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Comparative morphology and diet of young cichlids in the dammed Sinnamary river, French Guiana, South America

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The growth of most mensural characters of *Krobia guianensis* and *Crenicichla saxatilis* during early development was explained by a split regression indicating inflection in allometry at specific standard lengths. Double-centred PCA revealed morphological transformations during ontogeny mostly under the influence of the maximum body depth and the maximum caudal peduncle width, the area of the caudal fin and the horizontal diameter of the eye contributing also, but to a lesser extent. Young *K. guianensis* switched to larger prey at the end of the period when the growth of most of their studied mensural characters demonstrated an inflection, but young *C. saxatilis* changed their diet at a much smaller size than that at which an inflection occurred. However, in the lower reservoir sites, most young juveniles of *K. guianensis* and *C. saxatilis* did not switch to larger items during their ontogeny and micro-crustaceans occurred more frequently in their diet. It is hypothesized that the low net energy gained when eating such small prey may explain why the young of both species were thinner at these sites than in their undisturbed habitats. If food resources of young cichlids do not improve in the Petit-Saut reservoir, it is hypothesized that these species will develop stunted populations there.

Key words: Cichlidae; neotropics; ontogeny; *Krobia guianensis*; *Crenicichla saxatilis*; man-made lake.

INTRODUCTION

Ecomorphological studies generally focus on the relationship between the form of adult fish and their ecology (Gatz, 1979*a*; Wikramanayake, 1990; Winemiller, 1991, 1992). Some investigators have also addressed the changes in size, body shape, physiology and behaviour of early stages of fish (Paine & Balon, 1984; Kováč & Copp, 1996; Fuiman & Higgs, 1997; Gozlan *et al.*, 1999; Kováč *et al.*, 1999). These morphological changes enhance swimming ability (Webb, 1984; Gozlan 1998), resource use (Gatz, 1979*b*), predator avoidance (Keast, 1985; Webb & Weihs, 1986), and thus influence the growth and survival of young fish (Werner & Gilliam, 1984). In fresh waters, most studies of fish morphology and diet during ontogeny have addressed temperate species and only few data exist on the early development of neotropical fishes (Angermeier & Karr, 1983; Winemiller, 1989; Mol, 1995). Recently, Mérigoux & Ponton (1998) presented initial data on the body shape and diet of young stages for 66 fish taxa of the Sinnamary river (French Guiana, South America) and stressed the need for more detailed morphological studies during the ontogeny of these taxa.

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Immediately after impoundment on the Sinnamary river by the Petit-Saut hydroelectric dam in early 1994, Ponton & Copp (1997) observed that the young-of-the-year (YOY) assemblages in the reservoir differed from those in the tributaries and were dominated by the progeny of cichlids, especially *Krobia guianensis* (Regan, 1905) and *Crenicichla saxatilis* (Linnaeus, 1758). Ponton *et al.* (1999) confirmed that YOY of these two species were still dominant in the lower reservoir sites in 1995 and 1996, confirming the prediction of Winemiller (1995) that fish species of the equilibrium life history strategy (*sensu* Winemiller & Rose, 1992) are favoured in lenitic environments. However, other factors like food availability for early developmental stages may also influence the composition of the fish community in man-made lakes (Rodríguez-Ruiz, 1998).

The main aim of the present study was to document the early morphology and diet of two of the most ubiquitous (Ponton & Copp, 1997) and abundant (Ponton *et al.*, 1999) cichlids in the different sections of the dammed Sinnamary river: the generalist *K. guianensis* and the ichthyophagous *C. saxatilis*.

MATERIALS AND METHODS

STUDY SITES AND FISH SAMPLING

Young *K. guianensis* and *C. saxatilis* were collected in tributaries of the Sinnamary river downstream and upstream of the Petit-Saut reservoir and in the littoral zone of the lower- and upper-reservoir in 1995 and 1996 (Fig. 1). Details of the characteristics of the study sites can be found in Ponton & Copp (1997) and Mérigoux *et al.* (1999). In the tributaries downstream and upstream from the reservoir, fish were sampled during different hydrological periods: from January to May when water levels increase naturally, from June to September when usually they decrease, and from October to December when they remain low (Mérigoux *et al.*, 1999). Reservoir sites were sampled only once per year in August during the period of decreasing water levels (Ponton & Copp, 1997; Ponton *et al.*, 1999). Details of the sampling methods are presented elsewhere (Ponton & Copp, 1997; Mérigoux & Ponton, 1998). Briefly, at each site, an area of about 50 m^2 was enclosed with two or three 1-mm mesh stop nets and at least two successive doses of Predatox were applied mixed well with water (6·6% emulsifiable solution of rotenone extracted from *Derris elliptica* by Saphyr, Antibes, France). The specimens were collected with 1 mm mesh dip nets, preserved immediately in 75% alcohol, and brought to the laboratory in Cayenne (French Guiana) within five days after sampling where they were stored at 24 ± 0·5° C until processed.

MORPHOLOGICAL MEASUREMENTS AND DIET ANALYSIS

In the laboratory, YOY were identified and separated from adults. Based on the minimum size at first maturity of females in the Sinnamary river (Ponton & Mérona, 1998), the conservative size limits used for separating YOY from adults of *K. guianensis* and *C. saxatilis* were 75 and 140 mm standard length (L_S), respectively (Mérigoux & Ponton, 1998).

