Copeia, 1997(4), pp. 690–696

Ecology of *Cichla* (Cichlidae) in Two Blackwater Rivers of Southern Venezuela

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We investigated the ecology of peacock cichlids (*Cichla* spp.), diurnal piscovores and important gamefishes, in the Río Cinaruco (Río Orinoco drainage of the southern Venezuelan llanos) during the dry seasons of 1992–1993 and the Río Pasimoni (Río Negro-Amazonas drainage) during early 1993. In the Cinaruco, three *Cichla* species partitioned available habitats: *C. intermedia* near structure in primary river channel within or near swift current, *C. orinocensis* in shallow water along the shoreline of lagoons or slow channel reaches, and *C. temensis* in deeper waters along sandbanks and steeper rocky banks of lagoons and the river channel. During the dry season, *C. orinocensis* and *C. temensis* fed heavily on small characiform fishes, and *C. intermedia* consumed a variety of fishes, including loricariid catfishes. Only two peacock cichlids, *C. orinocensis* and *C. temensis*, were found in the Pasimoni, a more acidic and less seasonal ecosystem. These two species were larger in the Pasimoni compared with Cinaruco conspecifics; however, conspecifics from the two locations conformed to similar mass-length relationships. In both river systems, *C. temensis* were significantly larger than congeners, and *C. temensis* consumed larger prey than congeners in the Cinaruco. Examination of gonads and sizes of intraovarian oocytes indicated that reproduction by all five populations probably is initiated during the late low water period and may continue into the flooding period.

Investigamos la ecología de los pavones (Cichlidae, genero *Cichla*), picivores diurnos importantes en la pesca deportiva, en el Río Cinaruco (cuenca del Río Orinoco en el sur del estado Apure, Venezuela) durante la sequía de los años 1992–1993, y del Río Pasimoni (cuenca Río Amazonas, estado Amazonas) de Venezuela durante los primeros meses del 1993. En el Cinaruco, tres especies de *Cichla* reparten los hábitat disponibles: *C. intermedia* se ubica cerca de cobertura (arboles sumergidas, etc.) en el cauce principal cerca o dentro de la corriente rápida; *C orinocensis* se encuentra mayormente en agua de poca profundidad cerca de la orilla de lagunas o en el cauce principal sin mucha corriente; y *C. temensis* ocurre en agua más profunda al lado de bancos de arena y en lagunas y el cauce principal donde la orilla tiene una pendiente alta y es rocosa ("ripio o arrecife" de apureño). Durante la sequía, *C. orinocensis* y *C. temensis* se alimentaron principalmente de pequeños peces carácidos, y *C. intermedia* consumió una variedad de peces, incluyendo corronchos loricóridos. Solamente dos pavones *C. orinocensis* y *C. temensis*, se encontraron en el río Pasimoni, un ecosistema con menos fluctuación estacional y más acido. Estas dos especies alcanzaron tamaños mas grandes en el Pasimoni compararon con los pavones del río Cinaruco de la misma especie, sin embargo, su curva tallo-peso era la misma. En ambas cuencas, los *C. temensis* eran significativamente más grande que los otros pavones. En el rio Cincaruco, los *C. temensis* consumieron presas más grandes que las de los otros dos pavones. Examinación de la gónades y los tamaños de los huevos indica que la reproducción en las cinco poblaciones de pavones estudiados probablemente se inicia durante la parte final de la sequía (aguas bajas) y continua durante la etapa de lluvias e inundación.

PEACOCK cichlids (*Cichla* spp., Cichlidae) are one of the most widespread and abundant predatory fishes in clearwater and blackwater ecosystems of the Orinoco and Amazon Basins. Currently, systematists recognize five *Cichla* species (known as pavón in Venezuela and as tucunaré in Brazil), but additional species from the Amazon Basin require description (Kullander and Nijssen, 1989). Up to three coexisting *Cichla* species have been found in the upper Río Orinoco and upper Río Negro basins in southern Venezuela (Machado-Allison, 1971).

