tropical floodplain systems (Rodríguez and Lewis 1994, 1997), and thus predators likely induce changes in the fish community (Rodriguez and Lewis 1994, 1997) which, in turn, results in a shift in prey which they exploit (Winemiller 1990). In the Cinaruco River, decreasing prey size tracks seasonal changes in the overall size-structure of potential prey community, resulting in general patterns of prey selection by pisicvores. Although prey selection by piscivores is a function of many factors, including species-specific traits and spatial variability (e.g. differential predator and prey densities in patchy habitats), there nonetheless are general patterns of predation that provide a foundation for predicting predator-prey dynamics in species-rich tropical food webs.

CHAPTER VII

PEACOCK CICHLIDS' RESPONSE TO PIRANHAS, WITH IMPLICATIONS FOR VULNERABILITY TO COMMERCIAL NETTING

Introduction

Natural species interactions may render particular species more susceptible to human impacts, but there remains little study of how one species can indirectly decrease a second's fitness by altering its susceptibility to human activity (e.g. direct exploitation, habitat alteration, or other induced environmental change). For example, Relyea and Mills (2001) demonstrated how predator-induced stress on gray treefrog (*Hyla versicolor*) tadpoles increases the lethal effects of a pesticide. Parrish (1999) described how predatory attacks of large piscivores (e.g. tuna) on schooling prey forces the prey closer to the water surface, thereby making them more susceptible to seabird predators. Fisherman are able to more efficiently target commercially valuable piscivores by following feeding seabirds.

Figure 17 depicts a conceptual framework for such interactions. In Environment 2, the presence of species B affects species A in some manner, thereby making it synergistically susceptible to human impacts. This model is analogous to a "risk-enhancing emergent impact" of multiple predators (Sih et al. 1998) or a "positive behaviorally-mediated indirect interaction" (Dill et al. 2003), but broadens the scope of these frameworks by: (a) explicitly including humans, and (b) not limiting human activity to "predation", but allowing for a wide range of impacts. In this chapter I explore a possible instance of this synergistic interaction in the Río Cinaruco, Venezuela. I used a

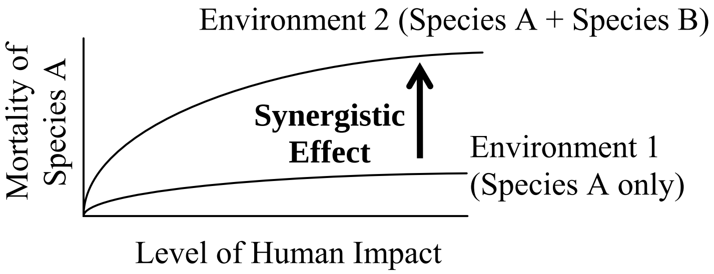


Figure 17. Synergistic effect on mortality of Species A resulting from an interaction with a second species. The effect is manifest only in environments where both Species A and B are present. The x-axis can depict impact of wide range of human activities, such as application of a pesticide or level of commercial fishing (see text).

field experiment to examine whether peacock cichlids *Cichla temensis* (hereafter referred to as *CT*) and *Cichla orinocensis* (*CO*) are constrained to shoreline habitats by the piranha *Serralsalmus manueli* (*SM*), thereby potentially rendering the peacock cichlids more susceptible to commercial netting.

Piscivore introductions have been shown to substantially alter prey assemblages in tropical lentic systems (Zaret 1979, Kaufman 1992, Gophen et al. 1995, Crisman et al. 2003), but there have been few studies in tropical freshwater systems that examine either the effects of, or factors contributing to, over exploitation of piscivores by fisheries. Net fishing is common in tropical waters, and may alter systems in dramatic ways (Goulding 1980, Bayley and Petrere 1989, Crisman et al. 2003). Large-scale netting is a relatively recent development in the Río Cinaruco, but the intensity of netting suggests ecosystem impacts will be severe (Chapter IV). Netters use long beach seines (~300 m in length, mesh size ~20 cm), which are deployed in a large semi-circle using a small boat, and then pulled onto shore. With these methods, netting activity is largely restricted to shorelines and near-shore habitat, and the middle of most lagoons can not be fished effectively.

