



Temporal patterns of resource partitioning among *Cichla* species in a Venezuelan blackwater river

D. B. JEPSEN*[‡], K. O. WINEMILLER* AND D. C. TAPHORN[†]

*Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, U.S.A. and [†]Universidad Experimental de Los Llanos Esequiel Zamora, Guanare, Portuguesa, Venezuela 3310

(Received 21 January 1997, Accepted 1 June 1997)

In channel and floodplain habitats of the Cinaruco River, Venezuela, *Cichla temensis* was more abundant and larger than *C. intermedia* and *C. orinocensis*. Seasonal variation in hydrology influenced habitat use, spawning, and predator–prey interactions. The three piscivores partitioned habitat, with *C. intermedia* showing a strong affinity for structured habitats in the main channel during all water level fluctuations. *C. orinocensis* was most abundant in shallow areas with submerged structure in lagoons and, to a lesser extent, in low velocity regions of the channel, and *C. temensis* occupied a wide range of lotic and lentic habitats. During the low-water period, the feeding frequency and body condition of all three species declined, and this was related, in part, to preparation for spawning near the end of the low-water season. The diet of *C. intermedia* was least similar to its two congeners during falling and rising water. *C. orinocensis* and *C. temensis* had lowest diet overlap during the low-water conditions, the period when many individuals of these two species move into lagoons for nesting. Prey in stomachs were significantly larger during the falling-water than the rising-water period, and predation by *Cichla* and other large piscivores during the falling-water period may have reduced the abundance of large prey, particularly *Semaprochilodus kneri*. These migratory detritivorous fish were important prey for *C. temensis* during the falling-water period and probably contributed a substantial fraction of the annual energy intake for this species. Together, the three *Cichla* species consume a wide spectrum of prey from a diverse fish assemblage, but prey are subdivided based on habitat, prey type, and season. © 1997 The Fisheries Society of the British Isles

Key words: *Cichla*; competition; migratory fishes; Orinoco River; seasonal effects; *Semaprochilodus*; Venezuela.

INTRODUCTION

Most ecological research on piscivorous fishes has focused on their potential effect on prey populations, rather than the potential for competition between sympatric piscivores. Studies of resource use by sympatric piscivores in tropical fresh waters have been conducted on South American piranhas (Nico & Taphorn, 1988), a guild of South American piscivores (Winemiller, 1989a), African *Serranochromis* spp. Regan (Winemiller, 1991), African catfishes (van der Waal, 1985; Merron, 1993; Winemiller & Kelso-Winemiller, 1996), and African tigerfish *Hydrocynus* spp. Cuvier and pike *Hepsetus odoe* (Bloch, 1794) (Lewis, 1974; Van der Waal, 1985; Winemiller & Kelso-Winemiller, 1994). Based on results from temperate zone studies, the effects of habitat heterogeneity on piscivory can be major (Mittelbach, 1986; Werner & Hall, 1988), yet this has received little attention in tropical river ecosystems, many of which are highly heterogeneous and dynamic (Welcomme *et al.*, 1989).

[‡]Tel.: +1 409 862 1279; fax: +1 409 845 3786; email: djepsen@wfscgate.tamu.edu

Changes in habitat quality and resource availability associated with seasonal variation in hydrology strongly influences ecological interactions in tropical rivers (Lowe-McConnell, 1979). The response of tropical piscivores to seasonally shifting prey densities seems to follow no general trend, but relatively little information is available. Diet overlap among nine piscivores was lowest during the period of falling water and high fish densities in a creek/floodplain in the Venezuelan plains (Winemiller, 1989a). This was also the period when many young piscivores, spawned during the previous flood season, had grown large enough to shift from invertebrate feeding to piscivory. A similar interaction between ontogenetic niche shifts and seasonal variation in the degree of resource segregation was obtained for piscivorous cichlids (*Serranochromis* spp.) from the Zambezi River and its associated floodplain (Winemiller, 1991). In contrast, diet overlap between piscivorous tigerfish and pike in the Zambezi River/floodplain was virtually constant between high- and low-water seasons (Winemiller & Kelso-Winemiller, 1994).

Peacock cichlids, *Cichla* spp. (Cichlidae), are important piscivores in species-rich South American rivers. Zaret & Paine's (1973) study demonstrated well the major effects of *Cichla ocellaris* (Bloch & Schneider, 1801) on a lake fish community and its adjacent terrestrial community. *Cichla* are important food and game fish, which have been introduced into lakes in several tropical and subtropical regions, including southern Brazil, Panama, Puerto Rico, Hawaii, and Florida. Most of the literature deals with *C. ocellaris* but several species are known (Kullander, 1986), and some of the early reports may actually deal with other species. The largest species, *Cichla temensis* (Humboldt, 1833), attains over 11 kg (Winemiller *et al.*, 1997), and for this reason it has been introduced to several tropical and subtropical regions as a game fish. Much of the available ecological information is from non-indigenous lake populations (Devick, 1972; Zaret, 1980; Novoa *et al.*, 1989). Little information has been gathered on these fishes in their native fluvial ecosystems, the blackwater and clearwater rivers of the Amazon, Essequibo, and Orinoco river basins.

Three *Cichla* species sympatric in the southern savanna, or llanos, of Venezuela were studied during the dry season by Taphorn & Barbarino (1993) and Winemiller *et al.* (1997), and the latter also described the population structure of *Cichla orinocensis* (Humboldt, 1833) and *C. temensis* from a blackwater river in the forested Rio Negro drainage of southern Venezuela. The influence of seasonality on patterns of resource use by these tropical piscivores in their native ecosystems has not been investigated. Patterns of resource use by three sympatric *Cichla* species were compared in the context of resource subdivision. The influence of seasonality and habitat heterogeneity on patterns of resource use is of interest, because ratios of resource demand/supply are likely to vary accordingly.

STUDY AREA

The main study area was a section of the Cinaruco River between 6°34' N, 67°26' W and 6°31' N, 67°22' W. This river section included a complex of habitat types that were representative of features found in other portions of the system. The Cinaruco is a low-gradient, floodplain system that originates in the alluvial

plains of north-eastern Colombia and flows east through the plains (llanos) region of southern Apure State in Venezuela. The Cinaruco joins the Orinoco River at approximately 6° N and 67° W. Soils of the Cinaruco catchment are generally nutrient poor and support only sparse savanna vegetation. Using Sioli's (1984) limnological criteria, the Cinaruco has been described variously as clearwater (Meade & Koehnken, 1991) or blackwater (Winemiller *et al.*, 1997). Water velocity in the main channel ranges from zero in littoral areas to about 0.5 m s⁻¹ in some cut-bank locations. Water quality data indicate a nutrient-poor, acidic system with low suspended solids and high concentrations of dissolved humic acids, the latter giving the water a tea-stained appearance. Main channel substrata are dominated by fine white sands derived from erosion of the unstable alluvial deposits of the surrounding catchment. Most of the floodplain lagoons are oxbows, some of which are interconnected by anastomosing channels that are probably remnants of primary river channels. The river is fringed by evergreen gallery forests that extend laterally from the river by no more than 200 m. Taxonomically, the fish fauna is very diverse (*c.* 200 species) and shares elements with blackwater rivers to the east and south plus, to a lesser extent, with whitewater rivers to the north (Taphorn, Winemiller and Jepsen, unpublished data). Small and medium-sized characids and other charciform families contribute the most species (Table I).

The Cinaruco undergoes annual cycles of water level fluctuation. During the rainy season of May through September, the gallery forest and much of the adjacent savanna are inundated, and with the cessation of rains, water levels recede and aquatic environments contract. White sandbanks become visible in main channel areas during the low-water season (approximately February–March) when many lagoons become isolated from the river and do not receive any surface water until the start of the next rainy season in April. The early rainfall that begins at upstream locations causes the initial flooding in the study area before commencement of local rainfall. The mean low flow of the Orinoco in the vicinity of the confluence of the Cinaruco occurs during late March, and mean peak flow occurs during early September (Lewis, 1988).