Peacock cichlids are diurnal piscivores that consume a variety of prey and potentially can

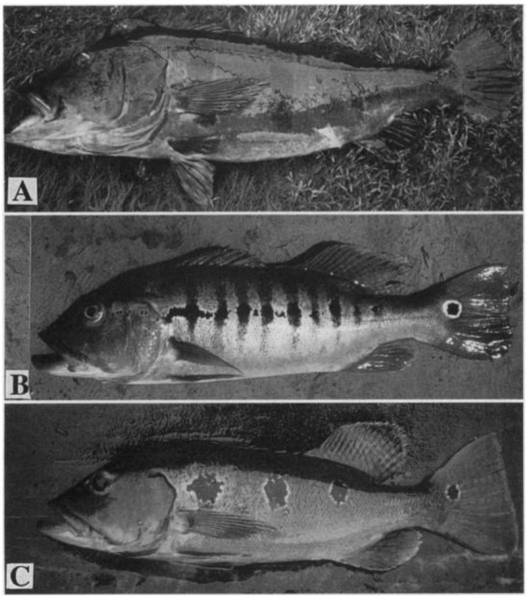

Fig. 1. (A) The banded peacock cichlid, *Cichla temensis* (81.5 cm SL), from the Río Pasimoni; (B) royal peacock cichlid, *Cichla intermedia* (39 cm SL), from the Río Cinaruco; and (C) butterfly peacock cichlid, *Cichla orinocensis* (43 cm SL), from the Río Pasimoni.

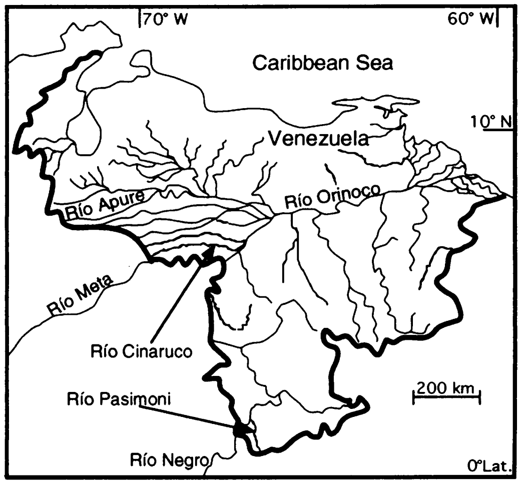

Fig. 2. Map showing the locations of the Río Cinaruco and Río Pasimoni in southern Venezuela.

influence prey populations. For example, the introduction of exotic peacock cichlids into Lake Gatún, Panama, was followed by massive changes in community composition and the structure of the aquatic food web (Zaret and Paine, 1973). A similar scenario of community transition followed the introduction of *C. orinocensis* and *C. temensis* into Las Majaguas (AB-D, Universidad Experimental de Los Llanos Occidentales thesis, unpubl., 1986; Winemiller, 1989), Guri (Novoa et al., 1989; Gil et al., 1993), and other reservoirs in Venezuela.

Zaret (1980) described the life history of a nonindigenous population of *C. ocellaris* in Lake Gatún, Panama. Characteristics of nonindigenous *C. ocellaris* populations in Hawaiian and Puerto Rican reservoirs were summarized in technical reports (W. Devick, Hawaii DLNR report, unpubl., 1972; C. Lilyestrom et al., Puerto Rico DNER report, unpubl., 1994), and the life history of *Cichla* in fish farms was investigated in Brazil (Fontenele, 1950; Braga, 1952, 1953). Very limited information on *Cichla* ecology in native rivers has been published (Lowe-McConnell, 1969; Goulding, 1980; Winemiller et al., 1995). Taphorn and Barbarino-Duque (1993) performed a mark/recapture study of *Cichla* populations in rivers and lagoons of Santos Luzardo National Park in Venezuela.

Currently, our understanding of the ecology of these important Neotropical piscivores is based more on nonindigenous populations in reservoirs than on fishes in their native fluvial environments. We examined local population structure, body mass–body length relationships, age at length, reproductive condition, patterns of habitat use, and diets of sympatric *Cichla* species in two rivers of southern Venezuela. During the dry season, *Cichla* ecology was investigated in a river draining the southern savannas (low llanos) and a river that drains forest watersheds in southernmost Venezuela. Three species (*C. intermedia, C. orinocensis, C. temensis*, Fig. 1) are sympatric in the Río Cinaruco (savanna). The same three species coexist in rivers of forested regions to the south (Machado-Allison, 1971), but *C. intermedia* apparently is absent from our Río Pasimoni study site.

