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Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan llanos

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Synopsis

Resource utilization by nine abundant piscivores from a diverse tropical fish assemblage was examined over the course of a year. All nine species exhibited peak reproduction during the early wet season and a similar sequence of size-dependent shifts from a diet composed primarily of microcrustacea, to aquatic insects, and finally fishes. Three piranha species specialized on fish fins, particularly at subadult size classes (SL 30–80 mm). Gradual dessication of the floodplain during the transition season was associated with fish growth, increased fish density, and decreased aquatic primary productivity and availability of invertebrate prey. Based on 118 resource categories, average pairwise diet overlap was low during all three seasons: wet, transition, and dry. Of 72 species pairings, only one pair of fin-nipping piranhas exhibited high overlap simultaneously on three niche dimensions: food type, food size, and habitat. Adults of two species, a gymnotid knifefish and pimelodid catfish, were largely nocturnal. Patterns of habitat utilization indicate that piranhas may restrict diurnal use of the open-water region by other piscivores. Collective diet overlap of individual piscivore species with the other eight feeding guild members and collective overlaps with the entire fish community each revealed two basic seasonal trends. Four species that showed an early switch to piscivory also showed a high degree of diet separation with both the guild and community at large on a year-round basis. The five remaining species showed lowest collective diet overlaps during the transition season when availability of invertebrates was reduced and fish densities were maximal. Whereas predation may play a role in habitat separation, diffuse competition for food resources during the approximately four-month transition season probably is the principal factor yielding patterns of diet specialization.

Introduction

Most diverse taxonomic groups of organisms exhibit divergence in trophic biology (e.g., cichlid fishes, Greenwood 1981; ostariophysan fishes, Fink & Fink 1981). Whether or not ecomorphological divergence is random or adaptive in the context of community interactions can be debated (Strong et al. 1979, Grant 1981). The study of resource exploitation among syntopic feeding guild members provides the most straightforward means of attaining a preliminary assessment of the relative importance of interactive processes within natural communities. Whereas descriptive studies that reveal patterns of resource subdivision are limited in their abilities to demonstrate the mechanisms creating observed relationships (Toft 1985), thoughtful comparisons and the weight of evidence derived from numerous studies already have yielded much insight (Schoener 1974, Helfman 1978, Sale 1979, Werner 1979, Toft 1985). In a recent review of the literature on fishes, Ross (1986) observed greatest partitioning on food dimensions, followed by habitat and time. Many studies treating two or more niche dimensions have shown complementarity, indicating a potential effect of interspecific competition. An interactive effect between competition, predation, and temporal shifts in abiotic environmental parameters has been suggested for some systems (Werner & Hall 1977, Werner et al. 1983, Mittlebach 1984, and see Schoener 1974, Toft 1985). Ross (1986) observed a general pattern of studies revealing less evidence of interactive effects on community structure in harsher environments.

Seasonal changes in resource availability and ontogenetic diet shifts can affect both predator-prey and competitive interactions among size-structured fish populations. The present study explores seasonal and size-related patterns of resource exploitation within the piscivore guild of a diverse neotropical fish community. Although varying greatly in both duration and breadth of taxonomic comparison, several recent studies have shown marked resource partitioning among tropical fishes (Angermeier & Karr 1983, Power 1983, Moyle & Senanayake 1984, Schut et al. 1984, Watson & Balon 1984, Araujo-Lima et al. 1986, Hyslop 1986, Prejs & Prejs 1987, Nico & Taphorn 1988). Fish populations frequently are size structured due to small hatching or neonate size and continuous growth. Body size significantly affects the size range of food particles potentially available to consumers (Brooks & Dodson 1965, Werner 1974, Magnan & Fitzgerald 1984). Furthermore, size distributions of fish populations directly influence predation rates on different age classes and often the spatial distribution of fishes (Fraser & Cerri 1982, Mittlebach 1984, Power 1984, Werner & Gilliam 1984).

The study site, Caño Maraca, experiences highly seasonal rainfall that is characteristic of many parts of central and southern Venezuela. Most fishes reproduce during the early and peak wet season, a situation that leads to temporal changes in average body size for most species (Winemiller, unpublished). Although similar data were collected for all fishes that occurred at the site, this investigation focuses on the piscivore guild as a potential unit for competitive biological interactions. Given the climate and natural history of the Caño Maraca ecosystem, several basic questions can be asked: (1) Do piscivorous fishes partition food and habitat, and if so, what is the influence of seasonal changes in their environment? (2) What are the relationships between ontogeny, resource partitioning, and seasonal changes in resource availability? (3) Given seasonal patterns of resource availability and exploitation by consumers, is there evidence of interactive effects on piscivore feeding behavior? (4) Do seasonal trends of pairwise species diet overlaps follow patterns from collective diet overlaps within the piscivore guild or total fish community, and if not, which index offers a better assessment of the likelihood of interactive effects?

Methods

Study site

During every month of 1984, fishes were collected from Caño Maraca, a swamp-creek of the Río Apure-Orinoco drainage in the western llanos of Venezuela (8° 52′ 30″ Lat. N; 69° 27′ 40″ Long. W). The region studied (termed an 'estero') lies within low, flat terrain that experiences extensive sheet flooding during the wettest months (late May–August). During this time, a large region bordering the creek channel is converted from exposed, sunbaked soil and thorn-scrub habitat into a productive marsh with diverse aquatic vegetation dominated by *Cyperus* sp., *Eichhornia diversifolia,* and *Heteranthera reniformis.* During the driest months (Dec.–May), the aquatic habitat is reduced to a network of mud-bottom pools blanketed by *Pistia stratiotes, Salvinia* spp., and *Lemna* spp.. Dissolved oxygen concentrations are reduced at this time and many fishes rely on special respiratory adaptations for survival. Annual rainfall in the region was 1300 mm during 1984, with 860 mm falling between June and September (Fig. 1). Based on changes exhibited by stream physico-chemical parameters associated with rainfall and their effects on aquatic organisms (Winemiller 1987a,

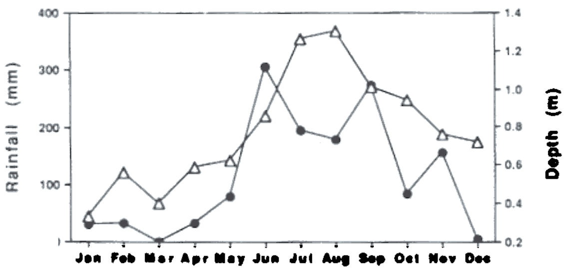

Fig. 1. Average monthly rainfall (closed symbols) and maximum midpool depth measured each month (open symbols) during the study period at Caño Maraca.

1987b), the annual cycle was divided into three terms of equal duration: dry season (Jan.–Apr.), wet season (May–Aug.), and transition season (Sept.–Dec.). Dry season conditions gave way to the wet season very abruptly with the commencement of heavy rains, whereas the wet season slowly graded into the next dry season over a prolonged period (i.e., transition season). During the transition season, fish densities increased and biotic interactions intensified within gradually diminishing aquatic habitats in the floodplain. Estimates of fish biomass at Caño Maraca at the end of the transition season are among the highest densities recorded for natural freshwater ecosystems (141–165 g m^{-2}, Winemiller 1987a). All available climatic and ecological information indicate that 1984 was not unusual in the sequence or magnitude of events. For example, the rainy season sometimes begins earlier or later than the last week of May, yet the first rains are typically heavy, persist for several months, slowly subside, and nearly cease all together for several months during the peak dry season.

Collections

Fishes were collected by seine (3.17 mm unstretched mesh, 2.5 m length; 12.7 mm mesh, 20 m length), experimental gillnet, and dipnet. On each outing, an attempt was made to sample the entire fish community such that the sample for each species reflected its relative abundance and size structure during each month. With the exception of three wet months, collecting effort expended was approximately equal during each sampling period. More total time was spent collecting during the first three months of the wet season due to the comparative inefficiency of adult fish captures in the newly-expanded aquatic environment. All aquatic habitats in the estero region were sampled for a minimum of six hours (habitats combined), and a collecting outing was terminated when two hours of sampling yielded no additional species. Collections used for comparisons of relative densities were made during either one or two days between the 11th and 28th of each month. Additional collections were made on other dates to supplement standard samples of uncommon species. A complete listing of collecting dates and sample sizes for preserved specimens appears in Winemiller (1987a). Collecting activities should not have affected natural fish densities between sampling periods, because (1) only a fraction of the total aquatic habitat was sampled on a given date and (2) fishes could move freely between the estero region and the permanent channel downstream (except during March and April). All collected individuals were preserved in 15% formalin rather than the usual 10% to safeguard against decomposition of stomach contents. The largest fishes were cut on the lateral wall of the visceral cavity to hasten penetration of formalin. Following examination, a portion of the fishes collected was deposited with the Museo de Ciencias Naturales de UNELLEZ, Guanare, Portuguesa, Venezuela. The remainder was deposited in the Natural History Collection of the Texas Memorial Museum, University of Texas, Austin, Texas.