In extensive standardized gill net sampling (>10,000 hours, see Chapter II), and in previous studies (Jepsen et al. 1997, Winemiller and Jepsen 1998), I have identified three of the most abundant large-bodied piscivores in the Río Cinaruco to be *CT*, CO, and *SM*, and these data suggest a largely non-overlapping distribution of the peacock cichlids and *SM*. *SM* accounts for 39% of all fishes captured by gill netting in deepwater habitats (>1,000 gill net hours, Chapter II). Alternatively, *CT* and *CO* are abundant along shorelines (Jepsen et al. 1997), where *SM* are typically absent. Many factors may contribute to the distribution peacock cichlids, but it is hypothesized that the threat of piranha predation is a primary mechanism (Winemiller 1989). In the absence of piranhas, I expect *CT* and *CO* would disperse into deeper waters (in addition to inhabiting structurally complex shoreline habitats), a pattern suggested by distributions in shallow lagoons where piranha are largely absent. If this hypothesis is correct, piranha likely render peacock bass more susceptible to commercial fishing by constraining peacock bass to shallow waters. The field experiments described in this chapter examine this hypothesis in more detail.

Methods

Field experiments were conducted in April 2004 along shoreline habitats in one lagoon (Laguna Larga) of the Río Cinaruco. The experimental areas (Figure 18) were constructed using chicken wire (diameter 5 cm) attached to 1.8 m metal poles at ~ 1m intervals. The total area enclosed was ca. 50 m^2. This design excludes all large-bodied fishes from passing in or out of experimental areas, while allowing full movement of most prey of *CT, CO,* and *SM*. A seine net (3.2 m x 1.8 m with 4 mm mesh) was suspended 5 m from the deep end of the experimental area, and that divided area into shallow and deep portions when deployed. A chain was secured with plastic cable ties to the seine lead line, to provide additional weight to sink the seine before sampling (see below). The bottom of the net was raised ~0.5m at the start of each experimental trial using a rope, threaded through the lead line, and attached to the metal poles on the side of each the experimental area. This allowed full movement of all fishes between the shallow and deep sections of the area during the duration of each trial. A ~9 m^2 area of sticks was placed in the shallow section of the experimental area to simulate woody "snag" habitats that are common along lagoon shorelines (Arrington 2002).

I employed 3 treatments within each experimental block (*n* = 4): (1) No fish added, (2) 12 peacock bass added (6 *CT* and 6 *CO*), and (3) 12 peacock bass (6*CT* and 6*CO*) and 12 *SM* added. These densities (0.24 peacock cichlids and 0.24 *SM* per m^2) are within the range of natural densities of these piscivores in lagoon habitats. For example, on multiple occasions I have identified locations with higher piscivore densities employed in the experiment, and have collected up to 27 *SM* and 19 *CT* in areas smaller than 50 m^2. Fish were collected by hook and line in lagoon habitats, transported immediately to experimental areas, and released at a random position.