Within each sample, up to 30 non-distorted or damaged individuals of each species were selected at random. For each specimen, two calibrated digital images, one lateral- and one ventral view, were captured with a Sony CCD camera model XC-77CE connected to a Data Translation Model DT3155 frame-grabber. Extension tubes between the camera and the 1 : 2·8 50-mm Tamron objective allowed adaptation of the magnification ratio to the size of the individuals. Images were processed later with UTHSCSA ImageTool version 2.0. From each specimen, a total of 10 external morphometric characteristics potentially associated with swimming ability and resource use (Wikramanayake, 1990) were measured to the nearest 0·1 mm: L_S, maximum body depth (*MBD*), maximum caudal peduncle depth (*MCD*), maximum body width (*MBW*),

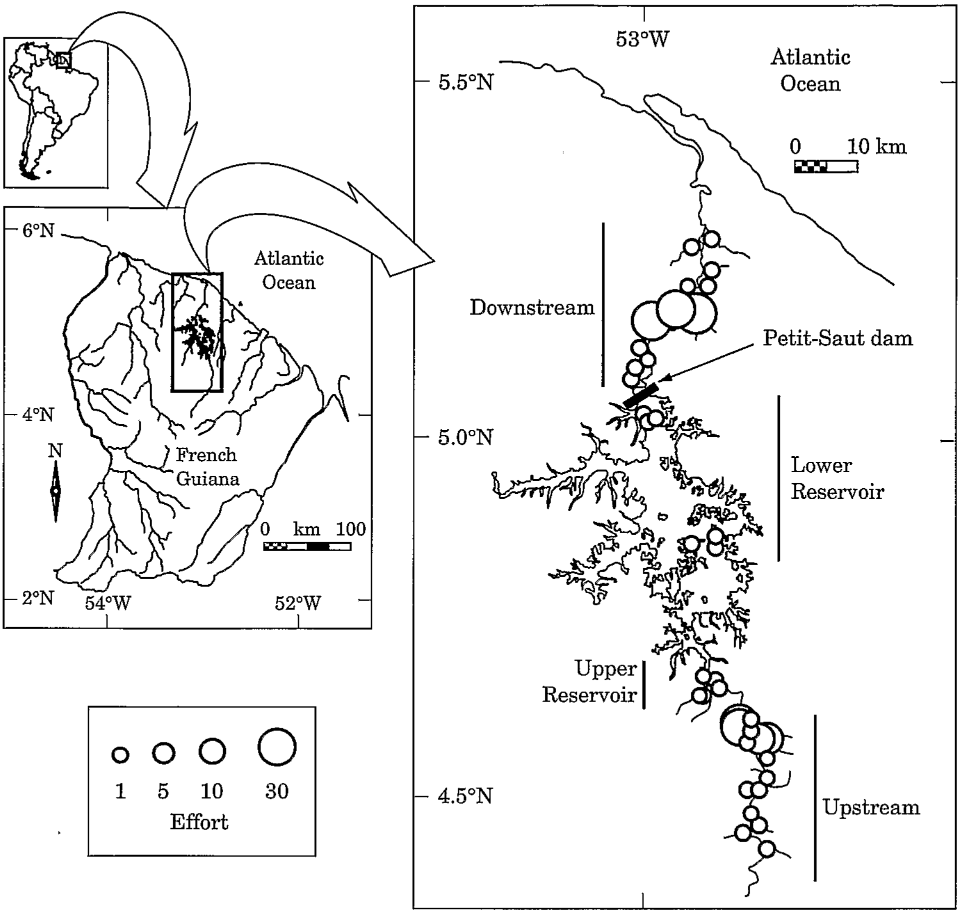

FIG. 1. Map of the Sinnamary river (French Guiana, South America), the reservoir at Petit-Saut as it appears when full, and the study sites in the downstream, lower- and upper reservoir and upstream sections in 1995 and 1996. The diameters of the circles are proportional to the number of samples (effort) taken at each site.

maximum caudal peduncle width (*MCW*), horizontal diameter of the eye (*HDE*), upper maxilla length (*ML*), distance between the tips of the lower maxilla or mouth width (*MW*), pectoral fin length (*PL*), and caudal fin area (*CA*). The digestive tract of each individual was then extracted and its length (*DTL*) measured to the nearest 1 mm with calipers. It was then opened under a dissecting microscope and its contents were examined (× 200 magnification). The presence was recorded of microcrustaceans (Copepoda, Cladocera and Ostracoda), large crustaceans (shrimps), aquatic insects, terrestrial insects and fish, and the width of the largest item of each prey category measured to the nearest 0·1 mm with an ocular micrometer.

DATA ANALYSIS

To examine the patterns of relative growth, simple linear, or linear piecewise (split) regression models were fitted to the ten morphometric characteristics (*CA* values square-root transformed) against L_S. Quadratic regressions were performed also but were not considered further as they never presented a significant improvement in fit over simple linear or split regressions (*F* tests as described in Kováč *et al.*, 1999). It was checked that the residuals of the simple linear or split linear regressions did not present systematic patterns when plotted against L_S (Wilkinson *et al.*, 1996) and then they were used for size-independent comparisons of the morphometric characters for each species (Reist, 1985). To assess the overall morphological transformations of the two species during their ontogeny, missing values were estimated using the simple linear or split linear models and then the resulting data sets were subjected to double-centred principal components analysis (PCA) on log-transformed data following Sagnes *et al.* (1997).

RESULTS

Young *K. guianensis* and *C. saxatilis* were present in 227 of the 266 samples collected in 1995 and 1996. In total 4374 *K. guianensis* and 1853 *C. saxatilis*, 98·3 and 98·9% respectively being YOY, were collected (Table I). Young *K. guianensis* occurred significantly more frequently than young *C. saxatilis* in the samples from January to May 1995 in the down- and upstream sections and from June to September 1996 in the upstream section ($P=0{\cdot}025$, 0·030, and 0·015 respectively, one-sided Fisher's exact test with 1 d.f.). They were significantly more abundant per 100 m^2 from January to May 1996 in the down- and upstream sections and in the lower reservoir in 1995 ($P=0{\cdot}009$, 0·027, and 0·002 respectively, *t*-test). Within each section of the Sinnamary river, densities of young *K. guianensis* and *C. saxatilis* did not differ significantly between periods (ANOVA) nor differed significantly between years (*t*-test). Finally, the densities of *K. guianensis* and *C. saxatilis* caught between June and September did not vary significantly between sections (ANOVA).