Separate samples were taken on 27 and 28 September, 25 and 26 October, 22 November, and 11 December from three habitats: open water midpool (day and night), shallow pool edge, and dense vegetation. The open water habitat was sampled in a large pool at the lower end of the estero with the 20 m, 12.7 mm mesh seine. These large seine samples were preserved in 15% formalin and kept separate from small seine (2.5 m, 3.17 mm mesh) samples taken from the same pool. Because the large mesh seine allowed small fishes to pass through, and large fishes easily avoided the small seine, values obtained for the number of individuals of each species in the two open water samples were later combined as one sample. Night samples were taken from the same open water location with both seines on 27 September and 25 October (1800–2400 h). The 2.5 m seine was used to sample open and sparsely vegetated, shallow shoreline habitat during the morning of each outing. For the vegetation habitat samples, the 2.5 m seine was rolled on poles attached to each end until the total area of exposed net was 4.2 m^2. The weighted end of the seine was passed below dense masses of floating vegetation and quickly brought to the surface on the other side, enveloping a quantity of aquatic vegetation approximately equal to the area of the seine and entrapping all fishes contained therein. The vegetation was then hauled to the adjacent shoreline where fishes were extracted and preserved.

Diet analysis

All preserved specimens were identified, counted, and measured for standard length to the nearest 0.1 mm (all lengths are reported hereafter as SL). Fish species names were provided by Donald Taphorn of UNELLEZ and Francisco Mago-Leccia of UCV (Caracas), and voucher specimens are available in the Museo de Historia Natural (UNELLEZ) and The Texas Natural History Collection (TMM, UT, Austin). Many Venezuelan species could not be given tentative species names due to the current state of taxonomic confusion. Consequently, a few species were designated as distinct forms by 'sp.'. Two piranhas were initially identified as *Serrasalmus eigenmanni* and *Serrasalmus* sp. (Taphorn & Lilyestrom 1985). The piranha subfamily (Serrasalminae) is currently under revision. According to William L. Fink (personal communication), these species correspond to *Serrasalmus* cf. *irritans* and *Serrasalmus* cf. *medini*, respectively. *Caquetia kraussii* was formerly listed as *Petenia kraussii* (Mago-Leccia 1970, and see Kullander 1983).

Whenever available, 30 specimens of each species from each monthly collection were dissected for stomach content analysis. For certain piscivorous species, such as *Hoplias malabaricus* and *Pygocentrus notatus*, all available specimens were dissected. When more than 30 specimens were available, a subsample was chosen for dissections that included representatives spanning the total spectrum of size classes in the collection. During the course of one year, 83 fish species were collected from the estero. Each monthly sample produced between 40 and 60 species (Winemiller 1987a). This paper reports findings for the nine most abundant piscivorous species only: *Hoplias malabaricus* (Erythrinidae), *Charax gibbosus* (Characidae), *Pygocentrus notatus* (Characidae), *Serrasalmus* cf. *irritans* (Characidae), *Serrasalmus* cf. *medini*, *Serrasalmus rhombeus*, *Gymnotus carapo* (Gymnotidae), *Rhamdia* sp. (Pimelodidae), and *Caquetia kraussii* (Cichlidae). For the purposes of this study, piscivores were defined as fishes averaging at least 50% fish prey in the diet of the largest adult size class. Six piscivorous species were rare in the local ecosystem and omitted from the analysis [i.e., *Acestrorhynchus microlepis* (Characidae), *Ageneiosus brevifilis* (Ageneiosidae), *Crenicichla saxatilis* (Cichlidae), *Hoplerythrinus unitaeniatus* (Erythrinidae), *Pseudoplatystoma fasciatum* (Pimelodidae), and *Sternopygus macrurus* (Sternopygidae)]. Additionally, four common species that consumed fishes in minor proportions were excluded from the comparisons [*Aequidens pulcher* (Cichlidae), *Astronotus ocellatus* (Cichlidae), *Parauchenipterus galeatus* (Auchenipteridae), and *Synbranchus marmoratus* (Synbranchidae)].

Food items in the anterior half of the gut were removed, examined under a dissecting microscope, and identified at the species (fishes) or ordinal level (invertebrates). Broader food categories were not used for numerical analyses, because (1) lower taxonomic categories generally represented one or more renewable resources, and (2) lumping resource states often inflates niche overlap values (Greene & Jaksic 1983). Prey items then were sorted, carefully blotted with a dry paper towel, and while still moist, measured in an appropriately sized graduated cylinder by water displacement. The degree of resolution for very small items was 0.005 ml. For volumes less than 0.005 ml, a value was estimated by spreading the item on a glass slide and comparing it to a similarly spread substance known to equal 0.005 ml. Except for highly fragmented material, the size interval associated with each identified prey item was recorded (10 mm intervals measured along the longest particle axis). An ocular micrometer aided linear measurements of small prey items. Diet breadths were calculated by Simpson's measure (Simpson 1949). Asymmetrical diet overlaps were calculated by MacArthur & Levins' (1967) formulas:

$$\varphi_{jk} = \frac{\sum_{i=1}^{n} p_{ij} p_{ik}}{\sum_{i=1}^{n} p_{ij}^{2}}$$

and

$$\varphi_{kj} = \frac{\sum_{i=1}^{n} p_{ij} p_{ik}}{\sum_{i=1}^{n} p_{ik}^{2}}$$

where p_{ij} is the proportion of prey item i consumed by species j, and p_{ik} is the proportion of the ith prey item consumed by species k. These measures reflect differences in the magnitude of overlap between two populations due to unequal niche breadths. For example, one would expect diet overlap of the more specialized bluegill sunfish, *Lepomis macrochirus*, on the green sunfish, *L. cyanellus*, to be less than that of the latter on the former (Werner & Hall 1977). The asymmetrical measure has been viewed as desirable in the sense that potential for exploitation competition for resources is more realistically portrayed as unequal for species having different diet breadths (Slobodchikoff & Schulz 1980). Whereas this and other measures of niche overlap present difficulties for statistical inference when three or more species are compared, they at least provide a simple, reliable index of diet similarity. All p_{ij}s were based on the total volumes of the food items consumed during a specified period. This method assumes that stomach contents from a large sample of individuals mirrors the feeding habits of the population at large. This study employed niche overlap (φ) as a measure of similarity only, and not as a direct estimate of interspecific competition (α) in the manner previously used by some investigators.

Following the method of Lawlor (1980), electivities were used in place of p_{ij}s for an additional set of diet overlap measures adjusted for prey relative abundances (hereafter referred to as diet similarities). Consumer electivities (e_{ij}) were calculated as

$$e_{ij} = \frac{p_{ij}}{R_i^{b}},$$

where R_i is the relative proportion of food item i in the environment, and p_{ij} is the proportion of item i in the diet of consumer species j. The relative abundance of each prey item in the environment was estimated from the column sums in the community resource matrix (items summed across all fish species examined, both piscivorous and nonpiscivorous). Although it is labor intensive, this method of calculating R_i has the advantage of basing total prey availability on the overall performance of the entire fish community. Assessment of prey R_is based on independent sampling efforts risk (1) underestimating availability when microhabitats available to fish are undersampled, and (2) overestimating availability when large numbers of prey that are actually invulnerable to predation are sampled (Wallace 1981). In effect, the method estimates food availability using fishes rather than humans as samplers of their environment. The method is more reliable when based on diverse assemblages containing many ecomorphotypes, because any single species would have a relatively small influence on estimates of availability.

Ecological measures and statistics were computed from the three seasonal resource matrices (9 predators × 118 potential prey categories). For analysis of ontogenetic diet shifts, dissected specimens were grouped into either 10 or 20 mm intervals, depending on the total range of SLs recorded for each species. The average proportion of microcrustacea, aquatic insects, and fish prey items was determined for each fish size interval. Fish scales were omitted from this analysis, because scales comprised a minor portion of diets and none of the nine species are believed to rely on scales as a significant food resource (sensu Roberts 1970, Sazima 1983). Most scales not associated with flesh were probably taken during aggressive interactions by these species. All statistical tests were computed by SAS (SAS Inst. 1985). A generalized linear model (GLM) procedure was used for calculation of ANOVA statistics for comparisons of data sets with large unequal sample sizes.

Results

The piscivore guild of the dry season was dominated by adult *Hoplias malabaricus*, followed by *Caquetia kraussii* (17–185 mm), adult *Gymnotus carapo*, and adult *Rhamdia* sp. (Fig. 2). During the harshest months of the dry period (Feb.–early May), *Charax gibbosus* and the four piranha species (*Pygocentrus* and *Serrasalmus* spp.) emigrated from the estero region to deeper aquatic habitats downstream. Collections made on Caño Maraca at a location 14 km east (downstream) of the estero during the height of the dry season yielded several individuals of *Charax*, *Serrasalmus irritans*, and *S. medini*. Small juveniles of *Hoplias* and especially *Caquetia* were taken at various intervals during the four month dry season, indicating that at least portions of the local populations were reproductively active.

Charax, *Pygocentrus*, and *S. irritans* returned to the estero within one week of the abrupt onset of the rainy season. All individuals of these species taken during June were adults with gonads in advanced states of maturation. Eleven large male *Pygocentrus* in black nuptial coloration were taken in shallow water among emergent stands of aquatic macrophytes with one haul of the 2.5 m seine on June 6. Each male had milt-laden testes, and their stomachs contained either large cycloid scales or plant debris. Juveniles of all nine species were collected during July and August. During the wet season, small omnivorous and herbivorous characids (especially *Astyanax bimaculatus*, *Markiana geayi*, *Ctenobrycon spilurus*, and *Odontostilbe pulcher*), and the detritivorous curimatid, *Curimata argentea*, numerically dominated the estero (Winemiller 1987a).