Methods and Study Sites

The Río Cinaruco in southern Apure State (R. Orinoco Basin) and the Río Pasimoni in southern Amazonas State of Venezuela (R. Casiquiare-R. Negro-R. Amazonas Basin; Fig. 2) are low-gradient, blackwater rivers. The Cinaruco originates in the flatlands of eastern Colombia and flows eastward into Venezuela where it forms the southern boundary of Santos Luzardo National Park. The Cinaruco lies within a region that experiences markedly seasonal rainfall and contains sandy, nutrient-poor soils, savanna vegetation, and acidic streams. In southern Amazonas, the landscape is dominated by evergreen tropical forests. The Pasimoni originates on the northern slope of the Neblina mountain range and flows northward to the Río

TABLE 1. WATER QUALITY PARAMETERS FOR THE RÍO PASIMONI AND RÍO CINARUCO (5–12 FEBRUARY 1993).

	Río Pasimoni		Río Cinaruco	
	Channel	Lagoon	Channel	Lagoon
pH	4.6	5.1	5.7	5.8
Conductivity (μmhos/cm)	30	29	35	35
Total alkalinity (mg/l)	<0.5	<0.5	<0.5	<0.5
Hardness (mg/l)	<0.5	<0.5	6.0	6.0
Chloride (mg/l)	5.6	5.8	1.5	2.8
Color (ftu)	36	39	4	8
Total inorganic nitrogen (μg/l)	29.3	30.0	7.0	11.2
Total inorganic phosphorus (μg/l)	3.7	1.8	0.9	2.7
Temperature	26.0	26.0	30.0	31.0

Casiquiare and is surrounded by low, poorly drained terrain. Annual rainfall is greater, less seasonal, and less predictable in this rain forest region than in the llanos. We performed intensive surveys of the Cinaruco during 20–24 January 1992, 7–12 February 1993, and 31 March to 2 April 1993; we surveyed the Pasimoni during 31 January to 5 February 1993.

The following environmental parameters were estimated using meters (YSI, Inc.): conductivity, salinity, temperature, and dissolved oxygen. Standard titration methods were used to measure total alkalinity, chloride, total hardness, pH, water color, and total dissolved inorganic nitrogen and phosphorus; and visual estimates were used to record substratum composition, submerged woody structure, channel width, water depth, and relative current velocity. Fishes were sampled in the river channel and lagoons with seines, gillnets, castnets, and hook and line. Angling with lures produced almost all of our *Cichla* specimens (SL > 20 cm), and although no juvenile *Cichla* were captured, a few juveniles were observed in shallow backwaters and low velocity shoreline habitats of the Cinaruco channel. Sites were sampled to represent all major habitats (i.e., river channel, backwaters, lagoons, tributary creeks). A single *C. orinocensis* was taken from a Cinaruco creek and is not included in this dataset. The remaining sampling effort was divided approximately equally between river channel versus lagoons and backwaters. All captured *Cichla* were measured (SL to nearest 0.5 cm) and weighed (nearest 5 g). Voucher fish specimens were preserved in 15% formalin and later deposited in the MCNG, Guanare, Venezuela; TCWC, College Station, Texas; UF, Gainesville, Florida; and INHS, Champaign, Illinois (institutional abbreviations follow Leviton et al., 1985).

For each *Cichla* species, a subsample from the total spectrum of size classes was sacrificed for stomach contents analysis; plus the number of growth checks on saggital otoliths were determined for a few large individuals (*C. temensis*—Pasimoni n = 4, *C. temensis*—Cinaruco n = 3; *C. orinocensis*—Cinaruco n = 2; *C. intermedia*—Cinaruco n = 2). Recent research at the Cinaruco (D. Jepsen, Texas A&M University, unpubl. thesis, 1995) indicates that growth checks are annuli that form during the late dry season (March to April) when fish prepare for spawning. Most *Cichla* specimens were handled in the field, but a few were preserved in formalin and returned to the Universidad Experimental de Los Llanos Occidentales or Texas A&M for stomach contents analysis.

RESULTS

Water samples from the Pasimoni and Cinaruco revealed classic blackwater features (Sioli, 1984) of low pH, conductivity, solute, and nutrient concentrations (Table 1). Water chemistry varied little between lentic lagoon and lotic channel habitats within each river.