Identification of the YoY of these two species was relatively easy (Fig. 2). In aquaria, young *K. guianensis* hatch at a mean size of 3·5 mm (D. Ponton, unpublished observations) but first appearance in the field samples was at 4–5 mm L_S. At that size, they were distinguishable from other young cichlids of the Sinnamary river, especially young *Cleithracara maronii* (Steindachner, 1882), by three bands of melanophores along their sides and the dark spot on their cleithra [Fig. 2(a)]. At 5–6 mm L_S their fin rays developed [Fig. 2(b)] and when young *K. guianensis* achieve *c.* 10 mm L_S, they begin to acquire an adult-like appearance [Fig. 2(c)]. Size at hatching of young *C. saxatilis* is unknown (Ponton & Tito de Morais, 1994), but individuals 8–9 mm L_S captured with rotenone were in an advanced stage of development, with fin ray formation advanced [Fig. 2(d)]. At *c.* 19 mm L_S, young *C. saxatilis* obtain an adult-like morphology and coloration [Fig. 2(e)], with the exception of one longitudinal black bar on each flank which disappears at *c.* 30 mm L_S.

For both species the relative growth of mensural characters conformed well to simple linear or split linear models (Table II). Pectoral length (*PL*) and digestive tract length (*DTL*) presented a high dispersion of their residuals (high values of S.D., Table II) and thus were excluded from further analyses. Linear in piece models indicated that the growth rates of some mensural characters changed markedly at given breakpoints. Based on the size at which these breakpoints occurred, young *K. guianensis* were classified into four size groups: <13 mm L_S; between 13–25 mm L_S when all breakpoints except one occurred (13·3 mm L_S for *MW*, *c.* 17 mm for *ML* and *EHD*, *c.* 24·5 mm for *MBD* and *MBW*); between 25–51 mm corresponding to the breakpoint in the growth of *MCD*; and >51 mm L_S. All breakpoints observed in the growth rates of mensural characters of young *C. saxatilis* occurred when individuals were between 26–44 mm L_S

TABLE I. Sampling effort (total number of samples and total surface sampled), total number of fish caught, percentage of young stages (% of YOY), occurrence of young stages in the samples (% Occ. YOY), and densities of young stages (mean, minimum and maximum number of individuals per 100 m^2) of *Krobia guianensis* and *Crenicichla saxatilis* in downstream, lower (L), upper (U) reservoir, and upstream sections of the Sinnamary river in 1995 and 1996 and for different hydrological periods

Section	Year	Period	Total number of samples	Total surface sampled (m^2)	*Krobia guianensis*						*Crenicichla saxatilis*					
					Total number of fish	% of YOY	% occ. YOY	Densities of YOY (n 100 m^{-2})			Total number of fish	% of YOY	% occ. YOY	Densities of YOY (n 100 m^{-2})		
								mean	min.	max.				mean	min.	max.
Downstream	1995	Jan.–May	26	1234	349	99·1	73·1	36·9	1·6	175·9	267	99·3	46·2	76·3	1·8	692·7
		June–Sep.	30	1925	508	99·8	56·7	38·5	0·6	327·5	343	98·0	43·3	39·9	1·5	103·6
		Oct.–Dec.	10	623	484	99·6	70·0	107·7	3·9	306·1	417	99·8	80·0	84·6	2·5	565·8
	1996	Jan.–May	30	1843	560	100·0	73·3	38·8	1·4	194·4	50	98·0	56·7	4·3	1·0	26·7
		June–Sep.	20	1154	125	96·8	75·0	15·5	1·2	104·4	329	99·4	80·0	35·7	1·3	422·9
		Oct.–Dec.	10	586	364	98·9	100·0	65·0	1·7	241·6	24	95·8	80·0	4·4	1·7	8·4
L. Reservoir	1995	June–Sep.	6	269	238	97·5	100·0	82·0	28·9	168·1	41	95·1	100·0	13·6	2·4	25·4
	1996	June–Sep.	6	287	98	99·0	100·0	36·2	2·0	104·3	56	100·0	100·0	19·0	7·2	45·7
U. Reservoir	1995	June–Sep.	4	234	53	100·0	75·0	26·9	2·8	48·8	5	100·0	75·0	3·1	2·7	3·9
	1996	June–Sep.	4	281	185	99·5	75·0	86·0	2·8	246·1	12	100·0	100·0	4·3	1·3	7·0
Upstream	1995	Jan.–May	20	626	75	90·7	60·0	19·6	1·9	160·8	102	99·0	30·0	68·6	1·5	390·8
		June–Sep.	30	2086	240	92·5	63·3	17·8	0·8	157·0	64	95·3	53·3	5·4	0·7	27·1
		Oct.–Dec.	10	430	16	100·0	40·0	8·6	1·5	17·3	10	100·0	60·0	3·6	1·9	5·2
	1996	Jan.–May	30	1404	460	97·0	60·0	61·2	1·8	559·4	99	100·0	76·7	9·8	1·7	117·3
		June–Sep.	20	1349	539	98·0	90·0	44·4	1·3	329·7	22	100·0	60·0	3·0	0·9	7·3
		Oct.–Dec.	10	495	80	97·5	60·0	22·6	1·2	87·2	12	100·0	60·0	3·5	1·6	6·1