Average size of all nine piscivores was greater during the transition season than the wet season due primarily to growth of juveniles produced during June and July (Fig. 2). *Hoplias*, *Charax*, *Pygocentrus*, *Gymnotus*, and *Caquetia* were extremely abundant within shrinking aquatic habitats during the transition season. Populations of *Hoplias*, *Charax*, and *Caquetia* consisted of a mixture of adults, subadults, and juvenile size classes during the transition season. Both adult and subadult size classes of *Rhamdia* and *Gymnotus* were taken during the transition season, whereas the four piranha species primarily consisted of subadults. During late October, dissolved oxygen concentration exhibited a temporary reduction (mean dissolved $O_2 = 0.73$ ppm), which probably resulted from a pulsed increase in total microbial metabolism associated with the death of aquatic macrophytes in shallow standing waters of the drying floodplain (Winemiller 1989). At this time, all four piranha species were rare or absent from the estero region of Caño Maraca. The four species reappeared on the site after dissolved oxygen had increased within the stream channel ($O_2 = 2.8$–6.0 ppm) within six weeks. Young-of-the-year *Pygocentrus* (76–127 mm) were taken in large numbers during November and December (Fig. 2).

Ontogenetic diet shifts

Of 9929 specimens from Caño Maraca that were dissected for diet analysis, the nine major piscivores comprised 1980 (20%). Small juveniles of all nine species exploited aquatic microcrustacea and aquatic insects (Table 1, Fig. 3). *Pygocentrus* showed two distinct ontogenetic shifts in basic diet components: from primarily microcrustacea to aquatic insects (20–40 mm), and from aquatic insects to fishes (40–60 mm). *Rhamdia* experienced similar diet shifts between 20–40 mm and 60–80 mm respectively. A mixture of microcrustacea and aquatic insects dominated the diets of juvenile *Hoplias* (<50 mm), *S. irritans* (<30 mm), *S. medini* (<40 mm), *S. rhombeus* (<40 mm), *Gymnotus*

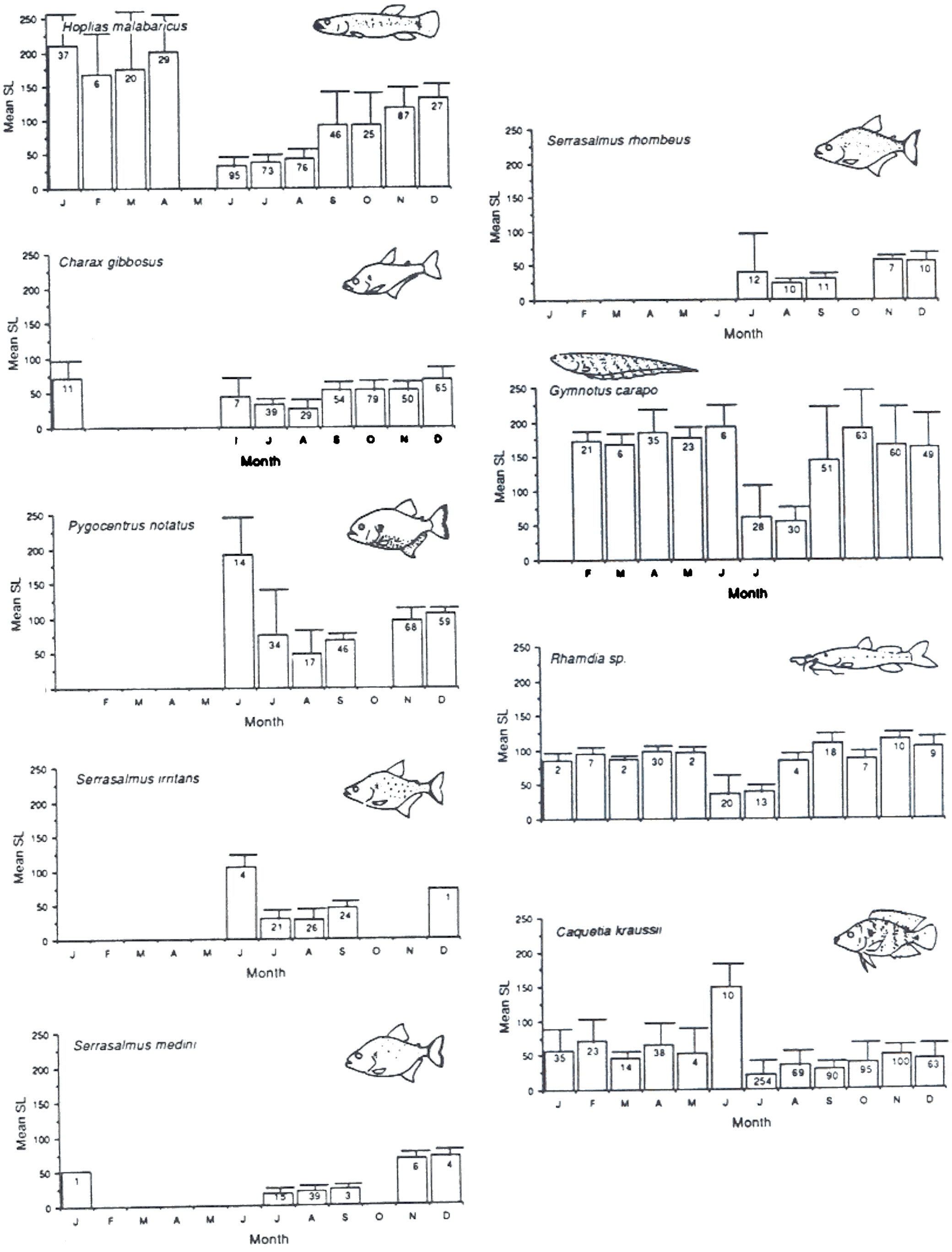

Fig. 2. Mean monthly standard lengths for each piscivore species at Caño Maraca. Error bars represent one standard deviation and collection sample sizes appear within each open bar.

(<120 mm), and *Caquetia* (<40 mm, Fig. 3). Ephemeroptera nymphs alone comprised 65% of the diet of juvenile *Charax* (<30 mm, Table 1). *Gymnotus* smaller than 40 mm consumed 62% chironomid larvae (Diptera), whereas between 120 and 240 mm, Ephemeroptera, Odonata nymphs, and chironomid larvae were predominant in *Gymnotus* stomachs. Juvenile *Caquetia* between 40 and 70 mm preyed heavily upon a wide variety of aquatic insects (Table 2).

The shift to a diet comprised primarily of fish components occurred between 20 and 30 mm for *S. irritans*, and between 30 and 40 mm for *S. medini* and *S. rhombeus* (Fig. 3). These narrow-bodied piranhas were fin specialists at subadult and adult size classes (Tables 2, 3). Fins comprised the major fraction of the diet of *S. rhombeus* larger than 80 mm, although this sample consisted of only 2 specimens. A 195 mm specimen contained nearly equal portions of unidentified fish fins and whole *Astyanax bimaculatus*. The largest *S. medini* specimens examined (71.6–80.6 mm) corresponded to subadult size classes, and all contained fins (the largest specimen contained fins and associated flesh of *Hoplias*). Between 40 and 50 mm, *Pygocentrus* shifted to a diet comprised primarily of whole fishes and sheared pieces of fish flesh. A wide variety of fish species were taken by *Pygocentrus*, but primarily *Curimata argentea*, small omnivorous characids, and the large detritivorous characiform, *Prochilodus mariae* (Prochilodontidae). Adult *Pygocentrus* consumed portions of other vertebrates (turtles, birds, mammals) when fishes were dispersed at low densities during the early wet season. *Hoplias* also shifted to a diet comprised of diverse fish species between 40 and 50 mm, but unlike *Pygocentrus*, *Hoplias* always swallowed its prey whole. *Hoplias* is capable of consuming rela-

Table 1. Resource matrix of dominant food items consumed by juvenile size classes of piscivorous fishes at Caño Maraca. Utilization is expressed as a percentage of the total volume of the prey item based on all specimens. Nine fish and 20 non-fish items with a combined volume of 45.2 liters are not listed (HMA = *Hoplias malabaricus*, CGI = *Charax gibbosus*, PNO = *Pygocentrus notatus*, SIR = *Serrasalmus irritans*, SME = *Serrasalmus medini*, SRH = *Serrasalmus rhombeus*, GCA = *Gymnotus carapo*, RHA = *Rhamdia* sp., CKR = *Caquetia kraussii*).