MATERIALS AND METHODS

DESIGNATION OF HABITATS AND HYDROLOGIC SEASONS

For broad spatial comparisons, lagoon and channel habitats were designated. Lagoons were lentic floodplain bodies that had no detectable flow, some of which were interconnected by anastomosing channels. Channel habitats were areas of the main river channel that usually contained submerged woody debris in littoral areas, erosional cut-banks, depositional sand banks, and occasional rocky outcroppings. Three hydrologic phases were distinguished that influenced both river and lagoon locations. The falling-water period occurred from November 1993 until early February 1994. This corresponded to a period of little or no rainfall and reflected the larger scale climatic pattern of the commencement of the dry season. A decrease in the aquatic connections between channel and floodplain habitats coincided with decreasing water levels. Prior to the falling-water period, the floodplain was inundated for several months by a seasonal hydrologic pulse that is characteristic for low-gradient rivers at this latitude. Lowest water levels on the Cinaruco occurred during February and March, the period designated low water. The rising-water period commenced with the rains of early April and continued after our sampling ended in mid-June, 1994. Then, the water level was

TABLE I. Cinaruco River fish orders and families, the number of species per family, and their adult length classes

Order	Family	No. of species	Length class	
Rajiformes	Potamotrygonidae	3	L	
Clupeiformes	Clupeidae	1	L	
	Engraulidae	1	S	
Characiformes	Anostomidae	7	M	
	Characidae	84	S (M, L)	
	Characidiidae	6	S	
	Chilodontidae	2	M	
	Ctenolucidae	3	L	
	Curimatidae	6	M	
	Cynodontidae	2	L	
	Erythrinidae	3	L	
	Gasteropelecidae	1	S	
	Hemiodontidae	5	M	
	Lebiasinidae	5	S	
	Prochilodontidae	2	L	
	Gymnotiformes	Electrophoridae	1	L
		Gymnotidae	1	L
Hypopomidae		2	M	
Rhamphichthyidae		1	M	
Siluriformes	Sternopygidae	3	M (L)	
	Ageneiosidae	1	L	
	Auchenipteridae	3	S (M)	
	Cetopsidae	1	S	
	Doradidae	8	M (L)	
	Loricariidae	10	M (S, L)	
	Pimelodidae	18	L (S, M)	
	Trichomycteridae	2	S	
Cyprinodontiformes	Belonidae	1	L	
	Poeciliidae	1	S	
Perciformes	Cichlidae	20	M (S, L)	
	Nandidae	1	M	
	Sciaenidae	2	L	
	Gobiidae	1	S	
Pleuronectiformes	Soleidae	1	M	
Synbranchiformes	Synbranchidae	1	L	

S, <50 mm; M, 50–150 mm; L, \geq 150 mm; designations in parentheses indicate size classes for a minority of species in the family.

approximately the same as when sampling began in the previous November. Although water levels were not measured, they fluctuated >4 m in the study region throughout the 8-month study interval.

Limnological data were collected monthly from river and lagoon habitats. Standard titration and colorimetric methods from a Hach™ water quality kit were used to estimate dissolved oxygen, pH, nitrite, nitrate, phosphate, hardness, and alkalinity. Temperature was measured with a thermometer, water velocity was estimated by timing the passage of a partially submerged sphere past a measured distance, and water depth was estimated using a weighted measuring tape.

FISH SURVEYS

Total sampling effort was approximately equal during the three hydrologic periods. Because this study emphasized resource use and interspecific interactions, and not absolute density estimates, sampling effort was focused on sites where *Cichla* captures seemed most probable based on previous research and our experiences at this site. A 4-m aluminum boat powered by a 15-hp outboard motor was used to access sampling sites. *Cichla* were captured using a variety of techniques, of which angling with rod, reel, and artificial lures was by far the most effective technique for fishes >100 mm standard length (L). A variety of lures was used to sample the entire water column and around various types of structure. *Cichla* <100 mm L were captured most efficiently from shallow littoral areas with seines or cast-nets. Experimental gillnets were set in lagoons and main channel areas, but these were relatively ineffective for catching *Cichla*.

For each *Cichla* captured, the presence or absence of submerged rocks, submerged woody debris, and visible water current was recorded. Fish that were to be returned to the river were handled while submerged in water in a 30-l tub to reduce stress. Species identifications were based primarily on external coloration following Machado-Allison (1971). For each fish, standard length was recorded to the nearest 1 mm with a tape held evenly across the body, and body weight (W) to the nearest 10 g using spring-loaded balances.

Stomach contents were obtained from most of the captured *Cichla* by means of a gastric lavage method that allowed collection of contents without harming the fish (Seaburg, 1957). Stomach samples were placed in separate plastic ziplock bags and frozen. Contents were identified to the lowest feasible taxonomic level (species, genus, family, or order for fishes, and usually order for invertebrates). Relative proportions of each prey category were determined from volumetric water displacement of identified prey items (to nearest 0.05 ml) as described by Winemiller (1990). The number of each prey category in each stomach was counted, then standard lengths were measured to the nearest 0.1 mm with dial calipers.

For each *Cichla* species, several individuals from a range of size classes were killed for sex determinations, visual assessments of gonad maturation and peritoneal fat reserves, and stomach contents analysis. Ovarian maturation was coded as three broad categories: undeveloped (egg diameter <1 mm); developing (1–2 mm); and mature (>2 mm). Testes were classified in a similar manner as undeveloped (small translucent cords), developing (large, translucent-white or tan testes), or mature (large, opaque, milky-white testes). To supplement samples sizes for condition and dietary analyses, *Cichla* were obtained opportunistically from sport anglers in the region. For these fishes, size, sex, and maturation data were recorded also. Reliable habitat information was not obtained for these fishes, so they were excluded from analyses that required location data.

PREY FISHES

To determine the relative abundance and availability of prey fish species, habitats in channel and lagoon sites were sampled with experimental gillnets (5.1, 10.2, 15.2 mm mesh, 50 × 2 m), seines (10 × 2, 15 × 2, and 30 × 2 m), hand-nets, and cast-nets. Time of day, gear type, sampling effort (duration of gillnet sets, distance of each seine haul), and environmental features were noted at each location. Prey samples were preserved in 15% formalin for later identification in the laboratory. Specimens then were counted and measured (nearest 0.1 mm L) with dial calipers. Voucher specimens were deposited in the Museo de Zoología, UNELLEZ and the Texas Cooperative Wildlife Collection, Texas A&M University.

DATA ANALYSIS

To characterize *Cichla* population structure, samples obtained from sport anglers were excluded. *Cichla* <200 mm were less vulnerable to hook and line capture, thus their relative abundances were underestimated in the length–frequency distributions. Body condition was estimated from the condition factor, K ($K=WL^3$). To examine spatiotemporal patterns of resource partitioning, *Cichla* were grouped according to

habitats and seasons a priori. Pianka's measure was used to evaluate diet overlap by prey order based on relative volumetric proportions, and Levin's standardized measure of niche breadth was used to estimate spatio-temporal variation in diet breadth (Krebs, 1989). Principal components analysis (PCA) based on $\log(x+1)$ transformed volumetric prey proportions and the correlation matrix were used to examine spatiotemporal variation in prey use. This exploratory procedure reduces the dimensionality in a multivariate data matrix by modelling variation among the original variables as vectors (i.e. principal components). When one or a few principal components explain a large portion of the variability, they can be plotted much like bivariate relationships to reveal patterns among observational units, in this case *Cichla* species sampled during different seasons. The category 'unidentified fishes' was eliminated from the data matrix for computations of diet breadth, overlap, and multivariate statistics.

Also, χ^2 contingency table analysis was used to examine species by habitat associations for each season, as well as species associations with habitat features (presence/absence of submerged structures and water current) that might reveal finer scale habitat partitioning. Logistic regression analysis examined the probability of capturing a given *Cichla* species from sites with different habitat features. For this analysis, potential habitats were those sites where at least one *Cichla* was captured. This method restricted the interpretation of habitat use to the frequency of a given species' occurrence in a habitat in relation to the frequency of occurrence of the other two *Cichla* species. A significant result for the association of a particular species with a given habitat variable or set of variables indicated either a negative or positive association in relation to the probability that the other two species would be found in the presence of that habitat variable or set. All statistics were computed with SAS (version 6; SAS Institute Inc., Cary, North Carolina, U.S.A.).

RESULTS

POPULATION STRUCTURE

A total of 817 individuals of the three *Cichla* species was examined. *Cichla temensis* was captured more frequently (56%) than *C. orinocensis* (27%) or *C. intermedia* (Machado, 1971) (17%). More males were captured than females for all three species (Table II), perhaps reflecting their greater vulnerability to capture during biparental nest-guarding during the low-water period. *Cichla orinocensis* and *C. intermedia* samples had similar unimodal size distributions (Fig. 1). The *C. temensis* sample had a bimodal distribution with <7% of the adult population falling within the size range in which *C. orinocensis* and *C. intermedia* were most abundant (301–350 mm). On average, *C. temensis* were significantly larger than the other two species (t_1 , tail=14.16, d.f.=625, $P<0.001$). The largest individual *C. intermedia*, *C. orinocensis*, and *C. temensis* were 429, 435, and 720 mm *L*, respectively.

HABITAT PARTITIONING

Cichla species used different aquatic habitats in response to seasonal changes in water level (Table III). Species were associated significantly with habitats (channel v. lagoon) within each of the three hydrologic seasons ($\chi^2=21.82-57.44$, d.f.=2, $P<0.001$). *Cichla temensis* was the most common species in both channel and lagoon habitats during the falling-water phase, and *C. orinocensis* was more common than the other two species in lagoons during the low-water period (59% of the sample). *Cichla orinocensis* was more common in lagoon sites than channel sites during all three seasons, and always was the least common species in the primary river channel. During the rising-water period, *Cichla intermedia*

TABLE II. *Cichla* population structure from surveys in the Cinaruco River, Venezuela, 1993–1994

Species	Total		Mean L (mm)	Mean W (g)	n		Mean L (mm)		Mean W (g)	
	n	%			Males	Females	Males	Females	Males	Females
<i>C. temensis</i>	399	56	381	1239	70	40	434	445	1808	1721
<i>C. orinocensis</i>	189	27	302	646	20	17	329	294	905	618
<i>C. intermedia</i>	119	17	308	636	20	3	306	299	666	575
Total	707				110	60	356	346	1126	971

Values for males and females are for specimens that were examined internally.