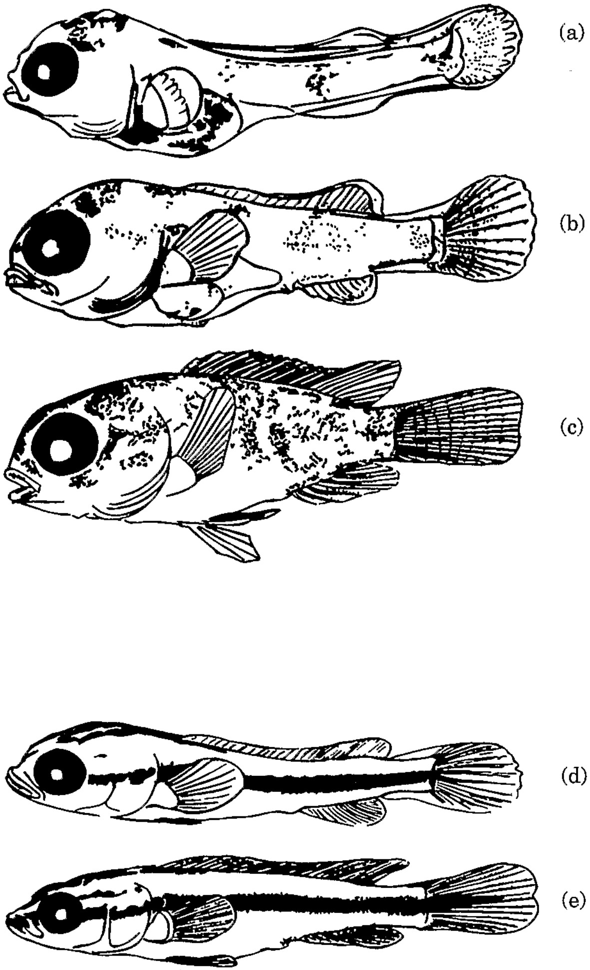

FIG. 2. *Krobia guianensis* at given sizes during early development: (a) 5·2 mm L_S, (b) 5·8 mm L_S and (c) 10·0 mm L_S and *C. saxatilis* (d) 9·5 mm L_S and (e) 19·0 mm L_S.

(26·3 mm for *MW*, *c.* 33·5 mm for *MBD*, *MCD*, and *ML*, and 43·2 mm for *EHD*) except one at 14·3 mm L_S for *MBW*. Consequently, four size-groups, corresponding to four periods in the ontogeny of this species, were retained: <14, (14–26), (26–44), and >44 mm L_S.

The first two components of the double-centred PCA explained 80 and 75% of the total variation of the data for *K. guianensis* and *C. saxatilis*, respectively (Figs 3 and 4). The characters contributing the most to the morphological changes of both fish species were the maximum body depth (*MBD*) and the maximum caudal peduncle width (*MCW*), the area of the caudal fin (*CA*, square root values), and the horizontal diameter of the eye (*HDE*) contributing also, but to a lesser extent. For both species, the lack of overlap between the 95% ellipses based on uniform weightings of size groups 1 and 4 indicated that the morphology of *K. guianensis* $L_S \leq 13$ mm and *C. saxatilis* $L_S \leq 14$ mm differed strongly from that of older juveniles [Figs 3(d) and 4(d)], groups 2 and 3 appearing to be only transitional size classes.

TABLE II. Parameters of linear- (regression 1 alone) or piecewise- (regression 1 and regression 2 successively) regression models adjusted to the growth of 10 mensural characters *v.* L_S

Species Mensural character	n	Regression 1		Breakpoint		Regression 2		r^2	Residuals (S.D.)
		Intercept	Slope	Value	Range	Intercept	Slope		
Krobia guyanensi									
Maximum body depth	1373	−0·958	0·428	24·2	21·9–26·5	−1·732	0·460	0·996	0·349
Maximum caudal depth	1376	−0·357	0·170	50·5	46·6–54·4	−1·771	0·198	0·989	0·216
Horizontal diameter of the eye	1361	−0·076	0·146	17·3	16·3–18·4	0·582	0·108	0·967	0·249
Maxilla length	1341	−0·394	0·125	16·9	15·7–18·1	0·062	0·098	0·973	0·201
Mouth width	1370	−0·094	0·105	13·3	10·4–16·2	−0·307	0·121	0·978	0·215
Maximum body width	1370	0·090	0·181	24·6	21·5–27·7	−0·451	0·203	0·982	0·312
Maximum caudal width	1377	−0·014	0·059	—	—	—	—	0·930	0·191
Pectoral length	1226	−0·853	0·307	28·6	24·2–33·0	−2·169	0·353	0·963	0·769
Digestive tract length	1362	−0·665	1·127	49·6	42·5–56·7	11·685	0·878	0·922	3·771
Caudal fin area (square root values)	1207	−0·470	0·264	—	—	—	—	0·984	0·392
Crenicichla saxatilis									
Maximum body depth	617	0·471	0·168	34·0	32·2–35·9	−1·672	0·231	0·990	0·397
Maximum caudal depth	616	−0·029	0·091	34·1	31·9–36·3	−0·950	0·118	0·990	0·204
Horizontal diameter of the eye	611	0·249	0·080	43·2	40·7–45·7	1·372	0·054	0·980	0·189
Maxilla length	582	0·152	0·085	33·5	31·5–35·6	−0·921	0·117	0·988	0·218
Mouth width	617	0·696	0·066	26·3	24·3–28·3	−0·645	0·117	0·977	0·308
Maximum body width	617	−0·009	0·173	14·3	11·9–16·6	0·691	0·124	0·981	0·344
Maximum caudal width	617	−0·078	0·046	—	—	—	—	0·952	0·201
Pectoral length	543	−0·127	0·200	—	—	—	—	0·987	0·454
Digestive tract length	605	−0·118	0·855	—	—	—	—	0·958	3·445
Caudal fin area (square root values)	547	−0·117	0·174	—	—	—	—	0·983	0·420

With n, number of observations; intercept and slope: parameters of the regressions; breakpoint: L_S values for which the piecewise regression models switch from regression 1 to regression 2; range: Wald 95% confidence interval of the breakpoint; r^2, square of the Pearson's correlation between the observed and the predicted values. Standard deviation (S.D.) of the residuals of the models are also given.