Prey category	HMA	CGI	PNO	SIR	SME	SRH	GCA	RHA	CKR
Vegetative detritus			0.32	-	0.17	0.61	6.01	0.12	0.05
Copepoda	0.07	0.20	1.82	0.24	0.57	-		0.61	0.45
Cladocera	2.29	1.27	17.10	11.96	16.30	5.18	9.61	9.12	0.85
Amphipoda	0.40	1.40	0.59	-		-	0.60	4.07	9.25
Eubranchipoda	0.02	2.09	-	-		-	4.50		0.29
Ostracoda	0.03	0.26	1.96		0.09		1.80	4.84	0.48
Ephemeroptera	17.98	65.40	71.79	16.73	63.89	20.78	1.80	10.66	37.18
Odonata nymphs	20.12	4.03	2.49		-	-		6.92	6.38
Misc. aq. Hemiptera	0.02	9.78	-			-		-	4.87
Corixidae (Hemiptera)	0.42	7.77	-	-		-		-	4.39
Trichoptera	-	0.20	0.72	1.04	5.66	0.21			0.04
Aq. Coleoptera (larv)	0.47	0.28	1.42	-	4.80	-	1.8	0.49	1.53
Aq. Coleoptera (adlt)	0.06	0.87	-	-		-		14.25	1.68
Chironomid larvae	1.86	21.82	1.60	1.72	4.35	1.04	61.86	25.84	2.41
Mosquito larv.(Diptera)	0.03	0.08	1.45	-	0.05	-	-	0.41	12.74
Misc. aq. insects	2.15	0.88			-	0.31	1.20	21.37	4.12
Fish fins				68.23	3.55	-	-	-	-
Misc. fish	8.63	4.19			-	2.45		-	1.53
Aequidens	5.82	-							
Poecilia	3.61								
Hoplias	3.88								
Rachovia	7.49								
Caquetia	7.21								

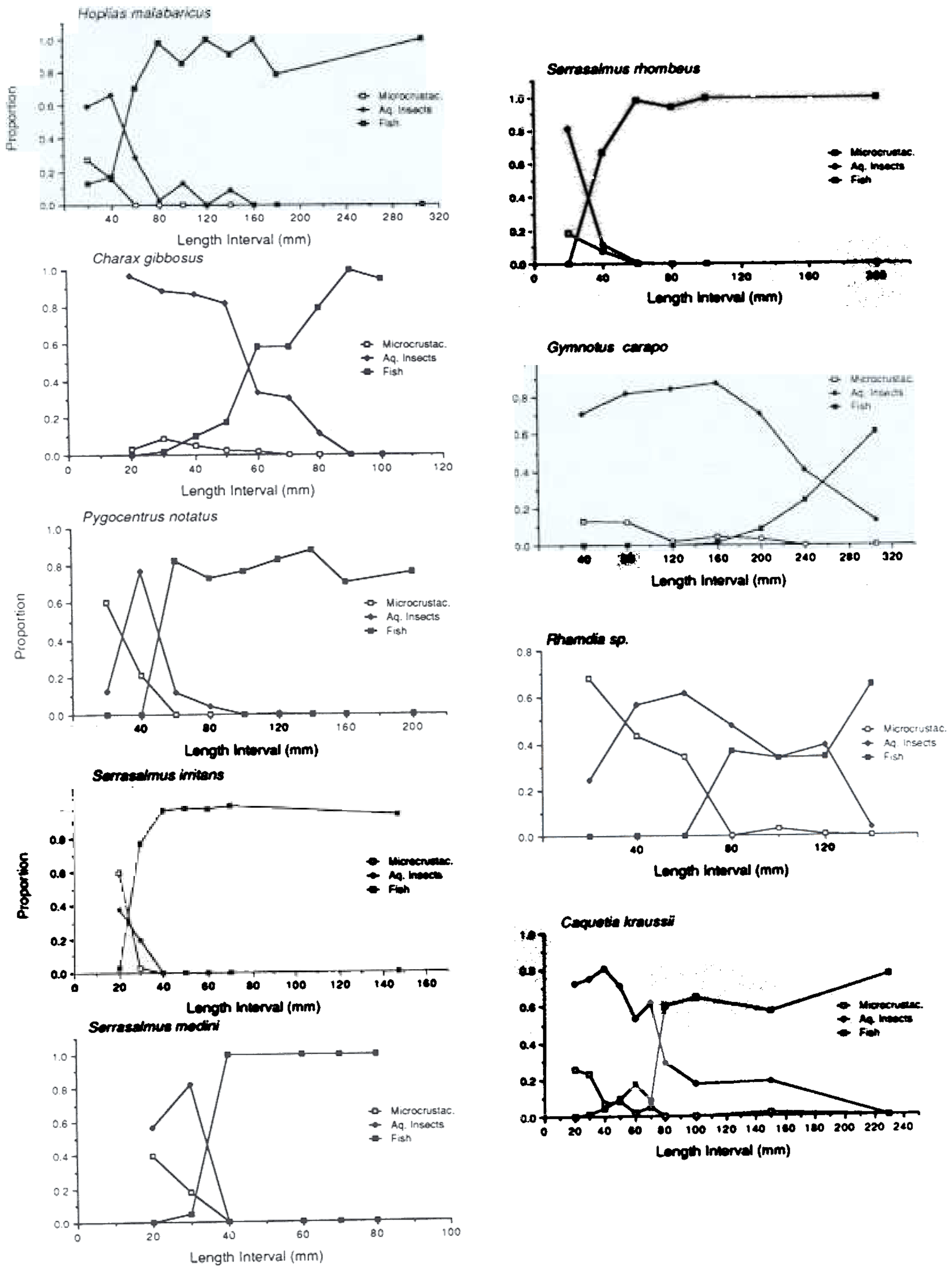

Fig. 3. Volumetric proportions of microcrustacea, aquatic insects, and fish prey categories taken by piscivores grouped by length interval.

tively large prey items. For example, a 305 mm individual had consumed a 95 mm specimen of the heavily armored, spined catfish, *Hoplosternum littorale* (Callichthyidae). A 288 mm *Hoplias* contained a subadult *Prochilodus* measuring over a third its own body length. Cannibalism was observed among all size classes of *Hoplias*.

Between 50 and 60 mm, *Charax* shifted from feeding primarily on aquatic insects to small characid fishes, particularly *Odontostilbe pulcher*. Like *Charax*, *Caquetia* over 70 mm preyed most heavily upon small characids, especially *Astyanax bimaculatus*, *Odontostilbe pulcher*, and *Ctenobrycon spilurus*. *Ctenobrycon spilurus* and *Curimata argentea* were the primary prey of large adult *Gymnotus* (>200 mm). *Rhamdia* larger than 60 mm consumed mostly whole *Curimata*, but also fresh remains of *Astyanax* and *Prochilodus* that apparently resulted from frenzied attacks by schooling *Pygocentrus*. The proportion of fish in stomachs was highly correlated with standard length (Table 4).

Table 2. Partial resource matrix of dominant food items consumed by subadult size classes of piscivorous fishes at Caño Maraca. Seven fish and 28 non-fish items totalling 43.4 liters are not listed.

Prey category	HMA	CGI	PNO	SIR	SME	SRH	GCA	RHA	CKR
Fine detritus	0.01	0.08	0.11	1.25	–	2.85	–	0.40	–
Aquatic vegetation	0.21	–	4.37	–	–	–	0.10	0.17	0.01
Clams (Mollusca)	–	0.02	–	–	–	–	–	8.35	1.24
Cladocera	–	0.05	–	–	–	–	3.44	1.85	0.79
Eubranchipoda	–	0.04	–	–	–	–	5.05	6.43	0.09
Shrimp (Decapoda)	–	–	0.46	–	–	–	–	3.89	7.72
Ephemeroptera	7.48	6.25	0.04	–	–	–	37.46	7.54	2.02
Odonata nymphs	4.76	10.35	0.57	–	–	–	20.82	20.12	2.41
Misc. aq. Hemiptera	0.57	2.52	0.03	–	–	–	–	5.07	
Corixidae (Hemiptera)	0.04	14.89	–	–	–	–	–	–	2.38
Aq. Coleoptera (larv)	0.10	0.36	–	–	–	–	2.84	4.03	2.77
Aq. Coleoptera (adlt)	–	0.45	0.11	–	–	0.02	–	0.40	12.63
Chironomid larvae	0.07	0.26	–	–	–	–	24.93	19.89	0.37
Misc. aq. insects	0.26	0.19	0.01	–	–	–	1.24	0.79	6.54
Orthoptera	–	–	1.05	–	–	–		0.99	15.21
Fish fins	–	0.72	0.07	96.17	100	80.77		–	–
Misc. fish flesh	–	0.18	32.51	–	–	–		3.58	1.16
Misc. fish (whole)	10.52	9.59	6.89	2.41	–	–		1.99	4.54
Corydoras	–	–	–	–	–	–		7.95	–
Odontostilbe	3.58	40.16	–	–	–			–	14.22
Aequidens	4.37	–	–	–	–			–	1.00
Gephyrocharax	–	7.56	–	–	–			–	0.50
Hemigrammus	3.73	–	–	–	–			–	1.00
Poecilia	2.01	–	–	–	–			–	1.33
Curimata	25.79	–	10.37	–	–			–	–
Astyanax	5.87	–	17.19						
Hoplias	8.31	–	–						
Rachovia	3.58	–	–						
Triportheus	–	–	4.37						
Markiana	–	–	5.59						
Caquetia	9.67	1.26							
Cheirodontops	–	3.60	–			–			
Gymnotus	–	–	9.93			–			
Hypostomus	–	–	–			15.68			
Apistogramma	5.16	–	–						

Table 3. Partial resource matrix of dominant food items consumed by adult size classes of piscivorous fishes at Caño Maraca. Twenty four fish and 32 non-fish items totalling 92.9 liters are not listed.