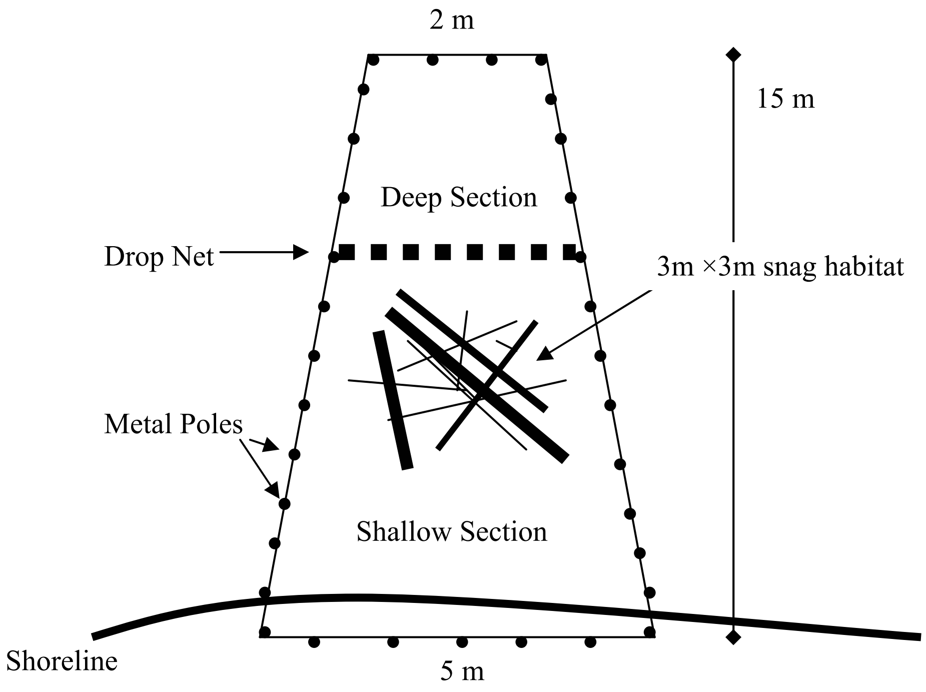


Figure 18: Experimental area design and dimensions.

Experimental areas were sampled 72 hours after the last piscivore was added. Two persons approached the area from each side, quickly lowering the bottom of the net to the substrate. One person immediately entered the area and further secured the bottom of the net by placing two metal poles lengthwise along the net lead line. No fish were able to pass from the shallow to deep areas after net deployment. Prey fishes were sampled in two ways. Cast net samples were taken adjacent to the snag habitat following the protocol described in Chapter IV. The sticks were subsequently removed and two hauls were made with a seine (12.8 m x 1.8 m with 4 mm mesh), starting from the divider net and directly to the shoreline. Prey fishes were preserved in 10% formalin, and later identified and measured (SL, ±1 mm) at Museo de Ciencias Naturales at UNELLEZ, Guanare, Venezuela. *CT* and *CO* collected were immediately transferred to water coolers. Seine hauls continued until 5 consecutive hauls yielded no additional *CT*, *CO*, or *SM*. The dividing net subsequently was removed, and seine hauls conducted in the deep section of the experimental area until 5 consecutive hauls yielded no additional *CT*, *CO*, or *SM.*

SM were euthanized, and stomachs removed for examination. *CT* and *CO* 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 (Chapter III). Recovered stomach contents were measured (when possible) and quantified volumetrically. After sampling, experimental areas were left for 72 hours until the next sampling day. For each of the 4 experimental blocks, different *SM, CT,* and *CO* were added, but within a block the same *CT* and *CO* individuals were used. *CT* and *CO* were returned immediately to experimental areas if the subsequent treatment of the block was either of the two containing peacock cichlids (#2 and #3 above). If the subsequent treatment was the no fish treatment, *CT* and *CO* and were held in a separate holding pen. Each experimental block lasted a total of 9 days (3 treatments, 3 days each) and was conducted at a different location along the lagoon shoreline. The depth of the experimental areas varied among bocks due to different shoreline morphologies.

Distribution of peacock cichlids was expressed as the % of total fishes collected in the shallow portion of the experimental area. Both univariate and multivariate statistics were used to analyze prey fish assemblages. Non-metric multidimensional scaling (MDS), a multivariate measure, was used to compare prey fish assemblage similarity/dissimilarity based on relative abundances of individual taxa among treatments and blosks. MDS constructs a 2-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).

Results

Significantly more peacock cichlid individuals (125% more) were found in the shallow section of the experimental area in the *SM* treatments than in treatments with peacock cichlids alone (Figure 19, paired t-test, $t = 3.7$, $p = 0.017$). This trend was consistent for both *CT* (SM treatment 0.31 ± 0.20; peacock cichlids alone 0.10 ± 0.11) and *CO* (*SM* treatment 0.16 ± 0.15; peacock cichlids alone 0.11 ± 0.13), and was significant for *CT* but not *CO* ($t = 1.64$, $p = 0.01$; $t = 0.81$, $p = 0.23$, respectively). Only 1 *SM* (2.1% of all individuals) was collected in the shallow section of the experimental area, providing further evidence of *SM* preference for deeper waters. Diets of all three piscivore species were dominated by relatively small prey fishes, primarily engraulids, *Microschemobrycon casiquiare*, and *Hemigrammus* spp. (Table 7). Mean prey/predator body size ratios (based on standard body lengths) were relatively low, 0.07 for both *CT* and *CO* and 0.11 for *SM.* Sample sizes were too small to evaluate potential stomach content differences for peacock cichlids among treatments.

