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Age structure and growth of peacock cichlids from rivers and reservoirs of Venezuela

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Cichla temensis collected in Venezuela attained a mean standard length of 440 mm, and *C. orinocensis* and *C. intermedia* mean lengths of 309 and 321 mm, respectively. There was little evidence of size differences between sexes. Opaque zones on otoliths corresponded to the period of peak of reproductive activity and low fish body condition (*K*). When aggregated across sites, linear estimates for growth of fish >age I were 57·5, 27·6, and 19·6 mm year^{-1} for *C. temensis*, *C. orinocensis*, and *C. intermedia*, respectively. Fish from the Cinaruco River appeared to spawn at age I, and prior to first maturation had grown 25, 21, and 23 mm month^{-1}, respectively, for *C. temensis*, *C. orinocensis*, and *C. intermedia*. There was little intersite variation in growth rates, and differences in sizes of conspecifics from different sizes were due to age differences. *Cichla* in captivity spawn several times per year. The present results indicate that the annual cycle or tropical wet/dry seasonality promotes reproductive seasonality in *Cichla*. The energetic cost of reproduction and brood defence probably constrains most individuals to one spawn per year. Conversely, populations living in relatively aseasonal reservoir environments may have several spawns per year, in which case growth zones on hard structures are difficult to interpret.

Key words: *Cichla*; otoliths; annuli; reproduction; age estimates; size structure; Venezuela.

INTRODUCTION

Calcified structures have been used to estimate growth and age for a great diversity of fishes (Bagenal & Tesch, 1978; Pannella, 1980; Secor *et al.*, 1995). In temperate regions, growth checks on hard structures usually correlate with responses to changes in water temperature or photoperiod (Beckman & Wilson, 1995). At tropical latitudes, variation in temperature and photoperiod is less pronounced and until recently, it was presumed that tropical fish lack skeletal growth characters amenable to age and growth analyses. Consequently, there are few reported studies of tropical fish growth based on skeletal structures, and most of these are studies of marine species (Fowler, 1995).

Many tropical regions experience strong and fairly predictable annual cycles of precipitation. Most large rivers undergo marked seasonal fluctuations in water levels (>6 m in the Amazon), and fish feeding opportunities and body condition are often associated with access to floodplain food resources during periods of high water (Lowe-McConnell, 1964, 1979; Goulding, 1980; Junk, 1985; Bayley,

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1988; Junk *et al.*, 1989; Winemiller, 1990; Jepsen *et al.*, 1997). Lowe-McConnell (1979) noted that many tropical fluvial fishes have distinct annual breeding seasons that are synchronized with seasonal flooding that ushers in a pulse of inorganic nutrients, production and food availability that promote juvenile growth. Discrete periods of spawning followed by rapid growth have been associated with variable growth zones on hard structures in temperate fishes, and there is no reason to expect tropical fishes to lack these zones. Recent studies have documented growth checks on scales or otoliths from fishes inhabiting tropical floodplain rivers (Boujard *et al.*, 1991; Winemiller, 1991; Winemiller & Kelso-Winemiller, 1994; Booth *et al.*, 1995).

The ecology of peacock cichlids *Cichla* spp. has been studied in their native rivers in Venezuela. *Cichla* are important piscivores and, when introduced into other tropical waters, can impact native fishes directly and indirectly and impact ecosystem structure (Zaret & Paine, 1973). Because of their natural abundance, sporting nature, and quality of flesh, *Cichla* are an important natural resource in many regions of South America. Exploitation of these species usually occurs without the benefit of ecological information, and little is known about the longevity and growth potential of these fishes in their native habitats. The few estimates available are from *Cichla* raised in captivity or introduced outside their native range (Braga, 1953; Devick, 1972; Rutledge & Lyons, 1976; Zaret, 1980).

Cichla are substrate brooders that guard young for several weeks after hatching, during which time adults cease feeding (Fontenele, 1950; Braga, 1952; Zaret, 1980). In Venezuela, Jepsen *et al.* (1997) found that *Cichla* feeding activity, maturation of gonads, and body condition were associated with seasonal fluctuations in water levels. Based on *Cichla* spawning behaviour and the effect of seasonal environmental conditions on feeding and reproduction, it was predicted that *Cichla* species would exhibit some degree of growth variation, and the timing of this variation would be recorded in fish otoliths. Here, length and weight data are assessed for several *Cichla* species, from natural and modified habitats in Venezuela. The objective of this study was to evaluate otolith macrostructure and field data to estimate age and growth in several species of *Cichla*, and compare these estimates across populations from several different habitats. The utility of hard structures to evaluate age and growth in neotropical piscivores has not been examined before. It was anticipated that populations from locations varying in ecosystem productivity and fishing pressure would have different length distributions, growth rates, and age structure. Estimation of age structure and growth rate is essential for management of these valuable stocks.

STUDY SITES

Cichla species were collected from a variety of freshwater habitats in Venezuela (Fig. 1, Table I) (Taphorn & Barbarino, 1993; Jepsen *et al.*, 1997; Winemiller *et al.*, 1997; Williams *et al.*, 1998). In this study, the most southern populations were from Amazonas State, a sampling site referred to here as Amazonas. Most samples from this region came from the Pasimoni and Siapa Rivers, tributaries of the Casiquiare River, which eventually joins the Rio Negro. Although there are limnological differences among rivers in this region, they are