Prey category	HMA	CGI	PNO	SIR	SME	SRH	GCA	RHA	CKR
Vegetative detritus	0.01	0.86	3.56	3.13	-	0.09	-	0.04	5.45
Aquatic vegetation	0.15	1.01	5.55	2.53	-	-	2.17	1.91	7.27
Hard fruits, seeds	-	-	0.29	0.31	-	-	0.09	0.84	7.27
Fish eggs	-	-	-	-	-	-	0.17	12.01	1.19
Snails (Mollusca)	-	-	-	-	-	-	4.86	-	1.88
Shrimp (Decapoda)	0.16	12.13	0.92	-	-	-	16.30	8.96	4.35
Odonata nymphs	0.26	-	0.04	-	-	-	15.60	1.24	3.46
Orthoptera	0.06	-	0.86	-	-	-	2.33	0.44	3.46
Arachnida	-	-	0.13	-	-	-	-	5.20	4.15
Ctenoid scales	-	-	-	3.15	-	-	0.05	2.00	-
Fish fins	-	-	0.31	51.53	76.19	56.54	-	-	-
Misc. fish flesh	0.05	0.47	14.46	-	-	-	-	3.64	0.89
Misc. fish (whole)	3.07	23.18	2.22	.50	-	-	6.70	1.20	22.19
Odontostilbe	0.08	37.13	0.07	-	-	-	2.81	-	7.90
Ctenobrycon	4.16	-	2.30	-	-	-	11.38	-	6.92
Pimelodella	-	-	2.34	37.55	-	-	-	-	-
Curimata	20.19	1.50	22.64	-	-	-	10.54	26.00	-
Astyanax	4.43	-	3.74	-	-	43.44	0.84	9.36	30.63
Prochilidus	25.23	-	7.91	-	-	-	-	9.88	
Rineloricaria	6.17	-	0.14	-	-				
Hoplias	2.24	-	-	-	23.84	-	-		
Triportheus	-	-	5.30	-	-	-	-		
Roeboides	-	17.17	-	-	-	-	3.10		
Hoplosternum	24.67	-	-	-	-	-	-		
Non-fish vertebrates	-	-	5.55	-	-	-	-		

Table 4. Product moment correlations between the proportion of fish in the diet and the standard length of piscivores containing food (* = P<0.05, ** = P<0.0001).

Species	r^2	F	DF	P
Hoplias	0.94	3.48	202	**
Charax	0.94	1.84	172	0.06
Pygocentrus	0.97	2.41	152	*
S. irritans	0.99	4.78	68	0.11
S. medini	0.95	2.10	56	0.17
S. rhombeus	0.89	0.34	47	0.93
Gymnotus	0.88	2.61	119	*
Rhamdia	0.89	0.93	71	0.61
Caquetia	0.75	3.15	121	**

Seasonality and diet

The proportion of empty piscivore stomachs was significantly affected by season (F = 3.67, 2 DF, $P<0.05$). Even though *Gymnotus* and the four piranha species did not contribute to the trend, significantly more empty stomachs were encountered during the dry season than the wet season (Table 5). Invertebrate and fish larvae production were supported by a burst of aquatic primary production following the heavy rains and flooding that initiated the wet season. Based on the total community-wide consumption, total aquatic invertebrate availability was higher during the wet season than the transition and dry season, whereas the inverse was observed for combined fish prey (Fig. 4). Presumably, several piscivores lowered their feeding rates during the peak dry season in response to physiological trade-offs associated with respiratory stress. On January 28, 1984, large numbers of *Hoplias* were observed dead or dying at the estero, asphyxia being the apparent proximate cause of death (Winemiller 1989).

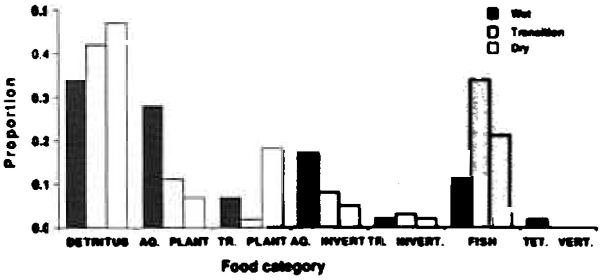

Fig. 4. Relative seasonal availability of fish food resources as indicated by total volumes consumed by the complete Caño Maraca fish fauna (total volumes recorded in liters for each season appear in the key; AQ = aquatic, TR = terrestrial).

To some degree, seasonal differences in the frequency of empty stomachs were due to ontogenetic diet shifts. Although no significant overall effect of fish size on frequency of empty stomachs was noted, the largest fishes had significantly more empty stomachs than the smallest size class (Table 5). The feeding rate of large piscivores, such as *Hoplias*, often is relatively low due to the time required for digestion of massive prey items prior to the initiation of a new feeding bout. All of the specimens of the largest size classes of the fin-nipping piranhas, *S. irritans*, *S. medini*, and *S. rhombeus* contained food (Table 5). *Pygocentrus* and *Gymnotus* in all three size classes appeared to be frequent foragers. To some degree, frequency of piscivorous feeding may be overestimated by stomach contents, because compact bones and stiff fin rays are digested more slowly than soft tissues. Additionally, different digestion rates for predominantly juvenile versus adult prey probably affects the frequency of empty stomachs. Chitinous matter associated with invertebrate feeding by smaller piscivores passes through guts more slowly than vertebrate flesh.

Diet breadth among piscivores showed no significant overall effect of season (ANOVA). Mean diet breadth among piscivores was 4.97 during the wet season, 4.72 during the transition season, and 3.89

Table 5. Percent empty stomachs encountered during three seasons and within three piscivore size classes.

Species	Wet	Transition	Dry	Total sampl
Hoplias	10.9	51.3	54.2	389
Charax	2.8	31.8	81.8	295
Pygocentrus	6.4	0	–	238
S. irritans	0	4.2	–	76
S. medini	0	0	0	68
S. rhombeus	4.3	3.3	–	50
Gymnotus	1.1	7.4	4.8	298
Rhamdia	0	18.6	29.3	124
Caquetia	5.5	4.1	13.8	370
Mean	3.4	13.4	30.6	F = 3.67, 2 DF, P <0.05
Species	Juveniles	Subadults	Adults	
Hoplias	6.5	31.2	57.1	
Charax	3.6	26.9	35.3	
Pygocentrus	0	2.0	2.4	
S. irritans	0	3.8	0	
S. medini	0	0	0	
S. rhombeus	6.4	0	0	
Gymnotus	0	3.0	6.8	
Rhamdia	0	12.0	21.2	
Caquetia	0.6	4.8	36.4	
Mean	1.9	9.3	17.7	F = 2.87, 2 DF, P = 0.07

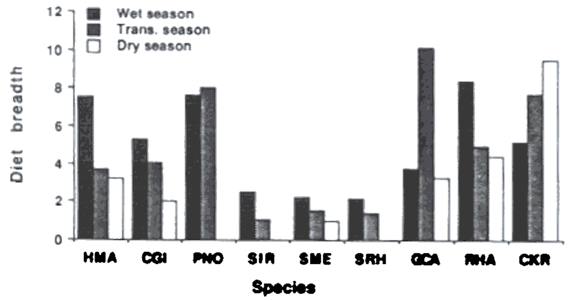

Fig. 5. Average diet breadths of piscivores during the wet, transition, and dry seasons at Caño Maraca (HMA = *Hoplias malabaricus*, CGI = *Charax gibbosus*, PNO = *Pygocentrus notatus*, SIR = *Serrasalmus irritans*, SME = *Serrasalmus medini*, SRH = *Serrasalmus rhombeus*, GCA = *Gymnotus carapo*, RHA = *Rhamdia* sp., CKR = *Caquetia kraussii*).

during the peak dry season. The three *Serrasalmus* species exhibited relatively narrow diet breadths as a result of their fin-nipping specialization. Diet breadths showed a trend of lower values during drier periods for *Serrasalmus* spp., *Hoplias*, *Charax*, and *Rhamdia* (Fig. 5). *Pygocentrus* and *Caquetia* exhibited trends of somewhat more generalized feeding during drier periods. *Gymnotus* was a more generalized feeder during the transition season than either the wet or dry seasons. During the transition season, *Gymnotus* (31–306 mm) took a variety of small fishes and aquatic invertebrates, especially Odonata nymphs and Hydracarina. *Gymnotus* was the principal predator of *Ctenobrycon spilurus*, a small characin that is abundant in the area throughout the year.

Average seasonal diet overlap among piscivores was low (0.18-wet, 0.19-dry, 0.25-transition; Fig. 6). For example, the proportions of cells within the p_{ij}-based overlap matrices with values less than 0.10 were 0.53 (wet), 0.57 (transition), and 0.65 (dry). During the wet season, the largest overlaps were between *Charax* and *S. medini* ($\varphi = 1.11, 0.46$), *S. irritans* and *S. rhombeus* ($\varphi = 0.70, 0.60$), and *Gymnotus* and *Rhamdia* ($\varphi = 0.34, 0.74$). Overlaps (p_{ij}-based) equal to or exceeding 1.0 were obtained for *Hoplias* × *Pygocentrus*, *Hoplias* × *Gymnotus*, *Hoplias* × *Rhamdia*, *S. irritans* × *S. medini*, and *S. irritans* × *S. rhombeus* during the transition season. Among 20 pairwise comparisons, only the *Gymnotus* by *Rhamdia* pairing showed large dietary overlap during the dry season ($\varphi = 0.64, 0.85$).