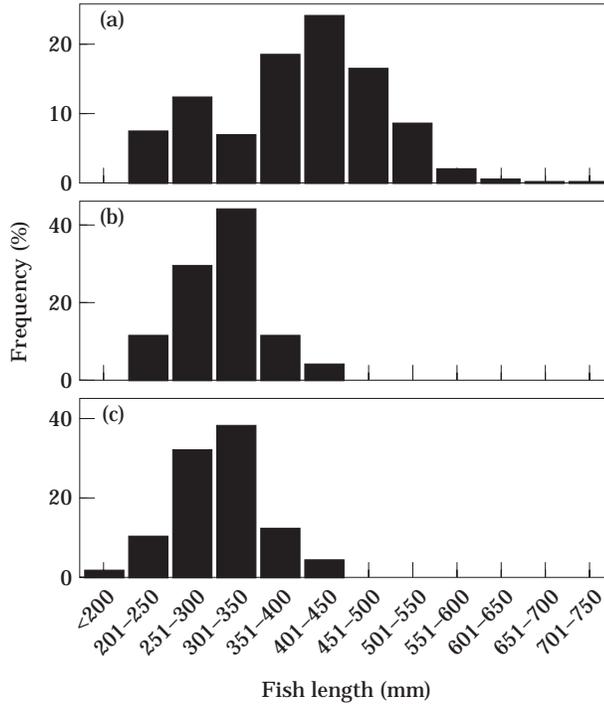


FIG. 1. Length-frequency distribution of *Cichla* species captured by hook and line from the Cinaruco River, 1993-1994 (a) *C. temensis* (n=399), (b) *C. orinocensis* (n=189), (c) *C. intermedia* (n=119).

TABLE III. Counts of *Cichla* species captured from lagoon and channel habitats of the Cinaruco River during three hydrologic seasons

Season Habitat	Falling		Low		Rising	
	Channel	Lagoon	Channel	Lagoon	Channel	Lagoon
<i>C. temensis</i>	100 (35)	84 (29)	46 (20)	39 (17)	26 (15)	94 (53)
<i>C. orinocensis</i>	18 (6)	49 (17)	36 (16)	59 (26)	3 (2)	23 (13)
<i>C. intermedia</i>	26 (9)	11 (4)	45 (20)	3 (1)	27 (15)	3 (2)
Total	144	144	127	101	56	120

Percentages for each season are in parentheses.

formed about 48% of the total *Cichla* sample from the river channel and <3% from lagoons. In general, *C. intermedia* was rarely encountered at lagoon sites, whereas *C. orinocensis* never constituted as much as a third of the *Cichla* sample from the river channel. Habitat partitioning between *C. intermedia*, *C. temensis* and *C. orinocensis* was greatest during the low- and rising-water periods (Table III). During low water, 93.7% of all *C. intermedia* were taken from river channel habitats, compared with 37.9 and 54.1% for *C. orinocensis* and *C. temensis*, respectively. Habitat partitioning between *C. temensis* and *C. orinocensis* was greatest during the falling-water period, with 73.1% of *C. orinocensis* from lagoons compared with 45.6% of *C. temensis*. Water quality parameters varied

TABLE IV. Results of χ^2 analysis of *Cichla* species association with structural and habitat variables ($n=642$)

Species	Rock		Wood		Current	
	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
<i>C. temensis</i>	1.982	0.159	7.431	0.0006	5.251	0.022
<i>C. orinocensis</i>	3.582	0.058	15.986	<0.0001	31.290	<0.0001
<i>C. intermedia</i>	16.601	<0.0001	1.233	0.257	91.985	<0.0001

more between months than between river channel and lagoon sites. Within an eight (months) by two (habitats) table, pH ranged from 5.4 (November lagoons) to 6.4 (March lagoons), temperature ranged from 28.5 (June channel) to 31.0° C (March lagoons), dissolved oxygen ranged from 6 (November lagoons, June channel) to 7.7 mg l⁻¹ (April channel), nitrate ranged from 24 (March channel and lagoons) to 53 mg l⁻¹ (June lagoons), and phosphate ranged from 0.2 (three samples) to 0.4 mg l⁻¹ (April channel and lagoons).

Finer scale habitat comparisons also revealed patterns. Although total sampling effort was not recorded, *Cichla* captures were more likely in littoral areas and around submerged wood or rock structure. *Cichla orinocensis* had a greater affinity for woody structure in lagoons relative to the other two species, and it never exceeded 10% of the sample when current was present, except in those cases in which woody structure was also present (Table IV; Fig. 2). In contrast, *C. intermedia* showed a strong association with current and rock structure, and it was found almost never in lagoons even when rock or woody structure was present (Fig. 2). *Cichla temensis* dominated samples from channel sites without structure (80%) and had a greater association with woody debris than *C. intermedia*. Shoreline areas with woody debris in the main channel yielded approximately equal proportions of the three species.

Logistic regression analysis produced a model that predicted significantly the probability of capturing *C. intermedia* in relation to the presence/absence of submerged rock (*r*), wood (*w*), and water current (*c*) (likelihood ratio $\chi^2=3.56$, d.f.=4, *P*=0.47). The multiplicative equation for the odds of capturing *C. intermedia* rather than another species in the presence of habitat variables was:

$$\text{Probability} = 5.93 \times 1.66^r \times 1.36^w \times 3.29^c.$$

Each exponent in this equation has a value of 0 for absence and 1 for presence, so that, for example, when rock was present at a site, the odds of capturing *C. intermedia* (as opposed to the other two species) increased by a factor of 1.66. Logistic regression did not predict habitat use by the other *Cichla* species with high confidence based on the same combination of variables (*C. temensis*, likelihood ratio $\chi^2=11.24$, *P*<0.025; *C. orinocensis*, likelihood ratio $\chi^2=28.77$, *P*<0.001).

FOOD PARTITIONING

Of the 570 *Cichla* stomachs examined, 137 had measurable prey. Prey identification was problematic because many samples were too digested, but

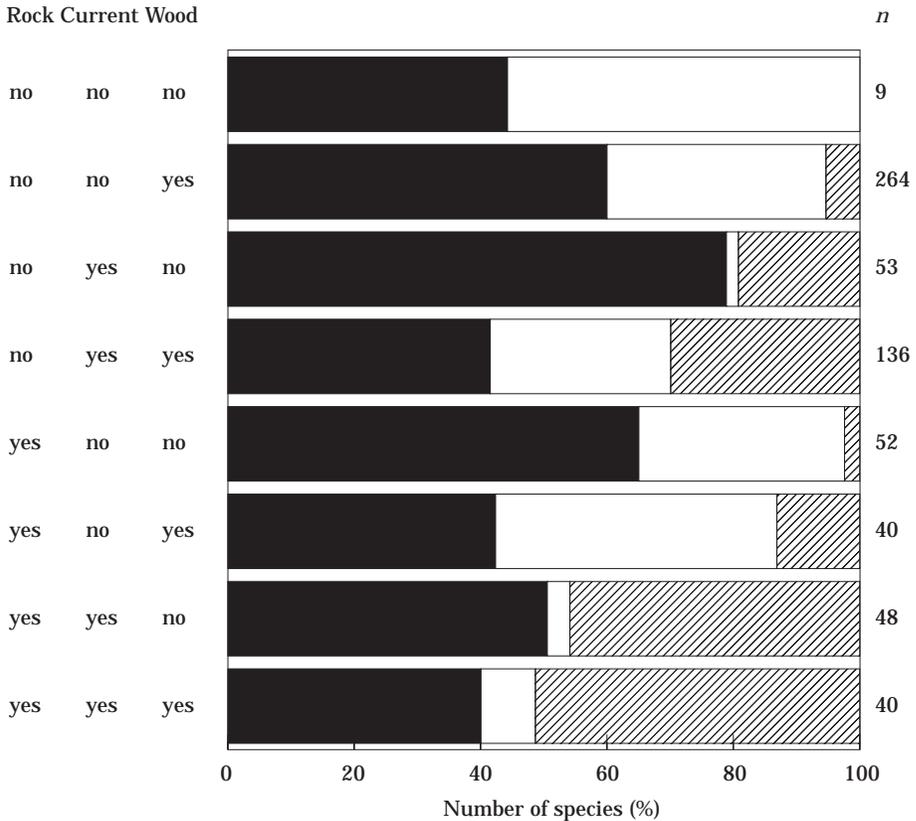


FIG. 2. Relative per cent occurrence of *Cichla* species captured in the presence or absence of structural habitat features. ■, *C. temensis*; □, *C. orinocensis*; ▨, *C. intermedia*.

resolution to taxonomic order was possible for most samples. It was not possible to collect adequate samples of small *C. intermedia* or *C. temensis*, but *C. orinocensis* < 80 mm fed predominantly on copepods and cladocerans (Table V). When *Cichla* switched to fish prey (51–200 mm for *C. temensis*), they consumed some of the smallest available prey fishes. Larger size classes of all three species were almost completely piscivorous, and larger *Cichla* consumed a wider spectrum of prey than smaller conspecifics and congeners (Table V).