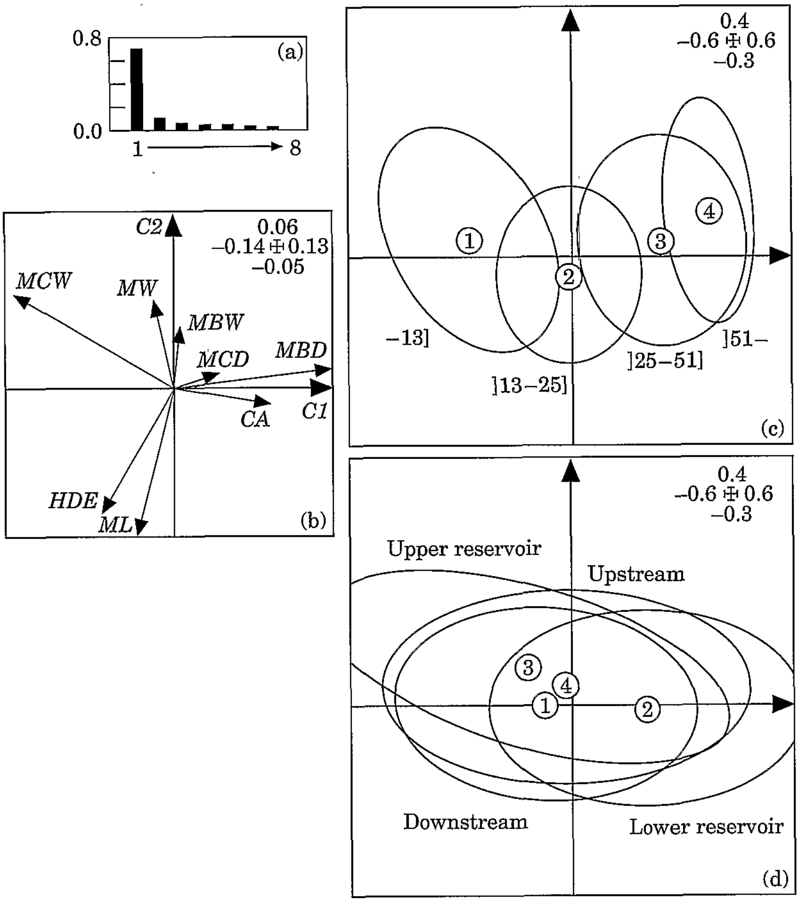

FIG. 3. Ordination of the 1378 *K. guianensis* individuals based on eight morphological variables (i.e. all except L_S, *PL* and *DTL*) in a double-centred Principal Components Analysis. (a) Eigenvalues of components. (b) Position of the eight morphological variables on the ordination plane with *MBD*, maximum body depth; *MCD*, maximum caudal peduncle depth; *MBW*, maximum body width; *MCW*, maximum caudal peduncle width; *HDE*, horizontal diameter of the eye; *ML*, upper maxilla length; *MW*, mouth width and *CA*, caudal fin area. (c) Size groups (1, <13; 2, (13–25); 3, (25–51); 4, >51 mm) delimited using the breakpoints obtained with split linear regressions (Table II). (d) Fish groups corresponding to the different sections of the river (1, downstream; 2, lower reservoir; 3, upper reservoir and 4, upstream) for the June–September period (data from 1995 and 1996 combined). Only 95% ellipses are drawn for clarity.

For both species, the 95% ellipses corresponding to individuals caught within different sections between June and September (data from 1995 and 1996 combined) showed considerable overlap but fish caught in lower reservoir sites (group 2) presented a tendency to differentiate by their morphology on C1-axis [Figs 3(d) and 4(d)]. Size-independent values of *MBD* (*C. saxatilis* only), *MCW*, and *CA* and YoY caught during that period varied significantly between sections (Fig. 5). More specifically, the young of both species were significantly thinner in the lower reservoir section than elsewhere.

For both species, diet spectra and maximum prey width varied little between seasons in the tributaries. *K. guianensis* L_S ≤ 25 mm [size groups 1 and 2,