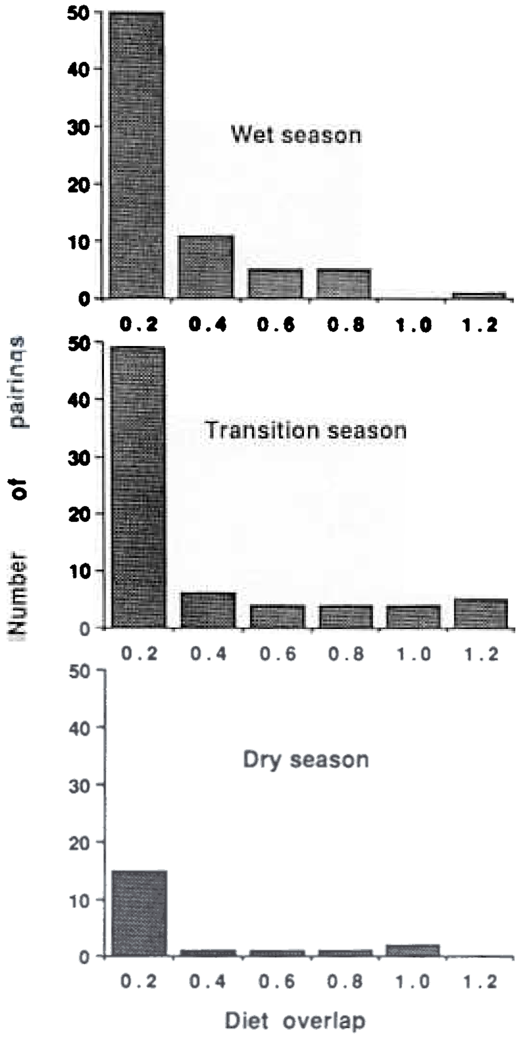

Fig. 6. Frequency histograms for piscivore diet overlaps during three seasons at Caño Maraca.

When diet similarities were calculated using electivities in place of p_{ij}s, little diet similarity was observed among piscivores during any season. The proportions of cells with electivity-based similarities less than 0.10 were as follows: 0.89 (wet), 0.76 (transition), and 0.75 (dry). Average seasonal diet similarities were 0.05 (wet), 0.08 (transition), and 0.10 (dry). Based on electivities, the highest diet similarity obtained for the wet season was $\varphi_e = 0.43$

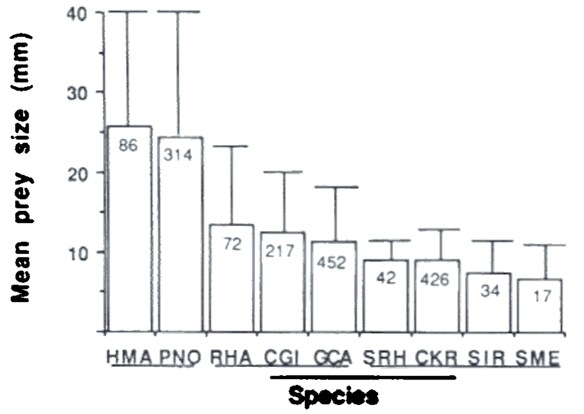

Fig. 7. Mean prey sizes encountered in diets of Caño Maraca piscivores during the transition season. Error bars represent one standard deviation, the number of prey items measured appears within each open bar, and means for species joined by lines below the x axis were not significantly different at $\alpha = 0.05$ according to Duncan's Multiple Range Test (species codes are the same as in Fig. 5).

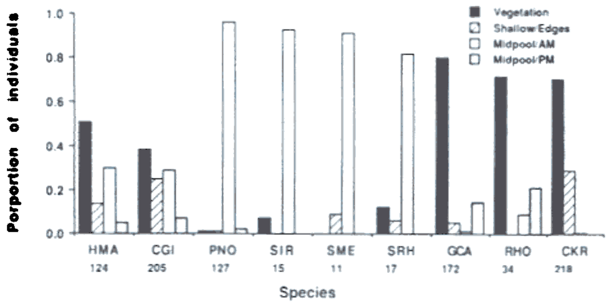

Fig. 8. Relative proportions of individuals of each species taken from four microhabitat samples during four months of the transition season at Caño Maraca (species codes are the same as in Fig. 5).

(*Pygocentrus* × *S. rhombeus*). Fin specialists, *S. irritans* × *S. rhombeus* provided the only transition season similarities exceeding 0.31 ($\varphi_e = 0.83, 1.19$), whereas *Hoplias* on *Charax* ($\varphi_e = 0.96$) represented the only pairing above 0.24 during the dry season.

Prey size

A significant relationship exists between prey size and piscivore species (F = 65.51, 8 DF, P<0.0001). *Hoplias* and *Pygocentrus* ate significantly larger prey than the other seven Caño Maraca piscivores, whereas *Caquetia* and the three *Serrasalmus* species exploited significantly smaller prey than the remaining five piscivores (Fig. 7). The latter finding should be qualified, however. Fin-nipping piranhas may actually exploit larger prey than *Caquetia*, since fin fragment measurements were used for the analysis, rather than estimates of host body length (Northcote et al. 1986).

Habitat utilization

Piscivores exhibited three basic patterns of habitat utilization during the transition season (Fig. 8). *Hoplias* and *Charax* were habitat generalists, occurring with similar frequencies in all three habitats and nocturnally in midpool regions to some degree. The four piranha species were essentially diurnal, midpool, open-water dwellers. *Serrasalmus rhombeus* appeared to utilize vegetation/edge habitats to a small extent. *Gymnotus*, *Rhamdia*, and *Caquetia* were primarily vegetation dwellers, particularly by day. Both *Gymnotus* and *Rhamdia* foraged in deeper, open-water nocturnally, the former aided by electroreception (Bullock 1982) and the latter by keen olfactory capabilities associated with its long barbels. *Caquetia*, large adults in particular, inhabited nearshore/edge habitats in addition to thick stands of aquatic macrophytes (29%).

In contrast with diet, habitat overlap (p_{ij}-based) among transition season piscivores was large. Only 18 percent of the cells in the habitat overlap matrix corresponded to overlaps less than 0.10, and mean overlap was 0.59. In addition to blocks of cells corresponding to habitat generalists (e.g., *Hoplias*, *Charax*), open water-dwellers (4 piranhas), and vegetation-dwellers (3 non-characiforms), large habitat overlaps were obtained for both *Hoplias* and *Charax* with each of the other seven relative habitat specialists (range of $\varphi = 0.32 - 1.14$). Whereas four categories (midpool day and night samples were treated separately for this analysis) provided only a coarse analysis of habitat partitioning, little opportunity for further broad subdivision was noted during the transition and dry seasons.

Although some opportunity for microhabitat specialization probably does exist within the turbid waters of the creek during these periods (e.g., benthic versus midlevel or surface), each habitat yielded rather consistent mixtures of species in seine hauls.

If one considers three niche axes simultaneously (prey type, prey size, habitat), and assumes conservatively that overlaps greater than 0.50 are biologically significant, then piscivores separated on at least one axis in all but four comparisons during the transition season (prey type overlap based on p_{ij}). Of 36 pairwise species comparisons, six separated on all three axes, 18 separated on two axes, and eight separated on one axis. Of the pairings that show high overlap on all three dimensions, *Hoplias* and *Pygocentrus* actually had equivocal overlap for habitat utilization ($\varphi = 0.32, 0.87$), sharing only open, midpool regions to any large extent. Patterns of foraging behavior of these species show striking differences as well (i.e., solitary, sit-and-wait *Hoplias* vs. gregarious, pursuit *Pygocentrus*). Other large, three-dimensional overlap pairings corresponded to fin-nipping piranha species (*S. irritans* × *S. medini* and *S. rhombeus; S. medini* × *S. rhombeus*). If electivity-based diet similarities greater than 0.50 are used as the criteria for significant dietary overlap, then only the *S. irritans* and *S. rhombeus* pairing showed significant three-dimensional overlap during the transition season.

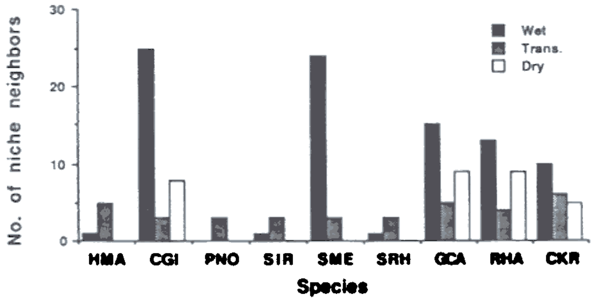

Fig. 9. The number of diet niche neighbors (defined by $\varphi>0.10$) possessed by each piscivore species during the wet, transition, and dry seasons at Caño Maraca (species codes are the same as in Fig. 5).

Collective diet overlap

As a coarse estimate of the potential for diffuse competition (sensu MacArthur 1972, Pianka 1974, 1980), I analyzed total diet overlap (p_{ij}-based) for each of the nine piscivores with other members of the fish assemblage. Diffuse competition (or diffuse overlap in this case) may occur when several niche neighbors, each exhibiting a weak interaction, have a significant collective effect on a potential competitor. In this instance, niche neighbor was defined as any species exhibiting overlap greater than or equal to 0.10 on the resource dimension in question. The opportunity for diffuse niche overlap should be great in species rich systems such as tropical fish assemblages. Total diet overlaps were calculated as the sum of all pairwise diet overlaps exhibited by niche neighbors during each of the three seasons. Two pools of potential niche neighbors were analyzed, the nine-species piscivore guild and the entire Caño Maraca fish community. Because not all species were present and response to aquatic hypoxia apparently superceded feeding during extended portions of the peak dry season, only wet and transition season diffuse overlap trends are presented.