The first two principal components derived from the prey resource matrix explained 40% (eigenvalue=2.39) and 72.5% (eigenvalue=1.96) of the cumulative variation. The first axis was influenced primarily by characiforms (eigenvector=0.53), perciforms (0.54), insects (−0.47), and macrocrustacea (−0.44). The second axis was strongly influenced by siluriforms (eigenvector=0.65), juvenile *Cichla* (0.55), insects (−0.30), and macrocrustacea (−0.32). Visual inspection of a bivariate plot constructed from PCA shows the importance of characiforms in the diet of *C. temensis* during falling- and low-water phases, and the increasing importance of siluriforms and juvenile *Cichla* as floodwaters rose (Fig. 3). During the rising-water period, *C. intermedia* consumed greater proportions of aquatic invertebrates. *Cichla orinocensis* had the lowest diet breadth during the falling-water period, when it fed primarily on characiform

TABLE V. Per cent frequencies and volumetric percentages of diet items in stomachs of Cichla by size category

	C. temensis size class (mm)			C. orinocensis size class (mm)			C. intermedia size class (mm)		
	51-200	201-400	401-600	0-50	201-400	201-400	0-50	201-400	201-400
Zooplankton	0	0	0	100 (100)	0	0	0	0	0
Macrocrustacea	0	0	0	0	0	0	0	11 (12.9)	0
Insects	0	0	0	0	0	4.5 (3.6)	0	5.5 (7.7)	0
Clupeiforms	16.7 (15.3)	0	0	0	0	0	0	0	0
Characiforms	16.7 (30.8)	25 (55)	47.2 (59.2)	0	0	27.3 (43.7)	0	5.5 (12.4)	0
Siluriforms	0	36 (9.1)	0	0	0	9 (6.6)	0	22 (5.7)	0
Perciforms	8.3 (25.6)	15.6 (10.1)	19.4 (24.2)	0	0	9 (4.7)	0	11 (23.2)	0
Other	75 (28.3)	67.9 (25.8)	44.4 (16.6)	0	0	54.5 (41.4)	0	66.7 (50.3)	0
Total number of stomachs with food	12	28	36	11	22	22	11	18	18
Total volume (ml)	3.9	71.62	854.3	1.74	43.96	21.78	1.74	21.78	21.78

Volumetric percentages in parentheses.

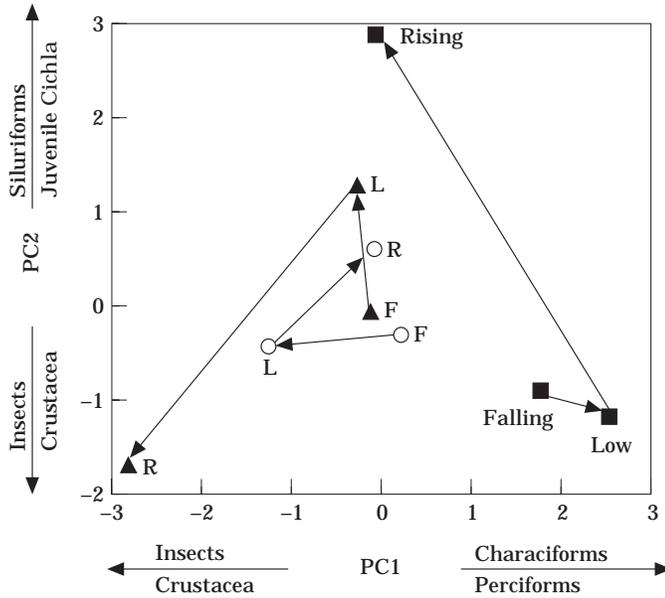


FIG. 3. Bivariate plot of the first two principal components from a resource matrix of prey taxonomic order. Data are based on per cent volumetric proportions of prey items from *Cichla* stomachs during different periods of the hydrologic season. ■, *C. temensis*; ○, *C. orinocensis*; ▲, *C. intermedia*.

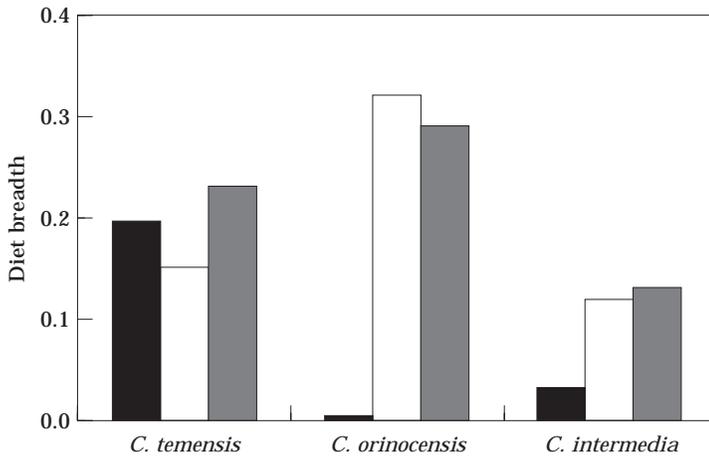


FIG. 4. Diet breadths (Levin's index; Krebs, 1989) of *Cichla* species by season. ■, Falling; □, low; ▒, rising.

fishes (Fig. 4). In contrast, *C. orinocensis* had the greatest diet breadth during the low- and rising-water periods when prey availability was lower (Fig. 4). Diet breadth of the other two species changed relatively little with seasons (Fig. 4), although *C. intermedia* had a trend similar to that of *C. orinocensis* with low diet breadth during the falling-water season.

Overall, the diet of *C. temensis* was more similar to *C. orinocensis* than *C. intermedia*, with the similarity of the latter pair intermediate (Table VI).

TABLE VI. Diet similarities of Cinaruco *Cichla* species during three seasons based on prey orders

Species pair	Falling	Low	Rising	Annual
<i>C. temensis</i> × <i>C. orinocensis</i>	0.97	0.40	0.92	0.88
<i>C. temensis</i> × <i>C. intermedia</i>	0.23	0.69	0.12	0.42
<i>C. orinocensis</i> × <i>C. intermedia</i>	0	0.90	0.06	0.76

When diet data were aggregated across seasons, *C. orinocensis* and *C. intermedia* had high diet overlap in lagoons (0.89) where *C. intermedia* was extremely rare, but low overlap in the channel (0.41) where the two species more often co-occurred. Furthermore, *C. intermedia* and *C. orinocensis* had almost complete overlap during low water, but partitioned resources almost completely at other times (Table VI). Diets of *C. temensis* and *C. orinocensis* were similar during falling and rising water, and were more similar than pairings of *C. temensis* and *C. intermedia*, except during low water. Overall, values were greater in lagoons than channel sites for all three species pairings.

Cichla feeding activity was associated with changing water levels. During February and March (low water), *C. temensis* and *C. intermedia* had high proportions of empty stomachs (Fig. 5). The greater frequency of stomachs with prey in May indicates that all three species increased feeding activity during inundation of the floodplain (Fig. 5). Body condition (*K*) changed markedly during the course of study and generally correlated with variation in feeding activity and gonad condition. The highest mean condition was in January for all three species (Fig. 6), and January values (falling water) were significantly greater than April values (rising water) for all three species (Tukey's multiple range tests, $P < 0.05$). Declining condition between the low- and rising-water periods coincided with maturation of gonads, especially in April and May when most of our observations of nesting activity were made (Fig. 6). Evidence from marginal increment analysis of otoliths (unpublished results) supports the hypothesis of reduced feeding activity during the reproductive period when somatic growth is retarded.