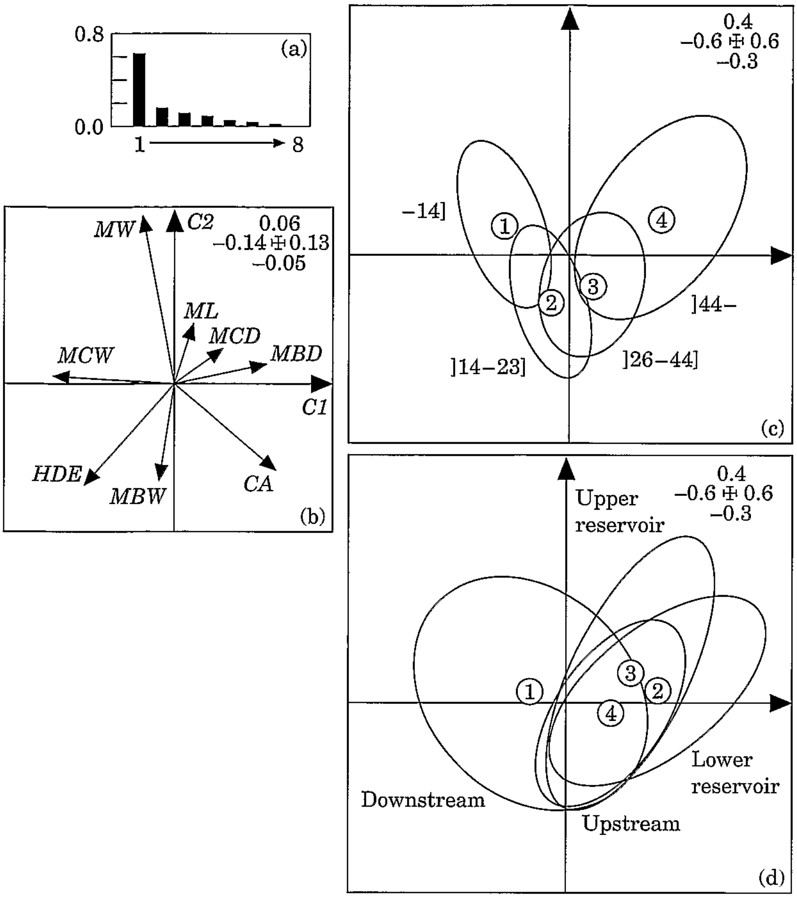

FIG. 4. Ordination of the 617 *C. saxatilis* individuals based on eight morphological variables (i.e. all except L_S, *PL* and *DTL*) in a double-centred principal components analysis. (a) Eigenvalues of components. (b) Position of the eight morphological variables on the ordination plane (see Fig. 3 for codes). (c) Size groups (1: <14, 2: (14–26), 3: (26–44), and 4: >44 mm) delimited using the breakpoints obtained with split linear regressions (Table II). (d) Fish groups corresponding to the different sections of the river (1, downstream; 2, lower reservoir; 3, upper reservoir and 4, upstream) for the June–September period (data from 1995 and 1996 combined). Only 95% ellipses are drawn for clarity.

Fig. 3(c)] and *C. saxatilis* L_S ≤14 mm [size group 1, Fig. 4(c)] preyed upon micro-crustaceans and aquatic insects <1 mm width (Tables III and IV). Larger *K. guianensis* [size groups 3 and 4, Fig. 3(c)] and *C. saxatilis* [size groups 2 to 4, Fig. 4(c)] switched to terrestrial insects and fishes (Tables III and IV). During their ontogeny, the mean maximal width of the prey ingested by young *K. guianensis* increased from <0·3 mm for individuals ≤13 mm L_S to >1·0 mm for those >50 mm L_S while young *C. saxatilis* of comparable sizes ingested prey two to three times wider. In the lower reservoir sites, *K. guianensis* L_S >13 mm and *C. saxatilis* L_S >26 mm ingested significantly smaller prey than in the tributaries (*t*-test, Tables III and IV).

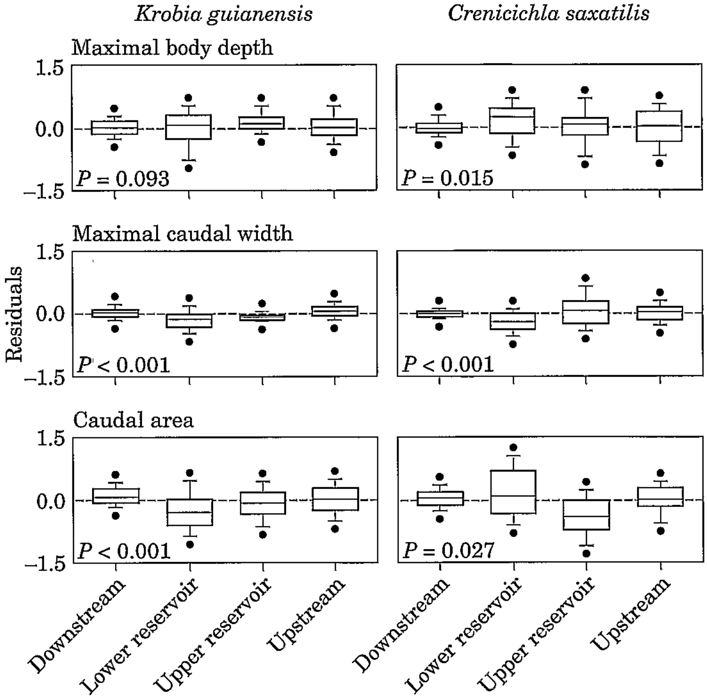

FIG. 5. Size-independent values (i.e. residuals of the regressions presented in Table II) of maximum body depth, maximum caudal width, and caudal fin area of young *Krobia guianensis* and *Crenicichla saxatilis* in downstream, lower reservoir, upper reservoir, and upstream sites for the June–September period (data from 1995 and 1996 combined). With *P*, exact probability of the Kolmogorov–Smirnov test.

DISCUSSION

ONTOGENETIC CHANGES IN MORPHOLOGY AND FEEDING ECOLOGY

The overall morphology of early developmental stages of *K. guianensis* and *C. saxatilis* differed from those of juveniles and their diet paralleled these differences. For both species, most individuals of size groups 1 fed upon micro-crustaceans and aquatic insects confirming previous observations on these species (Mérigoux & Ponton, 1998). The mean maximal width of their prey remained small (Tables III and IV), typically <50% of their mouth width that reached 1·3 mm for *K. guianensis* 13 mm L_S and 1·6 mm for *C. saxatilis* 14 mm L_S. Thus, the early developmental stages of these two cichlids do not seem to be gape-limited predators and thus differ from the larval stages of most fish species (Schael *et al.*, 1991). Their feeding abilities appear more limited by their swimming performances, their muscular masses, indicated by *MBW* and *MCW*, and their pectoral and caudal fins being under-developed. Juveniles of size group 4 presented not only most of the morphological features of the adults but also their diet: insect larvae and terrestrial insects for *K. guianensis* with fishes also for *C. saxatilis*.