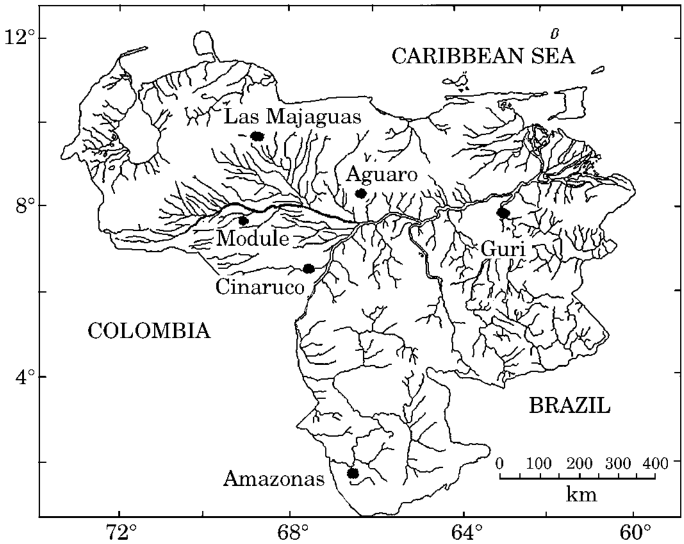

FIG. 1. Map of Venezuela indicating major drainages and sampling sites.

broadly similar in pH, transparency, substrate, nutrient impoverishment, and lack of aquatic vegetation. In Amazonas, four species of *Cichla* were collected; *C. temensis* (Humboldt, 1833), *C. orinocensis* (Humboldt, 1833), *C. intermedia* (Machado, 1971), and a species tentatively identified as *C.* cf. *monoclus*, based on external similarity to *C. monoclus* (Spix in Spix & Agassiz, 1831) collected from other localities in South America. Several earlier reports of *C. ocellaris* (Bloch & Schneider, 1801) may have dealt with *C. orinocensis* or a similar species. The taxonomic status of the genus *Cichla* is currently under study, and several new species may be described (S. Kullander, pers. comm.).

The Cinaruco River is a low-gradient, floodplain river in the savanna region (llanos) of Apure State. Rainfall is extremely seasonal in the llanos, with most rain (1200–1800 mm year^{-1}) falling between April and November (Taphorn, 1992), resulting in large seasonal fluctuations in water levels (1–5 m). The data collected in this river form the nucleus of the comparative analyses. At present, both the Cinaruco and Amazonas region support outstanding sportfisheries for *Cichla*, but increasing exploitation, including new illegal fishing may be affecting these populations.

The Aguaro River drains the central llanos region (Guarico State), and is similar to the Cinaruco in limnological attributes. According to informal reports, *Cichla* populations in this system have been impacted severely by illegal net fishing. Although *C. temensis* occurs in this drainage, its abundance has been reduced greatly in recent years, and samples are adequate only for *C. orinocensis*.

Fish were collected also from three modified sites. Guri Dam is a hydroelectric facility in eastern Venezuela (Bolivar State) that became operational in the early 1980s. Upon initial flooding, the 4250 km^2 reservoir supported an important sportfishery for *C. temensis* and *C. orinocensis*, but subsequently catches declined, probably due to overfishing and lack of a sufficient prey base to support *Cichla* biomass (Williams *et al.*, 1998). Las Majaguas is a storage reservoir (4250 ha) in north-west Venezuela (Cojedes State). Although historical

Table I. Summary of sampling sites, habitat attributes, and collection years where peacock cichlids were captured in Venezuela

Site	Characteristics					Sampling years	Species
	Flow	pH	Substrate	Aquatic macrophytes	Watershed		
Aguaro	Unmodified	5·7–7	Sand, rock	Abundant, submerged	Savanna	1996	CO
Amazonas	Unmodified	4–5	Sand, rock	None apparent	Forest	1993, 1997, 1998	CO, CT, CI, CF
Cinaruco	Unmodified	5–6·5	Sand, rock	None apparent	Savanna	1993–1994, 1998	CO, CT, CI
Guri	Impounded	4·8–6·7	Sand, rock	None apparent	Forest	1993–1994	CO, CT
Las Majaguas	Impounded	6·6–8·0	Sand, rock	Abundant, floating	Agriculture, woodland	1992	CO*, CT*
Module	Modified†	5·5–7·5	Silt, sand	Abundant, floating	Savanna	1993, 1996	CO

*Species introduction.

†See text for description.

Abbreviations for *Cichla* species: CO, *C. orinocensis*; CT, *C. temensis*; CI, *C. intermedia*; CF, *C.* cf. *monoclus*.

information is imprecise, *C. temensis* and *C. orinocensis* probably were introduced soon after dam completion, and presently there is a moderate artisanal fishery. The Module is a series of diked, low-gradient ponds in Apure State. The pond units provide water resources for livestock production in the dry season, and now provide aquatic refuges for fishes. It is not known whether *C. orinocensis* colonized the Module from adjacent rivers, or was introduced from another region of the country.

MATERIALS AND METHODS

FIELD SAMPLING

At all sites, *Cichla* were captured from a variety of habitats with several methods (gillnets, castnets, seines). By far the most effective method was by hook and line with artificial lures. For each fish, standard length (L_s) was recorded to the nearest 1 mm with a tape or measuring board, and body mass (W) to the nearest 10 g using spring-loaded balances. Most of the fishes were then released alive, but several individuals from a range of size classes were killed for sex determination and excision of sagittal otoliths (see below). *Cichla* from the Cinaruco River samples were examined to assess sexual maturity and peritoneal fat reserves following criteria in Jepsen *et al.* (1997).