Based on log transformed data aggregated across seasons, mean prey length was not different between *C. intermedia* and either *C. orinocensis* (t_2 tail, $P = 0.36$) or *C. temensis* ($P = 0.19$), but *C. temensis* consumed significantly larger prey than *C. orinocensis* ($P < 0.01$). The three *Cichla* species partitioned prey on the basis of size during the falling-water period (t_2 tail, $P < 0.05$ for each species pair; Fig. 7), and *C. temensis* consumed larger prey than its congeners during the low-water period ($P < 0.05$). After adjustment for the effect of predator size ($F = 43.71$; d.f. = 1, 133; $P < 0.0001$), prey length did not differ among species (ANCOVA; $F = 1.12$; d.f. = 2, 130; $P = 0.33$). *Cichla orinocensis* and *C. temensis* consumed progressively smaller prey through the falling-low-rising-water level sequence (Fig. 8). Mean prey length was significantly greater during the falling-water season relative to the rising-water season for both of these species (t_1 tail, $P < 0.0001$ for both species). During the falling-water period, large *C. temensis* consumed mostly immature *Semaprochilodus kneri* (Pellegrin, 1909)

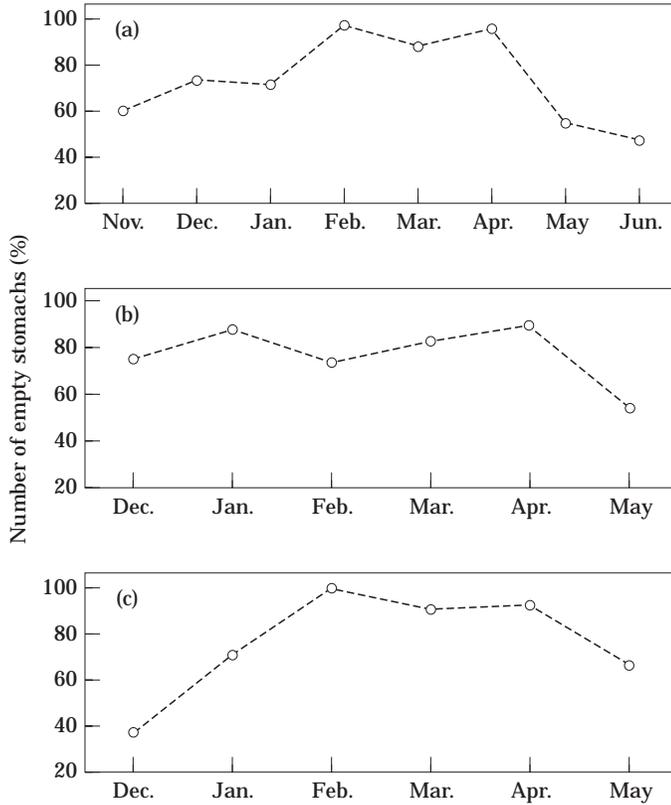


FIG. 5. Percentage of empty *Cichla* stomachs by month and species. (a) *C. temensis* ($n=381$), (b) *C. orinocensis* ($n=114$), (c) *C. intermedia* ($n=75$).

(100–170 mm), but as floodwaters rose, they switched to *Pimelodella* catfishes (<60 mm) and small cichlids, including juvenile *Cichla* sp. (<70 mm, species unknown).

During falling water, *Cichla* species consumed larger prey (log transformed mean=1.91) compared with prey from net samples (mean=1.54) t_2 tail=2.01, d.f.=578, $P<0.05$; Fig. 9). Mean prey sizes from *Cichla* diets and net samples were virtually identical during the low-water period (log transformed mean=1.67) but, during rising water, *Cichla* consumed prey significantly smaller than those from net samples (log transformed mean=1.57 v. 1.51, $t=1.99$, d.f.=1044, $P<0.025$; Fig. 9). Small characiforms dominated prey collections numerically throughout the study period, and this is reflected to some degree in *Cichla* diets, especially during low- and rising-water phases. However, numerical counts do not describe accurately the dietary importance of particular prey species. For example, a single species, *Semaprochilodus kneri*, formed 47.6% of the biomass in the diet of *C. temensis* during the falling-water period, but only 14% under low-water conditions. The near absence of *Semaprochilodus* from the diet during the rising-water period was associated with major reduction in the size of prey consumed by *C. temensis* (Fig. 8).

Estimated fish densities varied between seasons, with greatest densities recorded during low-water conditions and lowest densities recorded during the

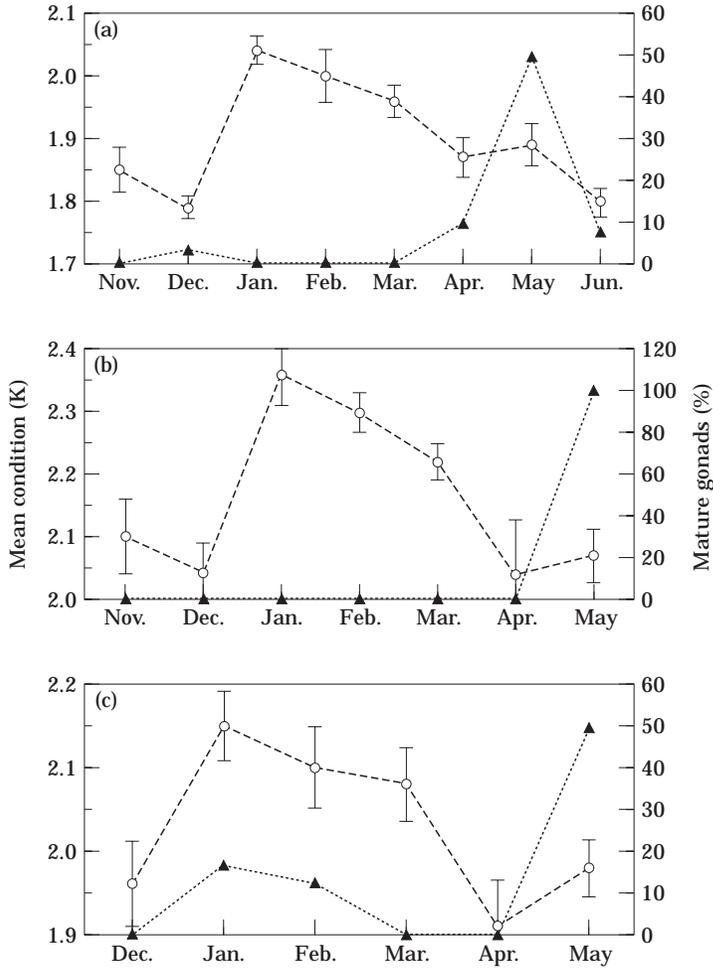


FIG. 6. Relationships between *Cichla* mean monthly condition factor (---○---, K) with standard errors and percentage of *Cichla* with mature gonads (▲). (a) *C. temensis*, (b) *C. orinocensis*, (c) *C. intermedia*.

rising-water period. Seine net catch per unit effort (cpue), expressed as number of fish per metre of seine per metre of net haul, averaged 0.13 during the falling-water period ($n=5$, s.d.=0.02), 0.50 during the low-water period ($n=3$, s.d.=0.19), and 0.07 during the rising-water period ($n=12$, s.d.=0.01). Gillnet cpue, expressed as number of fish h^{-1} of nocturnal set, averaged 0.18 during the falling-water period ($n=2$, s.d.=0), 0.21 during the low-water period ($n=3$, s.d.=0.09), and 0.10 during the rising-water period ($n=7$, s.d.=0.03).

DISCUSSION

SEASONALITY AND RESOURCE PARTITIONING

Seasonal fluctuations in food resource availability have been shown to modify resource partitioning among sympatric fish species in several neotropical freshwater systems. Whereas some tropical fish researchers have documented

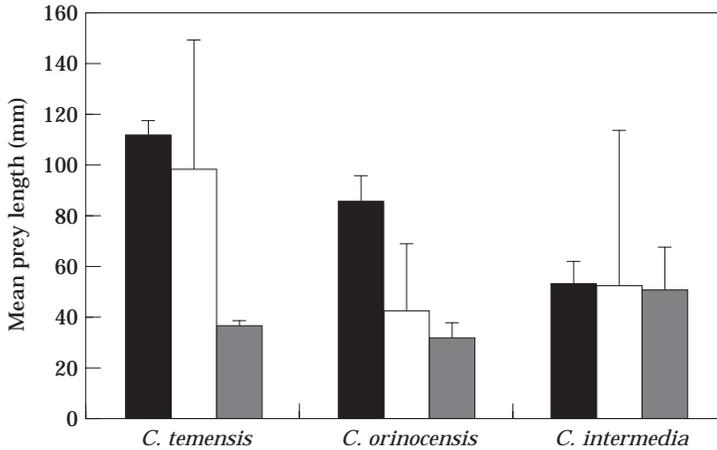


FIG. 7. Comparison of mean standard lengths and standard errors for prey taken from *Cichla* stomachs during different hydrologic periods. ■, Falling; □, low; ▒, rising.

increased diet similarity with a diminishing resource base (Goulding, 1980; Prejs & Prejs, 1987), others have shown that food partitioning increases during periods of resource scarcity (Zaret & Rand, 1971). Winemiller (1989a) concluded that diet specialization in a piscivore guild of a Venezuelan creek was a response to diffuse competition for food during the falling-water season. In the species-rich Cinaruco, *Cichla* appear to be opportunistic piscivores that consume many of the most abundant prey fishes. On the other hand, our study shows that sympatric *Cichla* use food and space in a manner that would reduce interspecific competition in the event that resource demand exceeds supply. The general patterns of resource subdivision by *Cichla* are similar to, but perhaps not as distinct as, those documented for piscivorous cichlids (*Serranochromis* spp.) of the Zambezi River floodplain ecosystem in Africa (Winemiller, 1991). In each system, a combination of spatial segregation and division of prey types resulted in resource segregation by piscivores during the falling- and low-water periods.