In both river systems, *C. temensis* were significantly larger than congeners (Fig. 3), and *C. orinocensis* and *C. intermedia* had similar size distributions in the Cinaruco. Mass-length relationships of the three species did not differ (ANCOVA F-tests for regression slopes and intercepts with $\log_e$-transformed data, n = 84, 77, 26, $P > 0.05$). Even though *C. temensis* and *C. orinocensis* from the Pasimoni had larger average and maximum sizes compared with conspecifics from the Cinaruco (Fig. 3), conspecifics from the two rivers conformed to similar mass-length regressions. The $\log_e$-$\log_e$ regression equations were as follows: *C. temensis*—Pasimoni, $M = 3.2L - 4.6$, $r^2 = 0.98$; *C. temensis*—Cinaruco, $M = 3.2L - 4.7$, $r^2 = 0.96$; *C. orinocensis*—Pasimoni, $M = 2.9L - 3.4$, $r^2 = 0.90$; *C. orinocensis*—Cinaruco, $M = 2.9L - 3.5$, $r^2 = 0.85$. Slopes and intercepts were not sig-

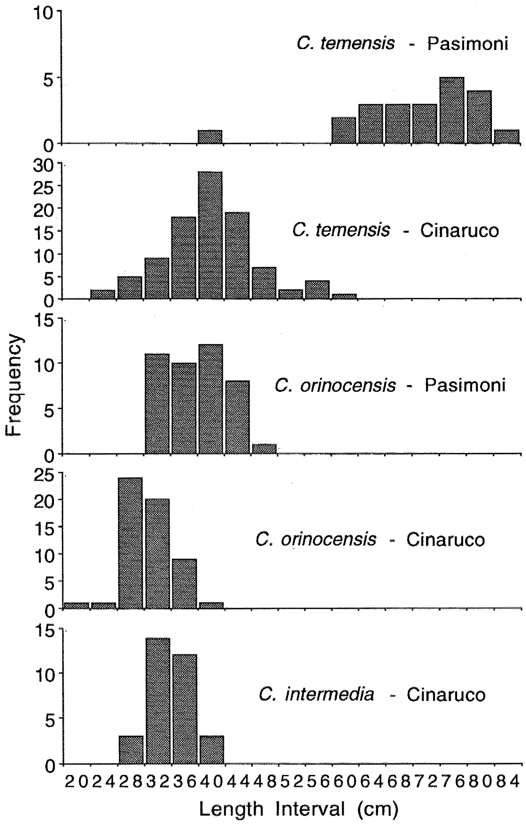

Fig. 3. Length frequency distributions of *Cichla temensis* and *C. orinocensis* population samples from the Río Pasimoni and Río Cinaruco and *C. intermedia* from the Cinaruco. Statistical comparisons are given in the text.

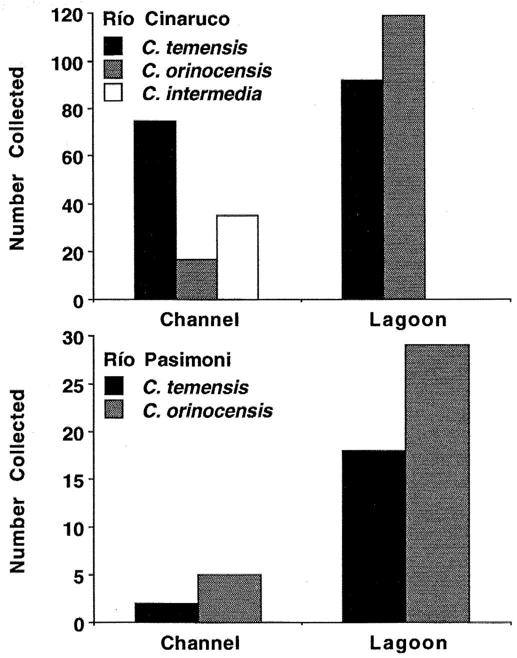

Fig. 4. Numbers of individuals of three *Cichla* species sampled from two habitats of the Río Cinaruco and Río Pasimoni. Sampling effort was divided approximately equally between channel and lagoon habitats. The association between species and habitat was significant for the Cinaruco (χ^2 = 101.4, df = 2, $P <$ 0.0001).

nificantly different (ANCOVA F-tests, Range for n = 17–60, $P > 0.05$).

Otoliths from *C. temensis* (68–75 cm SL, 6.5–9 kg) from the Pasimoni had 7–9 annuli. If one assumes that maturation occurs at 1–2 yr (Zaret, 1980), then our Pasimoni *C. temensis* sample was dominated by 9–11-yr fish that grew at an average of about 7 cm and 0.75 kg per yr.