Analyses of the number of niche neighbors and patterns of collective dietary overlap revealed two classes of seasonal response by piscivores. For five species, the number of niche neighbors and total dietary overlap were greater during the wet season than the transition (Fig. 9, 10). Extreme trophic specialization by subadult *S. medini* during the transition season was indicated by a large drop in total diet overlap relative to the previous sampling period dominated by juveniles ($\varphi_T = 17.8$-wet, 2.7-transition). The remaining four species (*Hoplias, Pygocentrus, S. irritans, S. rhombeus*) had comparatively few niche neighbors throughout the year (Fig. 9). Moreover, relatively low total diet overlap ($\varphi_T<4.0$) was observed for these piscivores throughout the year, both with other guild members and the community at large (Fig. 10). Although all three species specialized on fins as subadults, *S. irritans* and *S. rhombeus* switched to fins at smaller sizes than *S. medini*. Five of the nine piscivores showed lowest collective diet overlap

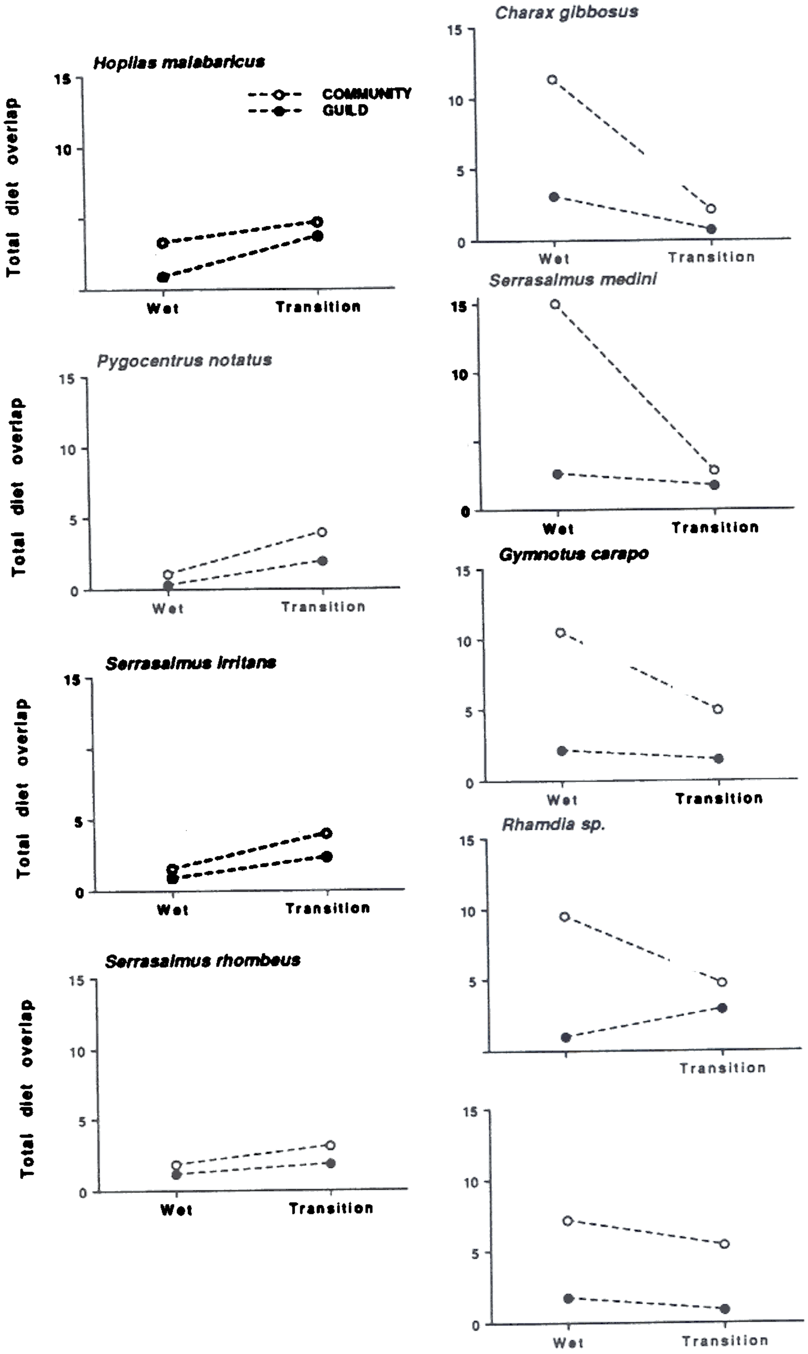

Fig. 10. Total diet overlap exhibited by each piscivore species during different seasons at Caño Maraca. Total community diet overlaps are represented by open symbols, and total piscivore guild overlaps are plotted as closed symbols.

during the transition season, both within the piscivore guild and the community at large (Fig. 10). In the cases of *Gymnotus*, *Caquetia*, and *Serrasalmus medini*, collective guild overlaps were low relative to overall community overlaps during both the wet and transition seasons. *Rhamdia* exhibited a slight increase in total guild overlap between the wet and transition seasons, although overall community overlap declined.

Discussion

Ontogeny and diet

All nine sympatric, tropical piscivores showed distinct shifts from invertebrate feeding by small juveniles to primarily fish feeding by subadult and adult size classes. Predominance of fin nipping by subadult and adult size classes of serrasalmine piranhas is consistent with earlier findings (Goulding 1980, Machado & Garcia 1986, Northcote et al. 1986, 1987, Sazima & Zamprogno 1986, Nico & Taphorn 1988). Three primary factors probably are involved in producing size-related patterns of feeding among piscivores. First, juvenile fishes are constrained by their small size to exploit relatively small food particles (Werner & Gilliam 1984, Keast 1985a, 1985b). Only following a period of initial growth can whole-fish swallowers switch to larger fish prey. Second, availability of small zooplankton and benthic invertebrates (e.g., aquatic insect larvae) was much greater during the wet season compared to either the transition or dry seasons at Caño Maraca (Fig. 4). Observed switching from invertebrate to fish prey largely coincided with changing food availabilities as indicated by feeding performance of the entire fish assemblage. Whereas total aquatic primary production and aquatic invertebrate availability declined during the gradual desiccation of the floodplain, fish densities increased markedly. Jackson (1961) made a similar observation for African fishes in seasonal aquatic habitats. Third, many predatory fishes exhibit changes in relative body proportions and other anatomical traits during growth that are associated with greater feeding specialization (Werner 1974, Werner & Hall 1979, Machado-Allison & Garcia 1986, Keast 1985b). Morphological changes associated with greater trophic specialization in the form of piscivory should reduce the efficiency of microinvertebrate feeding. Following this reasoning, Griffiths (1975) recognized a dynamic trade-off between maximizing prey number versus prey energy in the feeding strategies exhibited by piscivorous yellow perch, *Perca flavescens*, during ontogeny.

Resource partitioning

Food resource partitioning was widespread within the Caño Maraca piscivore guild, particularly during the transition season. Given the high concordance between ontogenetic diet shifts, prey availability, and seasonal rainfall, can high levels of resource partitioning be interpreted in relation to biological interactions, especially interspecific competition? Three general, alternative explanations could account for observed patterns of resource exploitation. First, resource exploitation could occur at random. Yet sufficient subdivision of available resources was observed among the nine piscivores as to render this null hypothesis unlikely. For example, average seasonal diet overlaps were considerably lower ($\varphi = 0.18 - 0.25$) than those obtained for series of randomly constructed 10-species communities ($\varphi =$ ca. 0.75, Pianka et al. 1979). Second, contemporary patterns of niche partitioning could be founded in genetically-based morphological and behavioral traits that evolved in response to past environmental conditions that differed from current conditions (sensu Connell 1980). This second hypothesis contrasts sharply with a third possible explanation, that contemporary patterns of resource subdivision are adaptive in the context of present day biotic interactions. Interspecific competition is foremost among biotic mechanisms cited in studies of community resource partitioning, although the role of predation has recently received greater attention, particularly with respect to habitat selection (Fraser & Cerri 1982, Sih 1982, Werner et al. 1983, Mittlebach 1984, Power 1984, Power et al. 1985, Hobson & Chess 1986).

In recent reviews of resource partitioning in lower vertebrates, Toft (1985) and Ross (1986) indicated that causal factors responsible for differences in resource use are rarely known. MacNally (1983) and others have argued that descriptive field studies alone cannot demonstrate competition. Whereas field experiments potentially can demonstrate interspecific competition (Schoener 1983), they are beset with problems of interpretation as well. Positive, negative, or even a complete lack of population response to experimental manipulations potentially are confounded by effects of indirect interactions (Bender et al. 1984, Tilman 1987) or measurement of inappropriate variables (Diamond 1983, MacNally 1983). Even though descriptive studies cannot demonstrate competition directly, they often provide strong circumstantial evidence with the potential to support or reject the hypothesis of interspecific competition. The inferential value of this circumstantial evidence depends upon the strength of comparisons based on interpopulation or temporal and spatial environmental variation.

In this study, trophic specializations were associated with lower diffuse diet overlap during the transition season when fish population densities were highest and availability of invertebrate prey was reduced. Due to the general pattern of interspecific synchrony in reproduction with the onset of the wet season, ontogenetic shifts toward more specialized piscivore diets largely corresponded with the progression of the transition season and fish growth. These observations are consistent with McKaye & Marsh's (1983) hypothesis that African cichlid fishes switch from more opportunistic, generalized diets to more specialized feeding during periods of relative resource scarcity (i.e., following the 'niche overlap hypothesis' of Pianka 1974). Morphological adaptations for specialized feeding may be selectively advantageous during a limited period during the annual cycle of ecological events. At Caño Maraca, four species that switched to piscivory at small sizes also exhibited low collective diet overlaps throughout the year (Fig. 10).