The young of both species preyed upon different items as they grew and one would expect that these diet shifts correspond to some important morphological changes. Young *K. guianensis* switched to larger prey at the end of the period

TABLE III. Percentages of occurrence (Hyslop, 1980) of micro-crustaceans, large crustaceans, aquatic insects, terrestrial insects, and fishes, mean maximum (max.) width and standard deviation (S.D.) of these prey in the diet of young *Krobia guianensis* of different size groups delimited using the breakpoints obtained with split linear regressions (Table II) in the downstream, lower reservoir, upper reservoir, and upstream sections for the June–September period (data from 1995 and 1996 combined)

Section	January–May				June–September				October–December			
	<13	(13–25)	(25–51)	>51	<13	(13–25)	(25–51)	>51	<13	(13–25)	(25–51)	>51
Downstream												
n	51	211	24	—	78	104	13	—	39	153	22	—
Micro-crustaceans	4	8	4	—	47	17	8	—	31	5	0	—
Large crustaceans	0	1	4	—	0	0	0	—	0	1	0	—
Aquatic insects	96	76	33	—	67	80	77	—	69	87	46	—
Terrestrial insects	6	10	46	—	0	5	31	—	8	6	46	—
Fishes	0	0	13	—	0	0	0	—	0	0	0	—
Mean max. width ± S.D.	0·4 ± 0·1	0·5 ± 0·4	1·2 ± 0·8	—	0·3 ± 0·1	0·7 ± 0·5	1·0 ± 0·5	—	0·2 ± 0·1	0·4 ± 0·5	2·2 ± 1·4	—
Lower reservoir												
n	—	—	—	—	13	59	77	29	—	—	—	—
Micro-crustaceans	—	—	—	—	77	25	12	0	—	—	—	—
Large crustaceans	—	—	—	—	0	0	1	0	—	—	—	—
Aquatic insects	—	—	—	—	62	76	48	31	—	—	—	—
Terrestrial insects	—	—	—	—	0	7	29	38	—	—	—	—
Fishes	—	—	—	—	0	0	4	10	—	—	—	—
Mean max. width ± S.D.	—	—	—	—	0·2 ± 0·1	0·3 ± 0·2	0·7 ± 0·4	0·8 ± 0·6	—	—	—	—
Upper reservoir												
n	—	—	—	—	29	10	8	—	—	—	—	—
Micro-crustaceans	—	—	—	—	72	20	0	—	—	—	—	—
Large crustaceans	—	—	—	—	0	0	0	—	—	—	—	—
Aquatic insects	—	—	—	—	65	90	62	—	—	—	—	—
Terrestrial insects	—	—	—	—	0	0	25	—	—	—	—	—
Fishes	—	—	—	—	0	0	0	—	—	—	—	—
Mean max. width ± S.D.	—	—	—	—	0·2 ± 0·1	0·4 ± 0·1	0·9 ± 0·8	—	—	—	—	—
Upstream												
Number of individuals	14	62	39	—	48	104	64	—	18	18	15	—
Micro-crustaceans	50	31	0	—	33	16	0	—	50	0	0	—
Large crustaceans	0	2	8	—	0	0	2	—	0	0	7	—
Aquatic insects	64	84	44	—	71	75	52	—	78	94	33	—
Terrestrial insects	0	11	49	—	2	10	28	—	6	0	60	—
Fishes	0	0	13	—	0	1	9	—	0	0	7	—
Mean max. width ± S.D.	0·3 ± 0·1	0·8 ± 0·5	1·3 ± 1·0	—	0·3 ± 0·1	0·3 ± 0·2	0·8 ± 0·7	—	0·3 ± 0·5	0·3 ± 0·2	0·9 ± 0·4	—

With *n*, number of individuals with items in their diet. Only data for $n>5$ are presented.

TABLE IV. Percentages of occurrence (Hyslop, 1980) of micro-crustaceans, large crustaceans, aquatic insects, terrestrial insects, and fishes, average maximum width and standard deviation (S.D.) of these prey in the diet of young *C. saxatilis* of different size groups delimited using the breakpoints obtained with split linear regressions (Table II) in the downstream, lower reservoir, upper reservoir, and upstream sections for the June–September period (data from 1995 and 1996 combined)