Cichla intermedia is a flowing channel habitat specialist, whereas *C. orinocensis* and *C. temensis* used a greater variety of channel and lagoon habitats. *Cichla orinocensis* was more common in lagoons and, when present in the river channel, it tended to occupy shallower lentic areas as opposed to the lotic areas occupied by *C. intermedia*. *Cichla temensis* was relatively evenly distributed across lagoon and channel habitats; however larger individuals tended to occupy deeper waters where neither of its congeners occurred. Habitat overlap tended to be greatest during the low-water period, and was influenced by reproductive ecology and possibly predation threat in the case of smaller individuals (see below).

Although overlap indices based on prey type indicated high diet similarity between *C. temensis* and *C. orinocensis* during the periods of falling and rising water, finer resolution of prey groupings (to genera or species) probably would reduce these values. Under low-water conditions, *C. temensis* tended to forage on larger cichlid and characiform prey from deeper littoral areas compared with *C. orinocensis*. In contrast, diet overlap was greatest between *C. orinocensis* and *C. intermedia* during the low-water period when small characiforms and cichlids are restricted to shallow littoral habitats of lagoons and the river channel owing

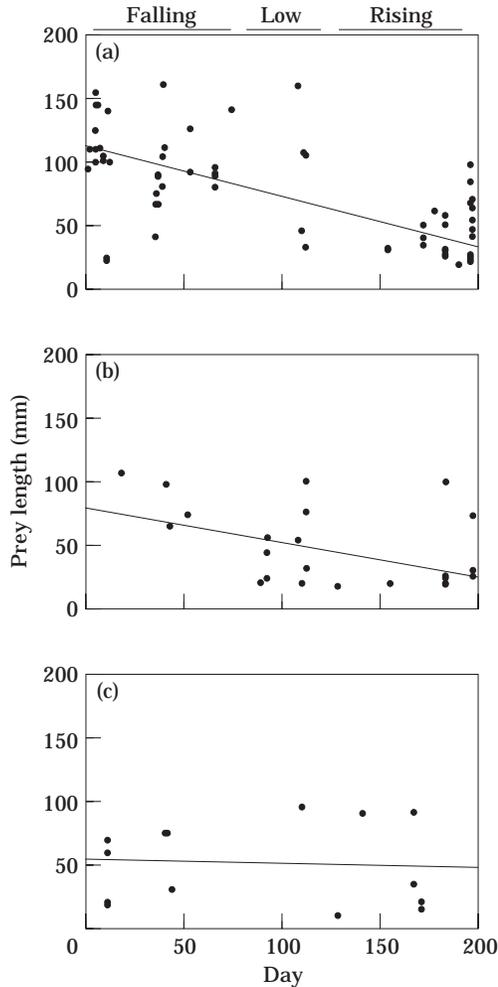


FIG. 8. Prey lengths from *Cichla* stomachs plotted over time. (a) *C. temensis*, (b) *C. orinocensis*, (c) *C. intermedia*. Day 1, 11 November 1993; day 200, 8 June 1994.

to the loss of ephemeral aquatic habitats on the floodplain. *Cichla intermedia* specialized to some extent on loracariid catfishes that cling to woody and rocky structure in flowing channel habitats, and adult *C. intermedia* tended to feed more on invertebrate prey compared with the other two species. During the falling-water period, *C. temensis* consumed significantly larger prey than its two congeners. Because of its larger size, *C. temensis* is able to consume a wider size spectrum of prey than the other two species. As shown for piscivorous largemouth bass *Micropterus salmoides* (Lacépède) (Winemiller & Taylor, 1987; Hambright, 1991), maximum prey size for *Cichla* most likely is gape-limited, and adult *C. intermedia* and *C. orinocensis* are unable to exploit the large *Semaprochilodus kneri* (100–170 mm *L*) during the falling-water period.

The reduction in the size of prey in diets of *C. temensis* and *C. orinocensis* during the low- and rising-water periods (Fig. 8) suggests that predation by *Cichla* and other piscivores might influence the size structure and density of some

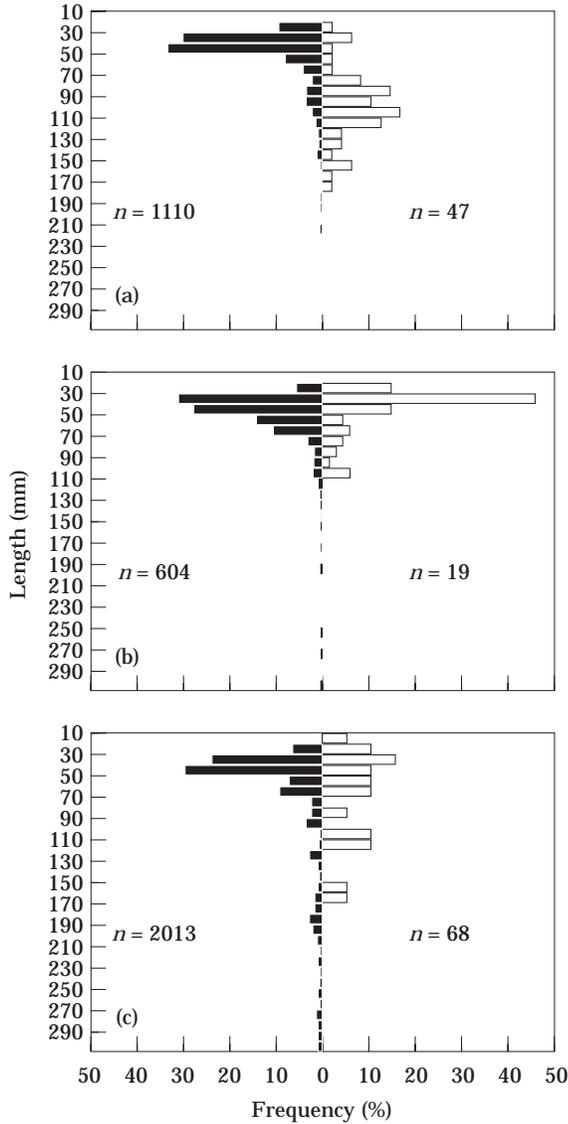


FIG. 9. Seasonal comparison of the length–frequency distributions of prey fishes from *Cichla* stomachs (□) and potential prey sampled from the study area (■). (a) Falling, (b) low, (c) rising.

prey populations. Densities of the most preferred medium-sized and large prey fishes probably are reduced to a fraction of their high-water biomass as waters recede, and they remain low until recruitment or immigration rebuilds stocks during the late wet season to early falling-water period. During falling-water, there were large groups of *Semaprochilodus* in both main channel and lagoon areas, but they became much less conspicuous as the dry season progressed. Feeding activity by large *Cichla* may reduce significantly the density of these important detritivores, or induce them to use habitats in structurally complex littoral zones where they are less vulnerable. In either event, *Cichla* either are forced to switch or find it more profitable to switch to the much smaller but more

abundant characids that inhabit open sandbank habitats. *Cichla* that became trapped in seasonally isolated lagoons during low-water conditions probably depleted their prey and *C. temensis* from these sites were in poorer condition than those from less isolated habitats. In addition, some of these fish had small *Cichla* in their stomachs, suggesting both cannibalism and that heterospecific prey had been cropped to low levels.

Seasonal fluctuations in water level of the Cinaruco appear to influence habitat use by *Cichla* and this seems to be influenced, in part, by predation threat and selection of spawning sites in addition to prey distributions. During low water, individuals of similar size (<300 mm) of all three *Cichla* species were often observed or captured in and around the same complex of woody debris in the main channel. These were probably not good foraging areas for *Cichla*, as indicated by high percentages of empty stomachs and our observations of few prey fishes in these habitats. The use of these structured refuges by small and medium-sized *Cichla* probably is due, in part, to higher predation risk in more open waters. Fish of similar size, regardless of species or trophic specialization, may be equally vulnerable to large predators. It was not unusual to observe up to eight fish species of similar size (including species of *Cichla*) swimming together in protected littoral zones. Even for larger *Cichla*, predators such as the river dolphin *Inia geoffrensis* (de Blainville, 1817) and piranhas (*Serrasalmus manuli* Fernandez-Yepey & Ramirez, 1967) may limit the use of deeper, open-water areas. Winemiller (1989a) hypothesized that piranhas exclude other piscivores from open-water areas in nutrient-rich streams in the llanos, and river dolphins in the Cinaruco have been observed to capture hooked or recently released *Cichla*. Some *Cichla* captured from the Cinaruco had wounds on their caudal and anal fins, and occasionally piranhas attacked hooked fish. The high affinity of all three *Cichla* species for littoral areas with protective cover suggests that these piscivores might reduce feeding opportunities in order to reduce their predation risk (Power, 1984; Mittlebach, 1986). As flood waters receded from the gallery forests and savannas, the availability of submerged structures declined and the ratio of refuge demand to supply probably increased.