In cast net samples, there were no significant differences among the three treatments in the number of individuals ($F = 3.4$, $p = 0.08$), mean length of individuals ($F = 2.3$, $p = 0.15$), abundance of individuals >40 mm ($F = 0.98$, $p = 0.41$), or the % of individuals >40 mm ($F = 3.3$, $p = 0.08$). MDS and ANOSIM analyses revealed no significant differences in assemblage composition according to treatment ($R = 0.21$, $p = 0.53$), although there was a significant effect of experimental block ($R = 0.30$, $p = 0.04$). Thus, as was found in experiments described in Chapter III, assemblages (as sampled by cast netting) were more similar among treatments within a block than for a given treatment among blocks.

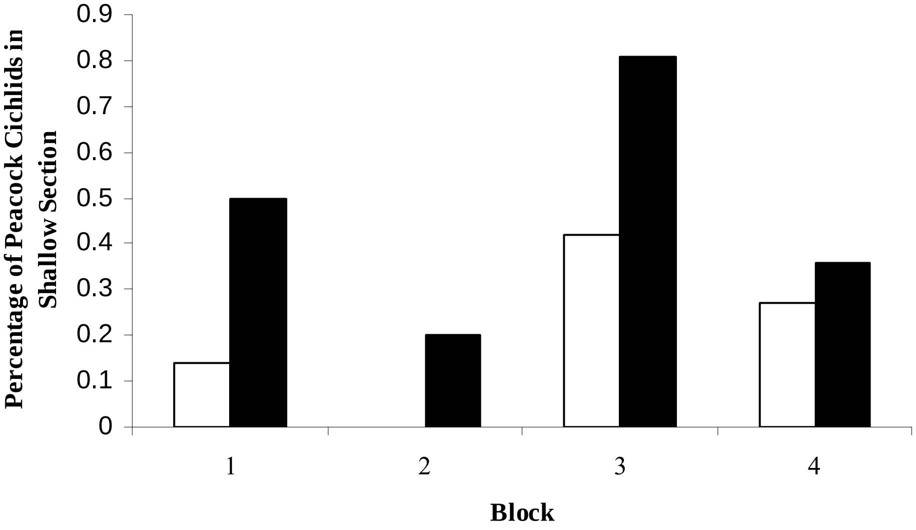


Figure 19. Peacock cichlids in the shallow section of the experimental area. Data expressed as a percentage of all peacock cichlids recovered from the shallow and deep sections combined. Open bars represent the treatment with only peacock cichlids, and filled bars the *SM* treatment.

Table 7. Results of stomach contents analysis of the three piscivores. Values of the prey taxa are expressed as a proportion (by volume) of all identifiable prey items recovered in stomachs of that piscivore species.

Piscivore Species	% Empty Stomachs	% Engraulidae	% *Microschemobrycon casiquiare*	% *Hemigrammus* spp.
Cichla temensis	69	5	40	35
Cichla orinocenis	67	16	53	31
Serrasalmus manueli	6	15	38	31

Discussion

In *SM* treatments, more *CT* and *CO* were found in the shallow section of the experimental area, suggesting presence of *SM* affects distribution of peacock cichlids. *CT* and *CO* tissue was not identified in stomachs of *SM*, suggesting that *SM* was not directly feeding on peacock cichlids within the experimental areas. Whether aggressive behavior by *SM* drives the shift in peacock cichlid distribution, or peacock cichlids shift their distribution simply in the presence of piranhas, remains unclear. The observed response of *CT* and *CO* to *SM* presence provides further evidence of the importance of trait-mediated (non-lethal) interactions, e.g. behavior (Dill 1987, Lima 1988, Trussell et al. 2004, Lima and Dill 1990), in understanding food web structure and dynamics.