SAGITTAE PREPARATION AND MACROSTRUCTURE ANALYSIS

The most efficient method to remove sagittae was to access the prootic bulla ventrally. This was then chipped away to expose the sagittal otoliths. Otoliths were cleaned and dried, labelled, then stored in plastic vials. Because of their opaqueness, whole *Cichla* otoliths could not be examined for macrostructure. Otoliths were fixed in an embedding medium (Ciba-Geigy, Dorval, Quebec), allowed to dry, then cut transversally near the focus with a low-speed precision saw. One to three thin sections (*c.* 1 mm), either adjacent to or incorporating the focus, were mounted on glass microscope slides with thermoplastic glue. Sections were polished with fine-grit sandpaper, cleaned, swabbed with immersion oil (glycerin), then examined under a dissecting microscope fitted with a micrometer. For each otolith, the thin section closest to the focus was examined for macrostructure. Alternating opaque (dark) and translucent (light, clear) zones were most visible under reflected light, and the number of opaque bands from the focus to the anterior otolith margin was counted. Each otolith was counted independently twice (no previous knowledge of count), by two researchers. Both within and between-reader agreement was high for most samples (Table II). When corroboration for a sample could not be achieved, that otolith was omitted from further analysis. Most count variation concerned a difference of one band, and was based on discerning the presence of the most interior opaque band. The distance from the focus to the margin was measured with the micrometer, and when possible the distance from the focus to the outside margin of each opaque band was noted. For Cinaruco River fishes, the seasonal deposition of opaque material was assessed by measuring marginal increments. Adapting the procedure of Casselman (1987), edge conditions were categorized as follows: translucent, opaque <50% width of most proximate complete band, and opaque >50% width of most proximate complete band. Opaque zones were interpreted ultimately as annual checks (annuli) associated with reproductive seasonality (see Results below).

DATA ANALYSIS

Literature reports for *Cichla* reared in captivity, and for fish introduced outside their native range, indicate that *Cichla* <200 mm L_s were young-of-the-year (YOY). As it was adult growth relationships that were of interest across a variety of aquatic habitats within the native range of *Cichla*, and there was little *a priori* knowledge of size at first maturity for fish in these habitats, fish <100 mm L_s were eliminated from analyses. The three species of *Cichla* from the Cinaruco River showed similar temporal patterns in gonad

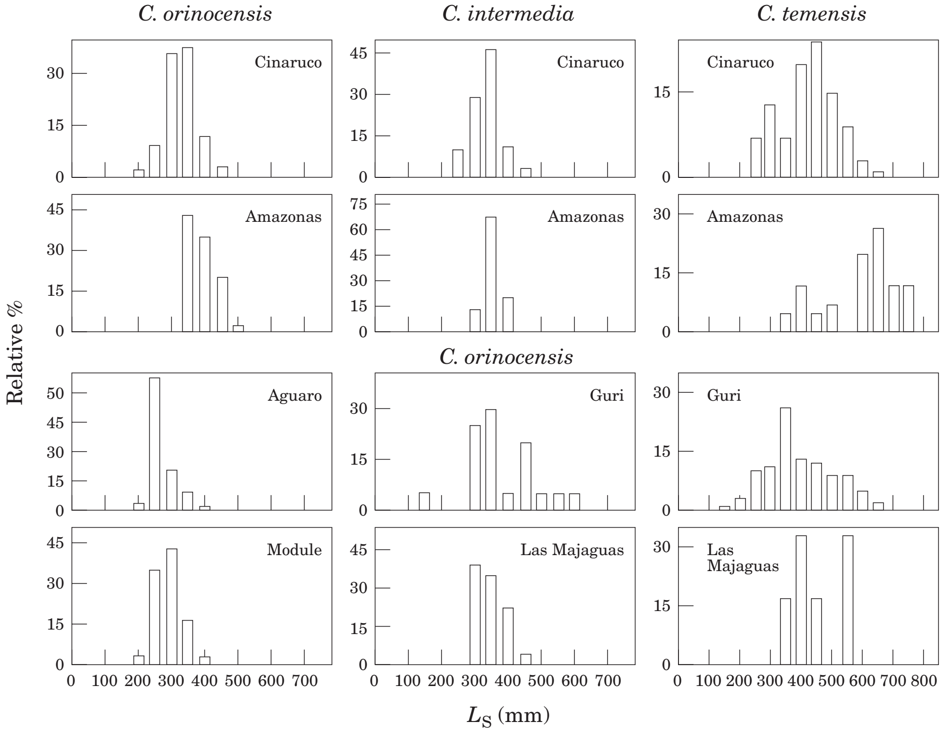

FIG. 2. Length–frequency histograms for species of *Cichla* from several sampling sites in Venezuela.

development, body condition ($W=aL_S^b$), and marginal increments. Thus for calculations of monthly mean values of these factors, data were pooled for the three species. The monthly relative increments were expressed as the width of opaque material at the margin, relative to the total width of the most proximate opaque zone (i.e. representing the previous year's growth check). Thus a mean relative increment >50% indicated a margin opaque zone >50% of the previous opaque zone. Least-squares regression procedures were used (analysis of covariance, ANCOVA) to calculate linear estimates of L_s with age, and ln transformed W on ln transformed L_s. Age data based on otolith bands and L_s were fitted to a von Bertalanffy growth function:

$$L_1=L_0\{1-\exp(-k(t_1-t_0))\}$$

RESULTS

Length and weight data were recorded for 1360 fishes from four species of *Cichla* (Table III). *Cichla orinocensis* occurred at all six sites, representing 32% of all fishes measured. *Cichla temensis* were collected at four sites and made up 56% of the total sample. *Cichla intermedia* (11% of sample) were found only in main channels of the Cinaruco and Amazonas Rivers. Only in Amazonas were *Cichla* cf. *monoclus* collected, and they made up only a small fraction of the samples ($n=15$). Although the sample size was small for this species, they appear to have a smaller maximum size than the other Venezuelan *Cichla*. Except at Guri, *C. temensis* were significantly larger than sympatric congeners (analysis of variance, ANOVA, $P<0{\cdot}001$), whereas *C. orinocensis* and *C. intermedia* were of similar size when sympatric.