Despite the fact that most cichlid species are capable of multiple clutches each year, predictable resource fluctuations in seasonal habitats probably induced reproductive seasonality in cichlids (Lowe-McConnell, 1964, 1969, 1979), which influences the ratio of demand to supply of spawning habitats for substratum nesters. When a combination of abiotic and biotic conditions restrict spawning times, demand for nesting sites cannot be offset by interspecific staggered spawning seasons, but can be achieved by differential use of nesting locations and substrata (McKaye, 1977). This appears to be the case for *Cichla* in the Cinaruco. *Cichla orinocensis* guarded nests in lagoon littoral zones at the same time *C. temensis* nested in more open areas of the same lagoons and when *C. intermedia* were observed nesting in low velocity areas along the edge of the main river channel. Simultaneous spawning may reduce interspecific predation among *Cichla* species. Selection should favour brood production during the annual period of curtailed feeding by *Cichla* (low water) followed by the annual floods that permit fishes to disperse across the vast fringing plains. Several postlarval *Cichla* (species unknown) occurred in stomachs of *C. temensis* from samples collected during the rising-water period. Other than the present study,

cannibalism in indigenous fluvial *Cichla* populations is not well documented. Gil *et al.* (1993) reported 12 and 35% (by weight) *Cichla* in the stomachs of *C. temensis* and *C. orinocensis* from Guri reservoir, but Zaret (1980) reported a low incidence of cannibalism for *C. ocellaris* in Gatun Lake, Panama.

POTENTIAL COMMUNITY EFFECTS OF *CICHLA* PREDATION

Although neotropical blackwater rivers, such as the Cinaruco River, have low levels of inorganic nutrients and little apparent autochthonous primary productivity, frequently they have high fish species diversity and relatively high fish biomass. This observation runs counter to the hypothesis that species diversity is enhanced by high primary productivity (MacArthur, 1965) but it is consistent with the predation model of species diversity (Paine, 1966). Although our study did not directly estimate the absolute densities of *Cichla* in the Cinaruco, standing stocks appear to be very high relative to some other native river populations (Winemiller *et al.*, 1997). The Cinaruco is a popular destination for international sport anglers, and catches of up to 200 *Cichla* day⁻¹ have been reported. Taphorn & Barbarino's (1993) mark-and-recapture study yielded dry season abundance estimates of 1750 *C. temensis* and 1080 *C. orinocensis* in a 3.5-km lagoon with a perennial connection with the Cinaruco River. Given the great abundance and voracity of these piscivores, the potential exists for prey communities to experience density-dependent predation, especially during the falling- and low-water seasons. Diurnal characiform fishes dominated the Cinaruco fauna and were numerically dominant in *Cichla* diets (Winemiller *et al.*, 1997). Fish samples from sandbank habitats of the Cinaruco revealed large variation in species relative abundances among sites, which suggests that few of these species are able to dominate this system numerically (Jepsen, 1997). *Cichla* might facilitate local species diversity via density-dependent predation and the periodic suppression of those species that might otherwise dominate inferior competitors (Paine, 1966, 1969). This contrasts with the community effects of non-indigenous *Cichla* in manmade lakes. In Lake Gatun, Panama, the introduction of *Cichla ocellaris* was associated with dramatic declines in fish biodiversity plus indirect effects within both aquatic and terrestrial food webs (Zaret & Paine, 1973).

During the high-water phase, both batch-spawning and repeat-spawning fishes increase in abundance in their expanded aquatic environment. Inputs of allochthonous food resources increase during flooding, and autochthonous aquatic production is enhanced by inputs of inorganic nutrients from the submerged landscape (Meyer, 1986; Goulding *et al.*, 1988; Bayley, 1989; Junk *et al.*, 1989). Survivorship is enhanced by the seasonal release from predation and competition (Lowe-McConnell, 1964, 1979; Winemiller, 1996). In turn, this surplus production can be cropped by *Cichla* and other piscivores during the falling- and low-water seasons. In regions where fishing mortality influences *Cichla* population structure, prey might be affected indirectly. Cinaruco anglers kept *C. temensis* that were significantly longer and heavier than those caught in this study (t_1 tail=8.67, d.f.=483, $P<0.001$ for mean L ; t_1 tail=9.15, d.f.=483, $P<0.001$ for mean W), and male *C. temensis* were more often retained than females.

Neotropical rivers are noted for their annual migrations of detritivorous fishes (Lowe-McConnell, 1987; Welcomme *et al.*, 1989). Among the largest and most migratory of these detritivores are species of the prochilodontid genera *Prochilodus* and *Semaprochilodus* (Bowen, 1983; Flecker, 1992). During the early wet season, adult prochilodontids migrate from river channels to productive river floodplains to spawn. In blackwater systems, *Semaprochilodus* frequently migrate to floodplains near the confluence of the blackwater river and its mainstem whitewater river. For example, *Semaprochilodus* of the blackwater Rio Negro in Brazil migrate to floodplains of the Amazon (Ribeiro & Petrere, 1990; Goulding *et al.*, 1988; Vazzoler *et al.*, 1989). *Semaprochilodus kneri* of the Cinaruco appear to spawn primarily in floodplains of the Orinoco River. During the falling-water phase, spent adults and immature *Semaprochilodus* migrate from nutrient-rich, natal habitats back into blackwater river systems (Ribeiro & Petrere, 1990; Vazzoler *et al.*, 1989). During the falling-water period, schools of migrating *Semaprochilodus kneri* (<200 mm) were attacked by groups of *C. temensis* within the main channel of the Cinaruco.

These observations, together with the diet data, suggest that migratory prochilodontids were a very important food resource for large *Cichla* during the falling-water season. Because feeding activity is greatly reduced and prey size declines during the low- and high-water seasons, *Semaprochilodus* captured during the falling-water period could constitute a major fraction of the annual energy intake of *C. temensis*. Like many tropical fishes in seasonal habitats, *Cichla* mobilize nutrients stored in muscle, liver, and fat deposits for gonad development and energy for reproduction (Junk, 1985; Winemiller, 1989b). The ability of *Cichla* to capture and sequester into biomass this essentially allochthonous food resource could promote local productivity in hyperoligotrophic blackwater rivers, because bacteria and autotrophs could then utilize nutrients and minerals excreted by *Cichla*. Fittkau (1973) proposed a similar role for crocodilians in floodplain lakes of the central Amazon. Fish production in these relatively productive lagoons was negatively associated with the reduction of crocodilians from overhunting. In hyperoligotrophic blackwater systems, these nutrient-transport and nutrient-cycling roles of migratory fishes and large piscivores would assume even greater importance.

Tropical fish communities show a high degree of guild structure, yet species within guilds can show significant patterns of resource subdivision (Winemiller & Pianka, 1990). Relative to other large piscivores in the community (e.g. nocturnal catfishes, shoaling piranhas), *Cichla* species share enough ecological similarities to be considered members of the same guild of diurnal, littoral-zone, pursuit predators that swallow their prey whole. Despite their broad diets and general morphological and behavioural similarities, sympatric *Cichla* subdivide space and food resources in a manner that indicates selection favouring efficient foraging and interspecific differences in performance. The key resource dimensions that determine differential performance appear to be water current (separating *C. intermedia* from the other two species), prey size (separating *C. temensis* from the other two species) and, to a lesser extent, prey type and microhabitat features such as depth and submerged structure. The strong seasonality of the Cinaruco River ecosystem appears to favour intense piscivory during the period of falling water, when abundant prey, many derived from

wet-season production, move from the drying floodplain into more permanent water bodies. Although the per unit area density of small fishes is highest during the low-water period, the absolute abundance of prey should be greatest during the initial stages of water recession. Among *Cichla*, patterns of food resource subdivision were associated with season and habitat overlap. In this dynamic ecosystem, temporal shifts in the intensity of competition and predation appear to interact in a manner that fosters greater ecological differentiation and species diversity in the contemporary realm. Comparative research that stresses seasonality and experimental manipulations of piscivore density and population structure are needed in tropical rivers.

Financial support for this research was provided by grants to KOW and DCT from the National Geographic Society and the Fundacion Fluvial de Los Llanos of Venezuela. G. Webb and C. Lofgren of Tour Apure and members of the Cinaruco Fishing Club provided food, lodging, and logistical support during aspects of the field work. BIOCENTRO (UNELLEZ) provided field equipment. T. McGuire, J. Williams, A. Barbarino, and several local guides assisted in field collections. We thank M. Sweet and T. Linton for reviewing earlier drafts of this work. The research was conducted under scientific collecting permit no. 1073 issued by the Servicio Autonomo de los Recursos Pesqueros y Acuicolas, Ministerio de Agricultura y Cria, Republic of Venezuela.