The distribution shift by *CT* and *CO* was not as strong as I had hypothesized, and this may be partially due to specific behavioral tendencies of individuals. For example, some individuals may be highly responsive to the presence of piranhas, while others may have a strong preference for structural complexity (e.g. the snag habitat) regardless of other factors. Such behavioral differences among individuals within a species are critical in determining outcomes of species interactions and effects on food web structure (Riechert and Hedrick 1993, Verbeek et al. 1994, Sih et al. 2003). Since snag habitat was only placed in the shallow water section, individual preferences for structurally complex habitats may have over-ridden the effect of *SM* in particular instances. Likewise, other individuals were collected in the deep section in treatments with and without piranhas, potentially suggesting individual preference for deep water habitats regardless of piranhas. The importance of intraspecific behavioral differences deserves further study in this context.

I have suggested (Chapter VI) that large-bodied piscivore diets may be largely passive (*sensu* Juanes and Conover 1994, Christensen 1996, Scharf et al. 1998, Sih and Christensen 2001) in this species-rich river, and the results of the experiment provide further evidence of this. For example, *SM* were never found to consume small-bodied prey taxa in the deep-water habitats in which they naturally occur (Chapter VI), but fed almost exclusively on small-bodied prey taxa in the experimental areas (93% of identifiable prey items were taxa with SL <50mm). Densities of small-bodied prey fish taxa are as much 500% greater on shorelines with structurally complex snag habitats than on debris-free shorelines (Layman, *unpublished manuscript*), and the addition of snag habitat within the experimental areas likely increased prey densities relative to surrounding areas. Thus, *CT*, *CO*, and *SM* fed on abundant prey taxa despite their relatively small size, consistent with the hypothesis that large differences in prey encounter frequency often overrides all other factors determining prey choice (Scharf et al. 2002).

In response to the habitat shift of peacock cichlids induced by *SM*, I observed no accompanying shifts in prey fish assemblages (termed a trait-mediated indirect effect, see Dill et al. 2003, Trussell et al. 2004, Grabowski 2004) in the shallow section of the experimental area. This is in contrast the results of the experiment presented in Chapter III in which piscivore exclusion had a significant effect on the abundance of fish (i.e. those >40 mm) within experimental areas. I attribute these inconsistent results to two possible factors: shorter duration of experiments and a smaller experimental area. The short duration may not have been sufficient for prey to respond to experimental treatments, especially since there may have been depletion of individuals through multiple sampling trials within the same area. Size of the experimental areas also may not have been sufficient to reflect potential behavioral responses of prey, as fishes could easily move in and out of the area. The results of the present experiment, along with those the larger-scale experiments described in Chapter III, suggest spatial scale of experiments may be critical to detect behavioral responses.

The behavioral interaction between peacock cichlids and *SM* has important implications at the landscape scale in the Río Cinaruco. In shallow shoreline habitats, peacock cichlids are more susceptible to commercial netting activity. Thus, in deep lagoons with high piranha densities, peacock cichlids are concentrated in a relatively small area around the lagoon’s shallow perimeter, making them especially vulnerable to netting. Understanding the interaction between peacock cichlids and *SM*, and framing this interaction in the context of lagoon morphology, is critical to prioritize conservation initiatives (i.e. choosing which lagoons to target fishing regulations) in this and similar floodplain rivers where netting activity is intense and on-going.

CHAPTER VIII

SUMMARY AND FUTURE DIRECTIONS

One of the most important challenges facing ecologists is describing food web structure in species-rich ecosystems, and assessing how this structure will be affected by human-induced perturbations. In complex food webs, this is especially difficult, as multiple species interact simultaneously, and resulting effects are typically complex, indirect, and diffuse (McCann et al. 1998, Yodzis 2000). In this work, I have described how multiple methodologies can be used to elucidate components of a very complex tropical river food web, and provide a context from which this, and similar, food webs can be better understood. Two themes unite findings presented: (1) substantial spatial and temporal variability in food web structure, and (2) the way in which body-size can be used to generalize species-interactions across this complexity.