TABLE II. Summary of between-reader variation for annuli counts on otoliths

System	*n*	% Agree	% Disagreement for annuli counts				No. of otoliths resolved
			1	2	3	4	
Aguaro	50	90	10	0	0	0	46
Amazonas	40	75	13	7	3	2	35
Cinaruco	86	56	30	9	2	1	81
Module	35	71	23	6	0	0	34
Average		71	20	6	2	1	
Total	211						196
Guri	26	15					0

In all cases, there was a significant relationship between length and weight ($P<0{\cdot}001$), and only fish from the Aguaro River had r^2 values $<0{\cdot}70$. Previous workers have noted sexual dimorphism in *Cichla* (Fontenele, 1950; Devick, 1972; Zaret, 1980; Jepsen *et al.*, 1997), with males being larger than females. With the exception of *C. orinocensis* at the Cinaruco River ($t_{\text{two-tail}}=2{\cdot}69$, d.f.=63, $P=0{\cdot}009$), sexes within sites were of similar length. A more useful expression of body size was the relationship between L_s and W. When aggregated across sites, *C. temensis* males had greater slope and intercept estimates than females (linear regressions of ln transformed W on ln transformed L_s: ANCOVA, $F_{1,333}=11{\cdot}5$; $P<0{\cdot}002$ for slopes; $F_{1,336}=23{\cdot}0$; $P<0{\cdot}001$ for intercepts). The two sexes of *C. orinocensis* had similar slopes and intercepts ($F_{1,204}=2{\cdot}68$; $P>0{\cdot}2$ for slope; $F_{1,207}=1{\cdot}74$; $P>0{\cdot}2$ for intercepts).

Length–frequency histograms showed a unimodal distribution for most samples (Fig. 2), revealing essentially no information about growth rates or age structure. However, the large sample size for *C. temensis* from the Cinaruco River does indicate some size class structuring, with bimodal maxima at 251–300 mm and 401–450 mm. There was a disjunct distribution for Amazonas *C. temensis*, perhaps the result of sampling from different rivers. *Cichla temensis* from the Pasimoni River were larger than those collected in other portions of Amazonas ($\bar{L}_s=616$ and 480 mm for Pasimoni and non-Pasimoni fish, respectively; $t_{\text{two-tail}}=3{\cdot}76$, d.f.=39, $P=0{\cdot}001$).

There was considerable intersite variation in the size structure of conspecifics. *Cichla temensis* and *C. orinocensis* populations differed in mean lengths among sites (ANOVA, $F_{2,757}=69{\cdot}6$ and $F_{5,426}=51{\cdot}99$; $P<0{\cdot}001$ for each, respectively). Fish from Amazonas had greater mean lengths than respective conspecifics at other sites ($t_{\text{two-tail}}=10{\cdot}76$ and 7·71; d.f.=779 and 445; $P<0{\cdot}001$ for both, respectively). *Cichla temensis* from the Cinaruco had greater mean length than those from Guri ($t_{\text{two-tailed}}=3{\cdot}27$, d.f.=713, $P<0{\cdot}001$), and *C. orinocensis* from the Cinaruco were larger than an aggregate sample of fish from the Module and Aguaro ($t_{\text{two-tailed}}=12{\cdot}29$, d.f.=272, $P<0{\cdot}001$).

GROWTH RATES AND SIZE-AT-AGE

Transverse sections of *Cichla* otoliths revealed a macrostructure of alternating translucent and opaque bands (Fig. 3). This banding pattern was more

TABLE III. Length and weight data and results of regressions of weight on length (both ln transformed) for species of *Cichla* from several river localities in Venezuela

Species	Total								Females					Males				
		L		W		Regression			Mean		Regression			Mean		Regression		
	n	Mean	Range	Mean	Range	b	r^2	95% CI	n	L	W	b	r^2	n	L	W	b	r^2
CO																		
Aguaro	70	239	184–323	0·3	0·2–0·8	2·49	0·68	2·08–2·91	43	238	0·3	2·40	0·73	27	244	0·3	2·72	0·67
Amazonas	51	364	305–455	1·1	0·6–2·6	2·81	0·90	2·54–3·07						8	390	1·4	2·59	0·97
Cinaruco	228	305	185–435	0·7	0·5–2·0	3·03	0·94	2·93–3·14	28	299	0·6	2·83	0·90	37	333	1·0	3·22	0·97
Guri	20	358	117–565	1·2	0·04–4·1	3·01	0·98	2·77–3·25	4	373	1·3	3·57	0·90	6	385	1·5	3·01	0·98
Las Majaguas	23	323	260–410	0·9	0·4–1·9	3·15	0·95	2·82–3·48	19	311	0·8	3·04	0·92	4	380	1·5	3·42	0·98
Module	37	270	195–370	0·6	0·2–1·3	3·02	0·94	2·75–3·29	18	261	0·3	3·25	0·90	14	261	0·3	3·29	0·97
Pooled		309		0·8						296	0·7				332	1·0		
CT																		
Amazonas	41	570	303–750	4·3	0·5–9·2	3·12	0·98	2·98–3·27	5	596	4·5	3·12	0·99	13	589	4·9	3·24	0·98
Cinaruco	529	397	158–720	1·4	0·1–6·8	3·13	0·98	3·09–3·17	80	408	1·5	3·08	0·98	142	402	1·6	3·21	0·98
Guri	186	370	124–621	1·3	0·03–5·4	3·15	0·98	3·09–3·21	40	368	1·3	3·01	0·98	51	399	1·7	3·08	0·99
Las Majaguas	6	425	340–520	1·9				1·94–3·70	4	417	1·9			2	440	1·9		
Pooled		440		2·2						447	2·3				457	2·5		
CI																		
Amazonas	15	332	295–400	0·8	0·5–1·5	3·90	0·91	3·17–4·62										
Cinaruco	139	310	205–429	0·7	0·2–1·6	3·08	0·94	2·95–3·21	12	318	0·7	2·88	0·89	25	312	0·7	3·01	0·96
Pooled		321		0·7														
CF																		
Amazonas	15	274	192–346	0·5	0·2–0·8	2·83	0·75	2·19–3·48										

P<0·001 for all individual slopes.