In our January/February Cinaruco samples, most individuals of all three species had inactive gonads or gonads in intermediate stages of recrudescence, and very few had fully ripe gonads (no *C. orinocensis* were ripe). In our March/April 1993 samples, 11 of 27 *C. temensis* were ripe, three of 13 *C. orinocensis* were ripe, and four of 10 *C. intermedia* were ripe. During the January 1992 and April 1993 surveys of the Cinaruco, one or more individuals of both *C. intermedia* and *C. temensis* were observed attending nests with eggs. On 2 February 1993, we observed a single *C. orinocensis* on a nest with eggs near the shoreline of a lagoon of the Pasimoni.

Based on Cinaruco data, the minimum standard lengths of fishes with ripe gonads were as follows: *C. temensis*, male = 36 cm, female = 32.5 cm; *C. orinocensis*, male = 31 cm, female = 27.0 cm; and *C. intermedia* male = 32 cm, female = 27 cm.

Cichla temensis and *C. orinocensis* occupied both channel and lagoon habitats in the Pasimoni and Cinaruco (Fig. 4). During our dry season surveys, *C. orinocensis* usually was observed and captured in shallow nearshore areas of lagoons and slow moving reaches of the river channel. *Cichla temensis* tended to occupy deeper littoral areas in lagoons and along sandy and rocky banks of the main river channel. In the Cinaruco, *C. intermedia* was always captured near submerged rocks or woody structure in the primary river channel within or near swift current. Mean lengths of *C. temensis* and *C. orinocensis* did not differ between habitats (Fig. 5); however *C. temensis* was significantly larger than *C. orinocensis* in lagoons (t = 5.21, df = 23, $P < 0.0001$) and the river channel (t = 2.14, df = 13, P = 0.05) and *C. intermedia* in the river channel (t = 2.91, df = 32, $P < 0.01$).

Small fishes (< 10 cm SL), especially the

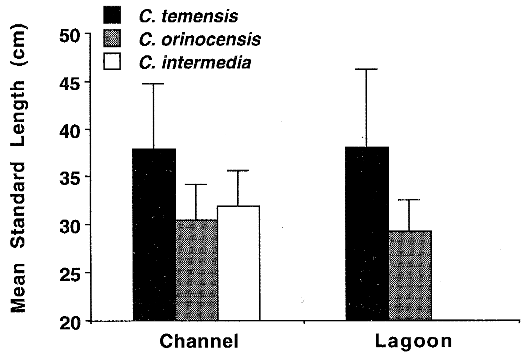

Fig. 5. Mean standard lengths (with SD bars) of *Cichla* species by habitat in the Río Cinaruco (Sample n for *C. temensis* = 98, *C. orinocensis* = 62, *C. intermedia* = 35). Statistical results are given in the text.

characids, formed the major diet component of all three *Cichla* species (Table 2). *Cichla intermedia* consumed a greater fraction of catfishes, primarily small loricariids, than did the other two species (Table 2). The species most frequently found in *C. temensis* stomachs was *Hemigrammus analis* (Characidae, n = 5), whereas *H. vorderwinkleri* was most frequent in *C. orinocensis* stomachs (n = 7). All three *Cichla* species consumed *H. analis* and small *Crenicichla* sp. (Cichlidae, probably *C. notopthalmus*). *Nannostomus* sp. (Lebiasinidae, n = 4) and anostomids (n = 4) were found in stomachs of *C. temensis* and *C. orinocensis.* Average prey length was greatest for *C. temensis,* followed by *C. intermedia* (Table 2). *Cichla temensis* prey were significantly larger than *C. orinocensis* prey ($t = 2.10$, df = 25, $P < 0.05$).

On several occasions, we observed large (60–80 cm SL) *C. temensis* attacking large characiforms (e.g., *Semaprochilodus kneri* [Prochilodontidae] and *Acestrorhynchus heterolepis* [Characidae] approximately 20–35 cm SL) in shallow shoreline areas. We captured several large *C. temensis* as they attacked a shoal of *S. kneri* that had exited a lagoon into a broad, shallow reach of the Cinaruco. On a few occasions at the Cinaruco, we observed *C. orinocensis* beach themselves during prey pursuit.