In summarizing work involving tropical fish communities, Lowe-McConnell (1987) suggested that competition is potentially most important during the late wet and dry seasons in floodplain ecosystems. During this 'crunch period', resources become increasingly limited (especially resources related to space) as local stocks of aquatic organisms become denser within shrinking bodies of water. Biotic interactions, especially fish predation, intensify at this time, but are piscivores necessarily resource-limited? Whereas apparent availability of fish prey may be high during the transition season, niche segregation and trophic specialization among piscivores should occur for two reasons. First, following optimal foraging theory (Krebs 1978, Pyke 1984), scarcity of invertebrate prey and temporary abundance of prey fishes would favor exploitation of the most profitable forms by predators, based on their morphology and innate components of feeding behavior. Profitability would be expressed here in terms of the ratio of energy gained by maximizing the rate of prey capture, divided by the total energy cost associated with searching, pursuit, handling, digestion, and assimilation. Evolutionary divergence of prey escape tactics increases requirements for specialization on a restricted number of prey species (Rand 1967). Second, the brevity of the season of high fish density, together with the high risk of mortality due to predation and dry season dessication/anoxia, conveys a tremendous fitness advantage to individuals that maximize their intake of temporarily abundant prey, then survive the ensuing dry season. A disproportionate fraction of the next generation would be founded by efficient piscivores that are larger and more fecund (or more effective in providing parental care) than less efficient conspecifics. In effect, a major fraction of the annual caloric intake of llanos piscivores is concentrated into the approximately four-month transition season. Relative to other seasons, growth and visceral fat deposition is maximal for most species during the transition season (personal observation).

Given the selective premium that is placed on highly efficient foraging by subadult and adult piscivores during the transition season, it appears likely that observed trophic specializations are adaptive in reducing the negative impact of diffuse competition within this rich fish assemblage. For competition to occur, resources must be in limited supply and contested by two or more populations. The presence of numerous heterospecific piscivores during the transition season of high fish density could restrict foraging to the most profitable prey types. Reductions in pairwise diet overlap during periods of reduced food availability have been shown in several earlier studies of fish communities (see Ross 1986). Though based on limited sampling, reduced diet overlap among fishes was reported by Zaret & Rand (1971) and Greenfield et al. (1983) during the dry season in Central American streams. Alternatively, Lowe-McConnell (1964), Knoppel (1970), and Goulding (1980) stressed high dietary overlap in South American fish communities, although no attempts were made to study trophic guilds quantitatively over time. The findings of the current study contrast sharply with those of Knoppel (1970), who interpreted his data as indicating a perplexing lack of correspondence between morphological characteristics and diets of fishes from five stream collections in central Amazonia. Also in opposition to the current findings was Knoppel's (p. 346) contention that 'stomach contents according to age of fishes did not merit close consideration'. Quite the contrary, Knoppel probably did not examine stomachs and size classes closely enough to discern the obvious patterns.

Recently, Prejs & Prejs (1987) observed higher dietary overlap during the dry season among small, vegetation-dwelling fishes in seasonal pools of the Venezuelan low llanos. These authors interpreted patterns of diet overlap as ecologically unimportant, because their data showed reduced feeding rates or a switch to detritivory during the dry season (apparently, the dynamic transition season of the llanos was not sampled). Lower availability of insect prey and increased predation pressure were believed to be the primary factors accounting for reduced dry season feeding; however, results obtained by Prejs & Prejs (1987) must be interpreted with caution for several reasons. First, their community subset of eight small, vegetation-dwelling fishes does not represent a trophic guild, but rather a diverse subset of small vegetation-dwelling fishes. Secondly, total sample sizes for stomach content analysis were small (N = 9–30), and prey biomass in stomach contents was estimated from length/mass relationships. Both of these factors increase risks of sampling error. Third, and most seriously, the taxonomic identities of the eight fish species are confused (see Taphorn & Lilyestrom 1985 for listing of regional ichthyofauna). The only unconfused species name, *Roeboides dayi* (Steindachner), is perhaps the most suspect of the eight. Prejs & Prejs (1987) found 99.9 and 100% vegetation and detritus in the stomachs of *R. dayi* during the dry season, whereas fish scales comprised 76 (N = 121) and 25% (N = 49) of the diet of *R. dayi* at Caño Maraca during the transition and dry seasons respectively. Scales formed 24 (wet) and 15% (dry) of the diet of *R. dayi* by volume at Caño Volcán, a small piedmont stream (N = 313, Winemiller 1987a). All other *Roeboides* species, for which data are available, specialize on scales in addition to aquatic insects (Sazima 1983, Winemiller 1987a). Most of the fishes referred to as '*R. dayi*' by Prejs & Prejs (1987) were probably *Ctenobrycon spilurus* (Valenciennes), a morphologically similar, omnivorous characid that is extremely common in shallow, productive environments throughout the llanos.

Some temperate zone studies also have demonstrated greater diet segregation among fishes during periods of reduced food availability (Nilsson 1955, Harrington & Harrington 1961, Thorman 1982). In addition to diet segregation, interspecific size and time related differences in habitat use have been demonstrated for both temperate and tropical fish assemblages (Werner & Hall 1977, Moyle & Senanayake 1984, and see Ross 1986 for others). Habitat segregation by Caño Maraca piscivores probably was as much a function of predator avoidance as food resource segregation. Fishes used aquatic vegetation as the principal form of cover for avoidance of predation by dense schools of red-bellied piranhas, *Pygocentrus notatus*. Additionally, and perhaps to a lesser extent, smaller fin-nipping *Serrasalmus* species posed a threat to diurnal, open-water dwellers. Where it is common, *Pygocentrus* may have a pervasive effect on the spatial structuring of fish communities, since only highly cryptic, heavily armored, or fast schooling fishes were generally taken from deep open-water regions of Caño Maraca and other ilanos streams during daylight. Nocturnal predators (e.g. *Rhamdia* and *Gymnotus*) leave the dense mats of aquatic vegetation to forage in the open water habitat under cover of darkness. Approximately 80 man-hours of nocturnal hook-and-line fishing at a stream in the low llanos of Apure state (location of Caño Maporal given in Nico & Taphorn 1988) yielded nine species of large piscivores (unpublished data). Diurnal hook-and-line fishing over the same period yielded 13 large piscivorous species, yet only three species occurred in both samples (e.g. *Pygocentrus notatus, Pseudoplatystoma fasciatus*, and *Plagioscion squamosissimus*). Sixty seven percent of the nocturnal sample was comprised of siluriforms (catfishes and knifefishes), whereas 92% of the diurnal sample belonged to the orders Characiformes (piranhas, tetras, and related forms) and Perciformes (cichlids and one freshwater drum). Furthermore, most diurnal piscivores were taken near cover at the stream margin, further supporting the hypothesis that *Pygocentrus* restricts diurnal use of the open-water, midpool habitat by other piscivores.

The three fin-nipping piranhas exhibited the highest similarities in diet and habitat niche parameters at Caño Maraca. As might be expected due to genetic and morphological similarities, closely related species frequently exhibit relatively less ecological segregation than more distant taxa. Lack of diet segregation among fin-nipping piranhas, especially *Serrasalmus irritans* and *S. rhombeus* subadults, was due in part to my inability to identify fin fragments at the species level in most instances. Records of the incidence of fin nips on preserved Caño Maraca specimens clearly indicate that not all fishes are equally vulnerable to *Serrasalmus* attacks (unpublished data). Preliminary tests of aquarium-housed juveniles and subadults suggest that *Serrasalmus* species possess distinct patterns of foraging behavior associated with either stealth in open water (*S. irritans*; see Nico & Taphorn 1988 for a brief description of field observation), persistent chasing with frequent remaneuvering (*S. medini*), or use of cover for ambushing (*S. rhombeus*). Similar behavioral patterns were observed among three syntopic piranha species in the Mato Grosso region of western Brazil (I. Sazima, personal communication). Further field and laboratory studies are needed to sort out the niche relations of fin-nipping piranhas more accurately.

Conclusions

High fish species diversity in the neotropics is associated with impressive morphological and ecological diversification (Roberts 1972, Fink & Fink 1979, Goulding 1980, Sazima 1986, Lowe-McConnell 1987). Coexistence of more than 100 fish species in some llanos creeks (Taphorn & Lilyestrom 1985) may be due in part to relaxed interspecific competition during horizontal flooding and the bloom of primary production that occurs during the wet season. Diets of five of the nine piscivores examined overlapped more with the rest of the fish community during this period than any other. Large diffuse overlap during the wet season largely resulted from heavy exploitation of abundant microcrustacea and aquatic insect larvae by juveniles. Lower collective overlap during the transition season probably was derived from complex interactions among several factors, including: (1) reduced availability of juvenile food resources, (2) fish growth and ecomorphological trade-offs favoring diet shifts, (3) increased fish densities and diffuse competition favoring maximal rates of prey exploitation, (4) differential prey profitability due to trade-offs associated with prey escape tactics, and (5) the threat of predation by piranhas restricting diurnal foraging by other piscivores in open-water microhabitats. In highly diverse communities, diffuse overlap with numerous niche neighbors represents a greater potential negative effect than isolated pairwise interactions.

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