References

- Bayley, P. B. (1989). Aquatic environments in the Amazon Basin, with an analysis of carbon sources, fish production, and yield. In *Proceedings of the International Large River Symposium* (Dodge, D. P., ed.) *Canadian Special Publication in Fisheries and Aquatic Sciences* **106**, 399–408.
- Bowen, S. H. (1983). Detritivory in neotropical fish communities. *Environmental Biology of Fishes* **9**, 137–144.
- Devick, W. S. (1972). Life history study of the tucunaré *Cichla ocellaris*. *Federal Aid in Sportfish Restoration Project F-9-1, Job Completion Report*. Honolulu: Hawaii Department of Land and Natural Resources.
- Fittkau, E. J. (1973). Crocodiles and the nutrient metabolism of Amazonian waters. *Amazoniana* **4**, 103–133.
- Flecker, A. S. (1992). Fish trophic guilds and the structure of the tropical stream: weak direct vs. strong indirect effects. *Ecology* **73**, 927–940.
- Gil, C. E., Andrada, J., Méndez, E. & Salazar, J. M. (1993). Estudio preliminar sobre alimentación en cautiverio y contenido estomacal de *Cichla temensis* del embalse Guri, Estado Bolívar, Venezuela. *Natura* **96**, 42–47.
- Goulding, M. (1980). *The Fishes and the Forest: Explorations in Amazonian Natural History*. Los Angeles: University of California Press.
- Goulding, M., Carvalho, M. L. & Ferreira, E. G. (1988). *Rio Negro: Rich Life in Poor Water*. The Hague: SPB Academic Publishing.
- Hambright, K. D. (1991). Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society* **120**, 500–508.
- Jepsen, D. B. (1997). Fish species diversity in sand bank habitats of a neotropical river. *Environmental Biology of Fishes* **49**, 449–460.
- Junk, W. J. (1985). Temporary fat storage, an adaptation of some fish species to the water level fluctuations and related environmental changes of the Amazon river. *Amazoniana* **9**, 315–351.
- Junk, W. J., Bayley, P. B. & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. In *Proceedings of the International Large River Symposium* (Dodge, D. P., ed.) *Canadian Special Publication in Fisheries and Aquatic Sciences* **106**, 110–127.

- Krebs, C. J. (1989). *Ecological Methodology*. New York: Harper and Row.
- Kullander, S. O. (1986). *Cichlid Fishes of the Amazon River Drainage of Peru*. Stockholm: Swedish Museum of Nature History.
- Lewis, D. S. C. (1974). The food and feeding habits of *Hydrocynus forskahlii* Cuvier and *Hydrocynus brevis* Gunther in Lake Kainji, Nigeria. *Journal of Fish Biology* **6**, 349–363.
- Lewis, W. M., Jr. (1988). Primary production in the Orinoco river. *Ecology* **69**, 679–692.
- Lowe-McConnell, R. H. (1964). The fishes of the Rupununi savanna district of British Guiana, South America. Part 1. Ecological grouping of fish species and effects of the seasonal cycle on the fish. *Zoological Journal of the Linnaean Society* **45**, 103–144.
- Lowe-McConnell, R. H. (1969). The cichlid fishes of Guyana, South America, with notes on their ecology and breeding behavior. *Zoological Journal of the Linnaean Society* **48**, 255–302.
- Lowe-McConnell, R. H. (1979). Ecological aspects of seasonality in fishes of tropical waters. *Symposia of the Zoological Society of London* **44**, 219–241.
- Lowe-McConnell, R. H. (1987). *Ecological Studies in Tropical Fish Communities*. Cambridge: Cambridge University Press.
- MacArthur, R. H. (1965). Patterns of species diversity. *Biological Reviews* **40**, 510–533.
- Machado-Allison, A. (1971). Contribución al conocimiento de la taxonomía del género *Cichla* (Perciformes Cichlidae) en Venezuela, Parte I. *Acta Biologica Venezuelana* **7**, 459–497.
- McKaye, K. R. (1977). Competition for breeding sites between the cichlid fishes of L. Jiloa, Nicaragua. *Ecology* **58**, 291–302.
- Meade, R. H. & Koehnken, L. (1991). Distribution of the river dolphin *Inia geoffrensis* in the Orinoco river basin of Venezuela and Colombia. *Interciencia* **16**, 300–312.
- Merron, G. S. (1993). Pack-hunting in two species of catfish, *Clarias gariepinus* and *C. ngamensis*, in the Okavango Delta, Botswana. *Journal of Fish Biology* **43**, 575–584.
- Meyer, J. L. (1986). DOC dynamics of two subtropical blackwater rivers. *Archiv für Hydrobiologie* **108**, 119–134.
- Mittlebach, G. G. (1986). Predator-mediated habitat use: some consequences for species interactions. *Environmental Biology of Fishes* **16**, 159–169.
- Nico, L. G. & Taphorn, D. C. (1988). Food habits of piranhas in the low llanos of Venezuela. *Biotropica* **20**, 311–321.
- Novoa, D. F., Koonce, J. & Locci, A. & Ramos, F. (1989). La ictiofauna del lago de Guri: composición, abundancia y potencial pesquero. II. Evaluación del potencial pesquero del lago Guri y estrategias de ordenamiento pesquero. *Sociedad de Ciencias Naturales La Salle* **49**, 159–197.
- Paine, R. T. (1966). Food web complexity and species diversity. *American Naturalist* **100**, 65–75.
- Paine, R. T. (1969). A note on trophic complexity and community stability. *American Naturalist* **103**, 91–93.
- Power, M. (1984). Depth distribution of armoured catfish: predator-induced resource avoidance? *Ecology* **65**, 523–528.
- Prejs, A. & Prejs, K. (1987). Feeding of tropical freshwater fishes: seasonality in resource availability and resource use. *Oecologia* **71**, 397–404.
- Ribeiro, M. C. L. de B. & Petre, M. Jr. (1990). Fisheries ecology and management of the Jaraquí (*Semaprochilodus taeniurus*, *S. insignis*) in Central Amazonas. *Regulated Rivers: Research and Management* **5**, 195–215.
- Seaburg, K. G. (1957). A stomach sampler for live fish. *Progressive Fish Culturist* **19**, 137–139.
- Sioli, H. (1984). The Amazon and its main affluents: hydrography, morphology of the river courses, and river types. In *The Amazon, Monographiae Biologicae, Vol. 56* (Sioli, H., ed.), pp. 127–166. The Hague: Dr W. Junk.
- Taphorn, D. C. & Barbarino, A. (1993). Evaluación de la situación actual de los pavones, *Cichla* spp., en el Parque Nacional Capanaparo-Cinaruco, Estado Apure, Venezuela. *Natura* **96**, 10–25.

- Vazzoler, A. E. de M., Amadio, S. A., Daraciolo-Malta, M. C. (1989). Aspectos biológicos de peixes Amazônicos. XI. reprodução das espécies do gênero *Semaprochilodus* (Characiformes, Prochilodontidae) no baixo Rio Negro, Amazonas, Brasil. *Revista Brasileira de Biologia* **49**, 165–173.
- Waal, B. C. W. van der (1985). Aspects of the biology of larger fish species of Lake Liambezi, Caprivi, Southwest Africa. *Madoqua* **14**, 101–144.
- Welcomme, R. L., Ryder, R. A. & Sedell, J. A. (1989). Dynamics of fish assemblages in river systems—a synthesis. In *Proceedings of the International Large River Symposium* (Dodge, D. P., ed.), *Canadian Special Publication in Fisheries and Aquatic Sciences* **106**, 569–577.
- Werner, E. E. & Hall, D. J. (1988). Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* **69**, 1352–1366.
- Winemiller, K. O. (1989a). Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan llanos. *Environmental Biology of Fishes* **26**, 177–199.
- Winemiller, K. O. (1989b). Patterns in variation in life history among South American fishes in seasonal environments. *Oecologia* **81**, 225–241.
- Winemiller, K. O. (1990). Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs* **60**, 331–367.
- Winemiller, K. O. (1991). Comparative ecology of *Serranochromis* species (Teleostei: Cichlidae) in the Upper Zambezi River floodplain. *Journal of Fish Biology* **39**, 617–639.
- Winemiller, K. O. (1996). Dynamic diversity in fish communities of tropical rivers. In *Long-term Studies of Vertebrate Communities* (Cody, M. L. & Smallwood, J. A., eds), pp. 99–134. Orlando, Florida: Academic Press.
- Winemiller, K. O. & Kelso-Winemiller, L. C. (1994). Comparative ecology of the African pike, *Hepsetus odoe*, and tigerfish, *Hydrocynus forskahlii*, in the Zambezi River floodplain. *Journal of Fish Biology* **45**, 211–225.
- Winemiller, K. O. & Kelso-Winemiller, L. C. (1996). Comparative ecology of catfishes of the Upper Zambezi River floodplain. *Journal of Fish Biology* **49**, 1043–1061.
- Winemiller, K. O. & Pianka, E. R. (1990). Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* **60**, 27–55.
- Winemiller, K. O. & Taylor, D. H. (1987). Predatory behavior and competition between smallmouth and largemouth bass. *American Midland Naturalist* **117**, 148–166.
- Winemiller, K. O., Taphorn, D. C. & Barbarino-Duque, A. (1997). The ecology of *Cichla* (Cichlidae) in two blackwater rivers of southern Venezuela. *Copeia* **1997**, 690–696.
- Zaret, T. M. (1980). Life history and growth relationships of *Cichla ocellaris*, a predatory South American cichlid. *Biotropica* **12**, 144–157.
- Zaret, T. M. & Paine, R. T. (1973). Species introduction into a tropical lake. *Science* **182**, 449–455.
- Zaret, T. M. & Rand, A. S. (1971). Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology* **52**, 336–342.