CO, *C. orinocensis*; CT, *C. temensis*; CI, *C. intermedia*; CF, *C.* cf. *monoclus*.

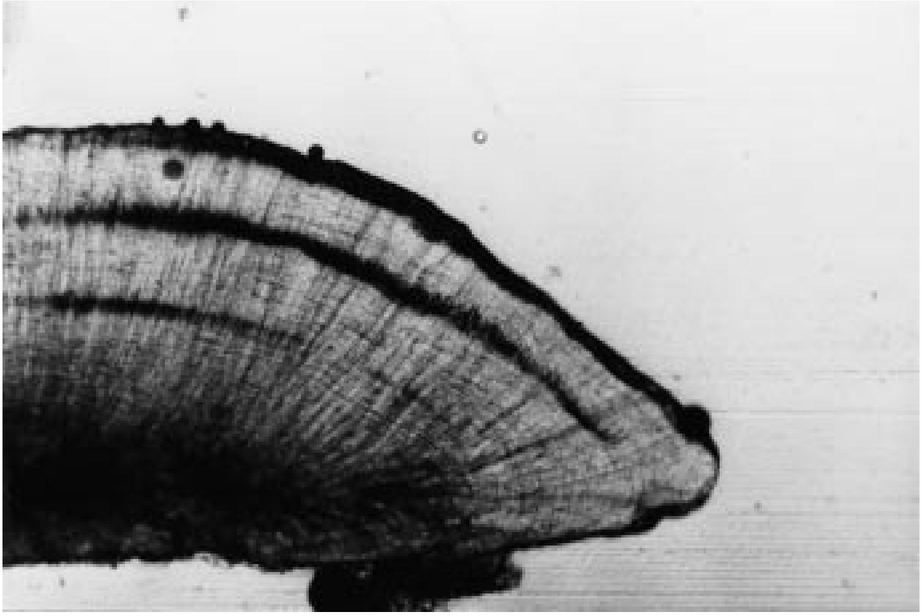

FIG. 3. Transverse view of thin section from sagitta of male *Cichla orinocensis* from the Cinaruco River, Venezuela. Captured on 22 May 1994. Fish length=332 mm L_s; weight=0·7 kg. Maximum diameter of the otolith in vertical dimension=1·0 mm.

pronounced in fishes from fluvial ecosystems (Aguaro, Cinaruco, Amazonas), and mostly diffuse in fishes from Guri reservoir. Sagittae from Guri could not be read with any confidence, and therefore were not used in age estimates. The 8-month record of marginal increments for otoliths from Cinaruco fishes showed a strong temporal pattern of opaque zone deposition that coincided with peak spawning activity and reduced body condition (*b*) (Fig. 4). Condition factor (*W*) was significantly lower during April–June than during any of the previous 3 months (Tukey's multiple range tests, $P<0{\cdot}05$), and generally was related to variation in feeding activity and gonad condition. For *C. temensis* and *C. orinocensis*, mean values of peritoneal fat reserves were lowest during May and June (Jepsen, 1995). Spawning and brooding behaviour were preceded by a protracted period of reduced feeding activity (low water, February–April), when the percentage of empty stomachs for all fish collected approached 100% (Jepsen *et al.*, 1997). Fishes containing food in their stomachs never had mature gonads. These patterns suggest that opaque zones in *Cichla* sagittae are formed during an annual period of slow somatic growth. Whereas the exact mechanism for zonation is not clear, the data indicate that band formation in *Cichla* sagittal otoliths was an annual event associated with spawning and variation in feeding activity in association with hydrological seasonality. Thus, a segment of one opaque and translucent band was interpreted as an annulus, which allowed estimation of fish age and growth rates.

The hypothesis that fish from different systems would have different body condition and growth rates was not supported. Slope and intercept estimates for linear regressions of *W* on L_s for both *C. temensis* and *C. orinocensis* populations among sites were not statistically different (ANCOVA; $F_{3,754}=0{\cdot}42$; $P>0{\cdot}5$ for

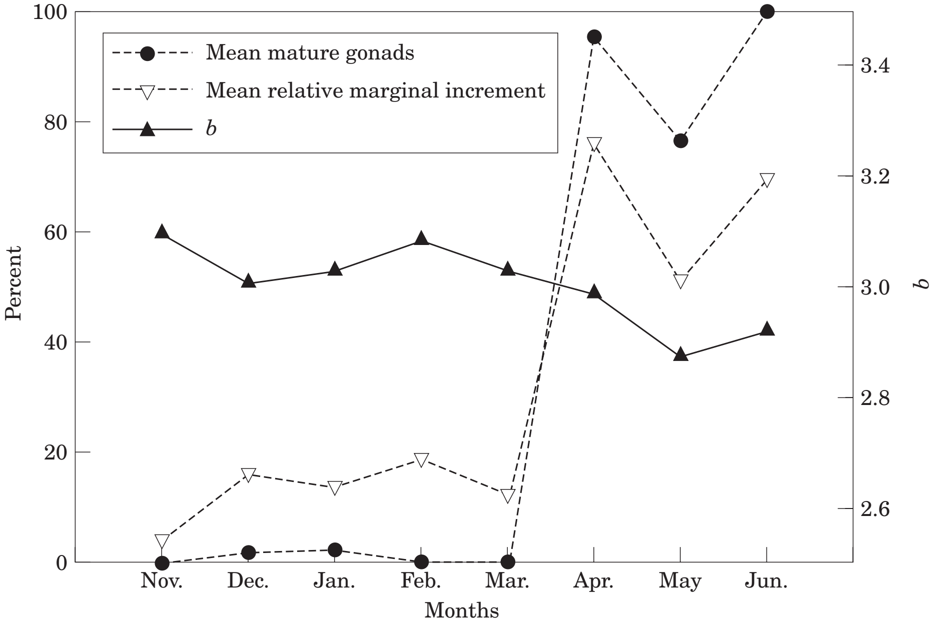

FIG. 4. Monthly progression in condition factor (*b*), mean % mature gonads, and mean relative percent of marginal increment development of opaque material on sagittal otoliths of *Cichla* species in the Cinaruco River, Venezuela.