The prey fields of the two river systems were similar, but fish densities were lower in the Pasimoni. Five sites in the Pasimoni yielded 80 fish species from 23 families; 31 sites in the Cinaruco yielded 211 fish species belonging to 35 families (voucher material and data in MCNG, INHS), and only about 40 species occurred in both rivers. The Pasimoni has not been surveyed as extensively as the Cinaruco, and additional species probably inhabit the former. We observed higher fish standing stocks in the Cinaruco compared with the Pasimoni. During the dry season, a single 10 m seine haul (6.1 × 1.8 m net) made either during day or night in the Cinaruco typically yielded from 15–30 species and 50–500$^+$ individuals. In shallow shoreline areas of the Cinaruco, hundreds of individuals and dozens of species were viewed at night with the aid of a flashlight. Far fewer individuals and slightly fewer species were observed in the same manner within similar shoreline habitats of the Pasimoni. Characiformes and Siluriformes dominated both river assemblages, comprising 52–60% and 16–20% of species, respectively. Cichlids also were an important group (17% of species in the Pasimoni; 10% in the Cinaruco).

Discussion

Although both would be characterized as blackwater ecosystems (low pH, humic acid stained, low conductivity; Sioli, 1984), the two rivers have very different watersheds. The Cinaruco drains savanna habitats where precipitation is strongly seasonal (virtually all rain occurs from May to August). The Cinaruco has a mostly ev-

Table 2. Percent Number of Prey Categories and Mean Total Lengths of Prey in *Cichla* Diets during the Dry Season at the Río Cinaruco. Values inside parentheses are percentages based on total numbers of prey excluding unidentified fishes.

	C. temensis	*C. orinocensis*	*C. intermedia*
Characiforms	53.8 (73.7)	81.5 (88.0)	61.5 (72.7)
Siluriforms	3.8 (5.3)	0 (0)	15.4 (18.2)
Perciforms	15.4 (21.0)	11.1 (12.0)	7.7 (9.1)
Unidentified fishes	26.9	7.4	15.4
Mean prey TL (cm)	4.62	3.34	3.72
Standard deviation	2.59	2.15	1.81
Number stomachs examined	87	51	31
Number empty stomachs	66	32	23
Total number prey items	26	27	13

ergreen gallery forest. The Pasimoni drains a heavily forested region that receives less seasonal precipitation (driest months are December to February). When compared with Cinaruco conspecifics, a greater proportion of Pasimoni *C. temensis* were captured from lagoons. Precipitation occurs frequently during the dry season in southern Amazonas, and the water velocity in the main channel of the Pasimoni may exceed the preferenda of *Cichla* or their prey. Additionally, the productivity of lagoons may be higher than the river channel to a greater extent in the Pasimoni than the Cinaruco. Although prey densities seemed higher in the Cinaruco, this apparent difference was not reflected in between-site comparisons of body condition.

Although *Cichla* body mass–body length relationships were virtually identical for conspecifics at the two locations, Pasimoni *Cichla* were considerably larger than their Cinaruco conspecifics. This pattern was particularly strong for *C. temensis.* Only one *C. temensis* smaller than 60 cm SL was captured at the Pasimoni, whereas only one *C. temensis* larger than 60 cm SL was captured from the Cinaruco. A few *C. temensis* exceeding 68 cm SL and 8 kg have been taken by anglers at the Cinaruco. *Cichla orinocensis* has the potential to attain a greater maximum size than those indicated by data from the Cinaruco and Pasimoni populations, as evidenced by a 55-cm SL, 5-kg specimen captured by one of us (KOW) from Las Majaguas reservoir in western Venezuela. Because of the remoteness of the region and government regulations restricting activities there, most *Cichla* populations in southern Venezuela had received little impact from fishing until very recently. Therefore, it seems likely that mortality for the largest size classes of *Cichla* is greater in the Cinaruco than the Pasimoni.

The among-species differences in the size structure of Cinaruco *Cichla* populations could be influenced by ecological differences. The largest species, *C. temensis,* occupied the greatest range of habitats and consumed the largest prey, including the migratory prochilodontid, *S. kneri.* Because mouth gape limits maximum prey size in these whole-fish swallowers, *C. temensis* may be the only *Cichla* that regularly surpasses a size threshold that allows it to exploit these seasonally abundant, large prey.