Winemiller (1990) suggested temporal and spatial variability is a basic characteristic of food web structure and function. This variability is substantial in floodplain systems such as the Cinaruco River. Temporal variability in food web structure was the dominant theme in Chapter VI, as predator diets were shown to vary substantially with the seasonal hydrological cycle. This is largely driven by prey availability as determined by biological interactions (e.g. predation, Chapters II, III, IV, VI), life history strategies of organisms (e.g. species migrations, Chapter II), and other species-specific traits (Chapters IV, V, VI). Determination of species' functional food web effects (Chapter III, VII) is further complicated by seasonal variability, as interactions that may be important in one season may not be in another. For example, the prey behavioral response demonstrated in Chapter III may not be as strong (or totally absent) in the high water period when fish densities are relatively low and food resources abundant. Likewise, the strength of the interaction demonstrated between peacock bass and piranhas (Chapter VII) likely varies seasonally.

Spatial variability was found to be substantial. In Chapter II, the differences in species composition across four major habitats in the river reveal the difficulty in generalizing about the overall "river" food web, when in reality the system consists of numerous sub-compartments that are interconnected to varying degrees. Underlying spatial heterogeneity may drive large-scale patterns of predator-prey dynamics, for example by influencing prey selection through differences in species density across habitats (Chapter VI). Spatial heterogeneity in food web structure is also influenced by humans, for example, by commercial netters who, by removing piscivorous fishes from the system, may induce distinct shifts in species composition at lower trophic levels (Chapter IV). Due to these impacts, lagoons separated by small distances and characterized by similar physical characteristics, can still have distinctly different web structures.

Despite great temporal and spatial variability, this work demonstrates how particular variables, such as body size, can be used to generalize patterns in food web structure. I have demonstrated three scales at which these patterns may be detected. First, body size was found to drive specific functional effects (sensu Paine 1980) within a module of the overall food web. Prey of a certain size responded to piscivore exclusion on river sand banks suggesting that, despite the diversity of the potential prey fish assemblages and spatial heterogeneity among sand bank habitats, body size may allow prediction of piscivore effects. This pattern was further substantiated at the landscape-scale, as differences in assemblage structure among netted and un-netted lagoons were largely size-based. Thus, size-structured interactions among individuals were reflected in landscape-scale patterns. Third, size-structured interactions were also apparent when analyzing predation patterns with data pooled across all habitats and study years. Predator and prey body size were highly correlated, the number of predators for each prey taxa was related to prey body size and, apparently, prey selection by predators has a distinct seasonal component based on body-size (Chapter V and VI). These basic size-structured patterns, integrated across the numerous sources of variability, provide promise for generating meaningful predictions of human impacts.

One of the biggest criticisms of ecology is the lack of predictive ability for some of the most pressing environmental problems of our time (Peters 1991, Brown 1995). This is often the case in species-rich systems in which predictive ability may be especially poor. Future research in Venezuelan floodplain rivers should continue to strive for a better understanding of the effects fishery exploitation will have on food web structure and function. Community-level effects of commercial netting seem to be remarkably consistent in the Ventuari River, Venezuela (Layman, *unpublished data*), suggesting that findings from the Cinaruco River may be directly applied to other systems. The approaches outlined in Chapters IV and VI will be especially interesting to test in other rivers, to project how robust patterns from the Cinaruco are in other locations. A comparative approach across multiple Neotropical rivers may be a powerful approach to understand human impacts on food webs.

Food web ecology has shown much progress in recent years, but there are still many problems to overcome. Most importantly, there are still far too few spatially and temporally robust descriptions of food webs. There is a great need to continue compiling extensive data sets on food web structure, especially to provide the foundation for modeling approaches that are increasingly being used to analyze webs. Studies which combine descriptive and functional analyses, such as those presented here, are especially important. To assess grave threats facing ecosystems all over the planet, but especially in species-rich ecosystems, the first step is to have the basic information necessary to understand the structure and dynamics of food webs.

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