TABLE IV. Growth parameter estimates for *Cichla* species from linear regressions and of the von Bertalanffy model, based on standard length and otolith annuli

Species	*n*	Slope Age (*b*)	Intercept *L* (*a*)	ANOVA (a=0·05)		von Bertalanffy			
				r^2	*P*	L_∞	*K*	t_0	r^2
C. orinocensis						650·5	0·079	− 5·2	0·69
Aguaro	46	30·7	231·9	0·22	<0·001				
Amazonas	15	25·9	252·6	0·52	=0·002				
Cinaruco	29	28·5	236·7	0·45	<0·001				
Module	34	26·3	229·1	0·42	<0·001				
C. intermedia						389·1	0·40	− 2·4	0·73
Cinaruco	22	19·6	262·0	0·54	<0·001				
C. temensis						843·7	0·162	− 2·3	0·66
Amazonas	24	46·0	364·9	0·42	<0·001				
Cinaruco	37	65·9	262·0	0·79	<0·001				

C. temensis; $F_{5,417}$=2·51; P>0·05 for *C. orinocensis*). Assuming linear growth between age I and VIII, *C. temensis*, *C. orinocensis*, and *C. intermedia* at the Cinaruco River had mean growth rates of 46·0, 28·5, and 19·6 mm year^{-1}, respectively (Table IV). For the four systems from which *C. orinocensis* otoliths were analysed, neither slope nor intercept estimates from linear regressions indicated between-site differences (ANCOVA; $F_{3,116}$=0·07; P>0·5 for slopes;

$F=1{\cdot}64$; $P>0{\cdot}2$ for intercepts). *Cichla temensis* from the Cinaruco River and Amazonas had similar slopes, but different intercepts ($P>0{\cdot}1$ for slopes, $P<0{\cdot}05$ for intercepts). Differences in intercepts were due to the lack of small fish (<age I) in Amazonas samples. For both species, the annuli data revealed that size differences among sites are probably the result of greater representation of older fishes in the samples from Amazonas, rather than differential growth rates (Fig. 5). Low r^2 values for all species and sites suggested that age and length relationships were curvilinear. Higher r^2 values in all cases, compared to the linear model, showed greater conformance with the von Bertalanffy model (Table IV and Fig. 5).

DISCUSSION

Cichla otoliths contain discrete opaque zones that correspond to reduced feeding activity, increased gonad maturation, and depletion of peritoneal fat reserves. This pattern suggests that opaque zones are deposited during a period of slow somatic growth. In contrast, opaque zone deposition appears to take place during periods of fast growth in many temperate zone fishes (Beckman & Wilson, 1995). Present results imply that translucent bands coincide with a period of greater body condition and intense feeding activity (Jepsen *et al.*, 1997). However, there is a possibility that opaque formation is delayed for 2–3 months in *Cichla*, which would correspond to peak feeding and body condition (falling water). The timing of annulus formation in tropical fishes is not well understood, but Fowler (1995) noted that most tropical marine species share a pattern similar to temperate fishes; fast growth synchronous with opaque zone deposition. The literature for tropical freshwater fishes is inconclusive. Yosef & Casselman (1995) interpreted the formation of translucent bi-annuli in otoliths of young *Oreochromis niloticus* (L.) to coincide with a decrease in water temperature, reduced feeding, and slower somatic growth. Winemiller (1991) reported that annulus formation on scales from young and adult *Serranochromis* Regan corresponded to a transition period between low and rising water (low feeding activity) in the Zambezi River system, and noted that false annuli found on adult fish during the rainy season were probably the result of multiple spawning bouts. Data from neotropical fishes indicate a pattern of opaque zone deposition resulting from several factors that reduce somatic growth seasonally. Lowe-McConnell (1964) found that female cichlids of several species had scale rings, whose placement on the scale margin was synchronous with the end of the dry season and low food availability. The rings were interpreted as condition rings, analogous to processes that impose a physiological winter on temperate zone fish. Growth zones found on opercula and scales in omnivorous anostomids were correlated with duration of floodplain inundation, presumably a response to increased feeding opportunity on the floodplain (Boujard *et al.*, 1991; Fabré & Saint-Paul, 1988). Growth checks on scales of prochilodontids were interpreted as resulting from decreased food intake during spawning migrations (Lilystrom, 1983; Barbarino *et al.*, 1998).

Due to the specific structure of *Cichla* otoliths, where opaque bands near the margin sometimes converged, it was impossible to use marginal increments to assess within-in season growth rates. Nevertheless, it appears that otoliths from