Two alternative mechanisms could account for the observation that *C. temensis* grows larger than its two congeners. Growth rates could be the same for all three species, but the largest *C. temensis* may be older than the largest *C. orinocensis* and *C. intermedia* (meaning that the former's adult mortality rate is lower). Alternatively, mortality rates may be similar, but *C. temensis* might grow faster than *C. orinocensis* and *C. intermedia.* At annulus 5, Cinaruco *C. temensis* were larger (mean = 54 cm SL and 3.5 kg) than *C. orinocensis* (mean = 35 cm SL and 0.975 kg) and *C. intermedia* (mean = 39 cm SL and 1.15 kg), which is consistent with the latter mechanism.

The primary nesting habitat appeared to be the littoral regions of lagoons (*C. temensis* and *C. orinocensis*) and slow moving side channels and back eddies along the shore of the main channel (*C. temensis*). When not nesting or brooding, adult *Cichla* partitioned habitat during the dry season, with *C. intermedia* restricted to flowing channel habitats with submerged structure, *C. orinocensis* in lagoons and shallow lentic areas of the river channel, and *C. temensis* in deeper littoral regions of both the channel and lagoons (see also Taphorn and Barbarino-Duque, 1993). Although large prey may be encountered occasionally in the shallow-water habitats occupied by *C. orinocensis* and *C. intermedia,* there would be many more opportunities to encounter larger prey, especially shoals of migrating *Semaprochilodus,* in the deeper littoral areas occupied by *C. temensis.* Larger mean prey size at the same intake rate and energy density would represent greater total energy intake. The high percentage (66–75%) of empty stomachs documented during the late dry season at the Cinaruco indicates that prey capture may be infrequent for all three species during that time of year.

Cichla temensis and *C. orinocensis* in our Cinaruco sample consumed more characids and fewer cichlids than those studied by Novoa et al. (1989) and Gil et al. (1993) in Guri reservoir. Although characids remain in Guri, their species richness and population abundances have declined relative to cichlids (Alvarez et al., 1986), as might be expected given the basic life-history differences of these two groups (Winemiller, 1989). Cichlids are brood guarders; and, in the absence of strong environmental seasonality, some species nest at frequent intervals. Our Cinaruco data for gonad condition indicate that a portion of each *Cichla* population was preparing to spawn near the end of the dry season (April). During April 1993, we observed a few schools of larval *C. temensis* accompanied by adult pairs. Yet, not all adults were in the same state of gonadal recrudescence during the late dry season, so some individuals may fail to reproduce, or they spawn during a different period of a given year.

Densities of most prey taxa probably peak as waters recede from the broad floodplain of the Cinaruco (November to January). Those *Cichla* that fail to optimize their intake of abundant prey during this falling water period could have difficulty capturing enough energy during the ensuing dry season to meet the requirements for successful reproduction. During the falling water period, immigrating *Semaprochilodus* may provide a particularly important source of nutrition for *C. temensis* in these oligotrophic rivers. In many regions of the Amazon and Orinoco basins, these abundant detritivores undergo annual migrations from their spawning and nursery grounds in productive floodplains of mainstem whitewater rivers into nutrient-poor, blackwater tributaries (Goulding et al., 1988; Vazzoler et al., 1989; Ribeiro and Petrere, 1990).

Acknowledgments

The National Geographical Society, La Fundación Fluvial de Los Llanos, and ASOMUSEO provided support for this research. PROFAUNA (Ministerio de Ambiente y Recursos Naturales of Venezuela) provided scientific collection permits to the authors. Several individuals assisted with fieldwork, especially P. Rodriguez and J. Lyons. We thank G. Webb, C. Lofgren, and the Cinaruco Fishing Club for rendering assistance during our field studies. Nutrient analyses were performed by D. Shormann. We thank D. Jepsen, L. Nico, and L. Page for reviewing and commenting on an earlier draft.

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(KOW) DEPARTMENT OF WILDLIFE AND FISHERIES SCIENCES, TEXAS A&M UNIVERSITY, COLLEGE STATION, TEXAS 77843; AND (DCT, AB-D) PROGRAMA POSTGRADUADO EN MANEJO DE RECURSOS NATURALES RENOVABLES, UNIVERSIDAD EXPERIMENTAL DE LOS LLANOS OCCIDENTALES ESEQUIEL ZAMORA, GUANARE, PORTUGUESA, VENEZUELA 3310. E-mail: (KOW) kow1956@zeus.tamu.edu. Send reprint requests to KOW. Submitted: 12 June 1996. Accepted: 28 April 1997. Section editor: S. T. Ross.

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