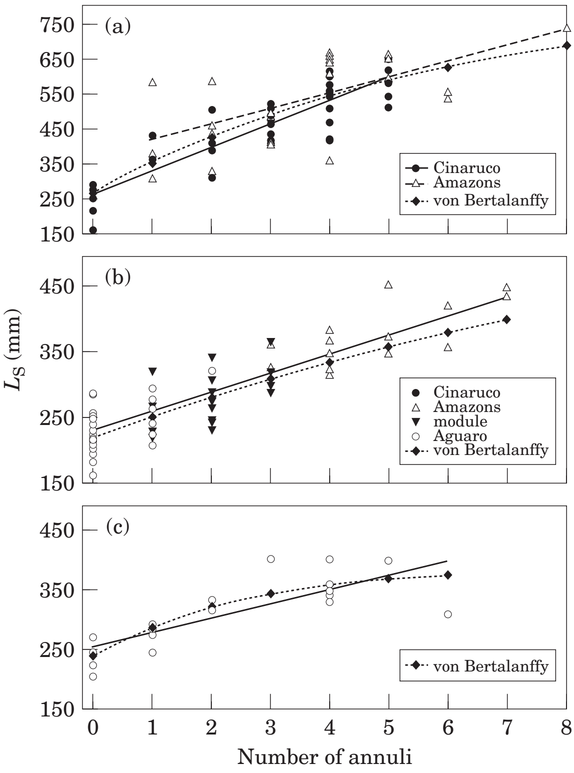

FIG. 5. Length at age relationships for *Cichla* species from several sites in Venezuela, based on counts of annuli on otoliths. Values for regression and von Bertalanffy estimates are given in Table IV. (a), *C. temensis*, (b), *C. orinocensis*, (c), *C. intermedia*.

Cichla living in strongly seasonal environments (e.g. Cinaruco and Aguaro Rivers) have an incremental growth structure that coincides with annual reproduction and reduced body condition. A limitation of the temporal analysis of annulus formation at the Cinaruco was that samples spanned only an 8-month period. Thus, it is possible that *Cichla* in this system form multiple bands each year in response to multiple spawning or other mechanisms, in which case, the age and growth estimates would be high. Conversely, otolith growth zones could form over intervals greater than a year, in which case they would coincide with annual hydrological events. At present there is no information that indicates growth checks are not true annuli, but several observations suggest that they are.

The family Cichlidae includes many species that are capable of multiple spawns per year, and in lake systems in Africa and Central America several species spawn throughout the year (McKaye, 1977; Lowe-McConnell, 1979). Fontenele (1950) reported that *Cichla* growing in fish culture ponds could spawn three to four times a year. Lowe-McConnell (1969) noted that in portions of Guyana with two rainy seasons per year, the timing of gonad maturation in *C. ocellaris* was more evenly distributed, and Zaret (1980) found evidence of two peak breeding seasons in Lake Gatun, Panama. A pattern emerges that cichlids living under more uniform hydrological conditions are energetically capable of multiple spawning annually. However, it is not clear if individual fish are capable of multiple spawns under natural conditions. Devick (1972) reported that individual female *C. ocellaris* in an Hawaiian reservoir spawn only once a year. Based on the life history and feeding of *Cichla* living under cyclical hydrology in the seasonal floodplain rivers of tropical South America, one would expect individual fish to spawn only once per year, which would validate the age and growth estimates. Several workers have noted that adult *Cichla* cease feeding during the 2–3-month breeding season (Devick, 1972; Zaret, 1980; Jepsen *et al.*, 1997), and results from the present study indicate large shifts in fish condition throughout the year. High quality or abundant prey may be available for only a portion of the year in floodplain rivers, and it may be important for large predators like *Cichla* to exploit these resources efficiently in order to survive unfavourable conditions later. Jepsen *et al.* (1997) found that all Cinaruco species had greatest feeding rates during a falling water period, and that migratory *Semaprochilodus kneri* (Pelligrin, 1909) comprised 47·6% of the diet of *C. temensis*. During the extreme low-water period, most *Cichla* stomachs were empty and spawning was initiated. Fat reserves were maximal during the falling-water period, and it is concluded that *Cichla* sequester seasonally abundant prey resources to meet energetic demands associated with spawning and fasting several months later. Fish that invest in extensive parental care to the exclusion of foraging activity may use somatic reserves as energy and nutrient sources during brooding, which may explain partially the appearance of alternating opaque bands on otoliths. For nest guarders with piscivorous habits, food intake during brooding may be particularly constrained, as pursuit of prey would leave eggs and larvae vulnerable to nest predators. Alternatively, fasting during brood guarding might be under hormonal influence, as it was observed that potential prey were not ingested, even when in close proximity to a brooding *Cichla* pair (D. Jepsen, K. Winemiller, per. obs.).

Otoliths from Guri fishes were much more difficult to interpret than otoliths from fluvial ecosystems, and in most cases no distinct bands could be identified. Guri reservoir experiences a 10 m annual fluctuation of water level which may influence seasonal availability of resources in the littoral zone occupied by *Cichla* (Williams *et al.*, 1998). Yet the area affected by the annual fluctuation at Guri is not as extensive as that associated with major lowland rivers of Venezuela.

CICHLA BREEDING BEHAVIOUR

Breeding behaviour for *C. temensis* has been described by Braga (1952) and Fontenele (1950), and for *C. ocellaris* by Sawara & Maranhão (1946), Braga (1952), Fontenele (1950), Devick (1972), and Zaret (1980). Briefly, *Cichla* are substrate spawners that form pair bonds for the duration of parental care. Approximately 7–20 days prior to spawning, *Cichla ocellaris* display secondary sexual characteristics (postorbital nuptial humps in males, and intensified body coloration in both sexes), presumably for mate attraction (Zaret, 1980). After a bond is formed, the pair clear a surface for spawning, then dig several small nest pits into which developing larvae are transferred eventually. After several days, the young leave the pits and, after absorption of the yolk sac at 5–6 days, commence independent feeding. One or both parents guard broods for *c.* 1–2 months, after which time the young begin independent life.

Lowe-McConnell (1969) reported reproductive seasonality in *C. ocellaris* in Guyana based on gonad data. In the Rupununi district, with one wet/dry cycle per year, *C. ocellaris* spawned just before and during the start of the rainy season. Lowe-McConnell noted that gonads became active 3–4 months in advance of peak spawning in April, then were quiescent through the end of the rains in September. Results presented here and observations of gonadal states and nesting behaviour corroborate these findings. Although fish were noted with developing gonads throughout the span of the Cinaruco study, the peak reproductive season occurs just before the transition between low and rising water in April–May.

AGE AT MATURITY AND PUBLISHED GROWTH RATES

The bands on many *Cichla* otolith thin sections were difficult to read, particularly for Guri fishes. Repeated polishings and manipulation with light sources under microscopy increased zonation clarity in most cases (excluding Guri fishes), and concordance between readers was improved during the second round of independent ageing. The most proximate band to the core was often diffuse, which accounted for most of the variation between readers. The age and growth estimates for fish older than age I depended on accurate interpretation of the first band as a spawning check. Based on the length at presumed age relationships (Fig. 5), and observations of gonad condition for fish of different sizes, it appears that most *Cichla* from the Cinaruco River reach sexual maturity at age I. For example, *C. orinocensis* <300 mm L_s were never observed without maturing gonads during peak spawning in April and May, and among all of the samples, there were only two fish <270 mm L_s with maturing gonads. For *C. temensis*, all fish >350 mm showed some degree of maturation during April–May. For *C. intermedia*, all fish >246 mm had maturing gonads. These observations support the slope estimates in Table IV, where *C. temensis*, *C. orinocensis*, and *C. intermedia* grew to *c.* 320, 260, and 280 mm L_s, respectively, prior to achieving maturation. Rutledge & Lyons (1976) reported no evidence of sexual maturity in female *C. temensis* of *c.* 298 mm total length (L_t), but they did note ripening eggs in fish between 310–364 mm L_t. Fontenele (1950) reported that both *C. temensis* and *C. ocellaris* were sexually mature following 11–12 months in captivity, and reached first maturity at a mean L_t of 340 and 280 mm, respectively. Devick (1972) reported that *C. ocellaris* in Hawaii reached first maturity at age I and 300 mm. Zaret (1980) reported that *C. ocellaris* living in Lake Gatun, Panama matured at about 270–320 mm L_s, and Lowe-McConnell (1969) reported that *C. ocellaris* in Guyana matured at 200 mm L_s.

The present study did not estimate growth rates of young fish, but values from the literature suggest that extrapolating the estimates in Table IV below age I would give reasonable estimates. Devick (1972) reported that, in the laboratory, *C. ocellaris* grew *c.* 25 mm month^{-1} for the first 3 months of life, and fish living in a reservoir grew to 64 mm within 3–4 months (about 16 mm month^{-1}). This suggests that fish living in natural conditions may grow more slowly than those reared in captivity. Lowe-McConnell (1964) noted that *C. ocellaris* growth is variable during the first year in native habitats. During a 4-month rainy period in the Rupununi, *C. ocellaris* YOY ranged from 60 to 200 mm L_s and grew at about 27 mm month^{-1} (based on Lowe-McConnell, 1964: p. 126). Braga (1953) found that *C. temensis* <50 mm grew 1·0 mm day^{-1}, and fish 50–100 grew 0·8 mm day^{-1} (linear extrapolation of these data for monthly rates would be *c.* 28–30 mm month^{-1}). Rutledge & Lyons (1976) noted that *C. temensis* reared in Texas ponds grew between 13–61 mm L_t month^{-1} for the first 6 months after hatching. Based on these data and their report that after 5 months, a cohort of 50 mm fish had grown to 218 mm L_s, growth during the first 5 months was estimated at 33 mm month^{-1}. For Cinaruco fishes (Table IV), estimates for first-year linear growth would be 27, 22 and 23 mm month^{-1} for *C. temensis*, *C. orinocensis*, and *C. intermedia*, respectively.

LENGTH/WEIGHT COMPARISONS

Zaret (1980) reported slope estimates from length/weight regressions for *C. ocellaris* from a variety of natural and introduced habitats in the neotropics. Notable was the significant decrease in slopes from the time when fish were introduced to a system compared with estimates several years later. Zaret interpreted this trend as indicative of predator introductions in general, where over time prey resources decline. Zaret's slope value for the Guariquito River was 2·83 (the fish species reported in Zaret's study was probably *C. orinocensis*), and in the present study for a nearby drainage (Aguaro) was 2·49. The values for the Aguaro appear low in relation to other sites, and the lower r^2 value suggests that data collection at this site was imprecise. Zaret gave a value of 2·82 for *C. ocellaris* from the Rio Negro in Brazil, near the present values for *C. orinocensis* and *C.* cf. *monoclus* from Amazonas (2·81 and 2·82, respectively). Estimates of the relationship between length and weight will be influenced by population size structure, time of sampling, and sexual maturity. Considering the wide range of habitats sampled in this study (rivers, ponds, reservoirs), slope values were remarkably uniform.

MANAGEMENT IMPLICATIONS

By all accounts, net fishing has reduced greatly the abundance and average size of Aguaro *Cichla* over the past two decades. Capture of *C. temensis* is now rare, and most *C. orinocensis* in the sample were age 0. There is some indication that *C. temensis* at the Cinaruco recently have undergone a reduction in body size as a result of size-selective mortality associated with sportfishing and recent limited illegal netting. Long-time sport anglers at the Cinaruco reported that 10 years ago it was common to catch *C. temensis* >650 mm L_s. In addition, Jepsen (1995) found that *C. temensis* collected at random were significantly smaller than those kept by anglers. Present otolith data suggest that most fish >550 mm (which comprised <2% of the catch) are age V or older. Strategies to increase the relative number of larger fish might include a size limit that allows a greater number of age IV fish (currently the size class 400–500 mm exploited by anglers) to recruit to age V and beyond. In addition, larger fish feed more heavily on larger prey such as migratory *Semaprochilodus* (Jepsen *et al.*, 1997). Reduction in the mean size of *C. temensis* could produce a cascading trophic effect on the fish community, resulting in greater competition among forage fishes at lower trophic levels (Winemiller & Jepsen, unpubl. data).

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