Section	January–May				June–September				October–December			
	<14	(14–26)	(26–44)	>44	<14	(14–26)	(26–44)	>44	<14	(14–26)	(26–44)	>44
Downstream												
n	30	10	58	6	104	60	8	13	30	—	46	12
Micro-crustaceans	13	10	5	33	63	33	12	0	13	—	13	0
Large crustaceans	0	0	0	0	2	2	12	31	0	—	2	8
Aquatic insects	77	40	45	67	67	70	50	23·1	90	—	65	33
Terrestrial insects	20	60	57	33	2	38	25	15	7	—	50	33
Fishes	3	0	0	17	0	0	0	31	0	—	0	8
Mean max. width ± S.D.	0·8 ± 0·3	1·2 ± 0·5	1·3 ± 0·6	1·2 ± 0·7	0·6 ± 0·3	1·4 ± 0·4	1·3 ± 0·7	3·2 ± 2·6	0·4 ± 0·2	—	1·3 ± 0·6	1·7 ± 0·5
Lower reservoir												
n	—	—	—	—	—	—	24	30	—	—	—	—
Micro-crustaceans	—	—	—	—	—	—	92	30	—	—	—	—
Large crustaceans	—	—	—	—	—	—	0	3	—	—	—	—
Aquatic insects	—	—	—	—	—	—	54	47	—	—	—	—
Terrestrial insects	—	—	—	—	—	—	12	40	—	—	—	—
Fishes	—	—	—	—	—	—	0	7	—	—	—	—
Mean max. width ± S.D.	—	—	—	—	—	—	0·9 ± 0·5	2·2 ± 1·7	—	—	—	—
Upper reservoir												
n	—	—	—	—	—	—	—	9	—	—	—	—
Micro-crustaceans	—	—	—	—	—	—	—	0	—	—	—	—
Large crustaceans	—	—	—	—	—	—	—	0	—	—	—	—
Aquatic insects	—	—	—	—	—	—	—	11	—	—	—	—
Terrestrial insects	—	—	—	—	—	—	—	44	—	—	—	—
Fishes	—	—	—	—	—	—	—	56	—	—	—	—
Mean max. width ± S.D.	—	—	—	—	—	—	—	3·8 ± 1·2	—	—	—	—
Upstream												
Number of individuals	34	32	—	10	—	—	30	12	—	—	—	11
Micro-crustaceans	91	75	—	10	—	—	23	0	—	—	—	9
Large crustaceans	0	3	—	0	—	—	3	33	—	—	—	27
Aquatic insects	29	50	—	40	—	—	93	33	—	—	—	45
Terrestrial insects	0	16	—	50	—	—	7	17	—	—	—	18
Fishes	0	3	—	20	—	—	3	67	—	—	—	0
Mean max. width ± S.D.	0·4 ± 0·1	0·9 ± 0·3	—	2·7 ± 1·7	—	—	1·2 ± 0·4	3·3 ± 1·8	—	—	—	1·4 ± 0·9

With *n*, number of individuals with items in their diet. Only data for *n*>5 are presented.

during which most of the measured characters demonstrated significant changes in their growth rates. For this species, the period from 13 to 25 mm L_S can be considered as a developmental threshold (*sensu* Kováč *et al.*, 1999), as not only most breakpoints coincided with each other but also with a behavioural change. Young *C. saxatilis* changed their diet when passing from size group 1 to size group 2, when only maximum body width presented a significant break and at a much lower size than when the shifts in relative values of most other mensural characters occurred (Table II).

These two cichlids presented other differences in morphological changes during their ontogeny that may explain the observed differences in diet spectra and prey size. The upper maxilla length and mouth width grew more rapidly for *K. guianensis* than for *C. saxatilis* at the beginning of their life. A first phase of strong positive allometry of maxilla length is a common pattern among perciformes such as marine Carangidae (Shirota, 1978) and freshwater Percidae (Wong & Ward, 1972). The growth pattern of the mouth gape of young *C. saxatilis* paralleled more that of elongated fish species such as *Cololabis saira* (Boulenger), a cyprinodontiform of the North Pacific (Shirota, 1978), than that of perciformes. The length of its maxilla presented a strong positive allometry only after a breakpoint occurring at 33·5 mm L_S. Despite this rapid growth of their mouth gape at the beginning of their life, *K. guianensis* ingested smaller prey than *C. saxatilis* in the same habitats. These differences in prey sizes may be explained better by the body shape of the two species than by the morphology of their mouth. The importance of the maximum body depth (*MBD*) in the overall ontogenetic changes in the morphology of *K. guianensis* [Fig. 3(b)] indicated that their body shape, typical of locomotor generalists (*sensu* Webb, 1984), was acquired early in life. Young *C. saxatilis* presented an elongated and flexible body from their early stage of development on (Fig. 2) and caudal fin area contributed importantly to their overall changes in morphology [Fig. 4(b)]. This body shape, characteristic of sit-and-wait predators such as Esocidae in the Northern Hemisphere and Hepsetidae in Africa (Webb, 1984), and a large caudal fin (Osse *et al.*, 1997), are known to confer on fish the capacity to develop maximum acceleration and thus catch large evasive prey successfully. In summary, young *K. guianensis* develop first a high body depth that may increase their ability to move rapidly in the different dimensions of space (Webb, 1984), and thus use food items of different origins, while the morphological changes of young *C. saxatilis* may improve their swimming abilities rapidly and thus their capacities to ingest large prey.

ARE RESERVOIRS FAVORABLE HABITATS FOR NEOTROPICAL CICHLIDS?

Cichlids usually spawn in still waters (Breder & Rosen, 1966); consequently, they are well adapted for using the littoral zone of tropical man-made lakes as breeding sites (Lowe-McConnell, 1987). Ponton *et al.* (2000) observed that YOY of cichlids were abundant relative to the other species in Petit-Saut lower reservoirs sites from 1994 on. However, the densities of YOY *K. guianensis* and *C. saxatilis* estimated for reservoir sites in the present study are roughly in the range of values obtained in downstream and upstream sites (Table I). Thus, these two species do not appear to find any advantage in terms of reproductive success in the littoral areas of Petit-Saut lake.

During early development, fish usually feed on increasingly larger prey in order to maximize energy intake (Werner & Gilliam, 1984). The present study confirmed that young *K. guianensis* and *C. saxatilis* follow this pattern in the tributaries of the Sinnamary river, their natural habitat (see above), but less obviously in the lower reservoir sites where the size of their prey remained smaller (Tables III and IV). Filling of the Petit-Saut reservoir induced major modifications immediately in the communities of aquatic invertebrates and several types of benthic (mainly Ostracoda) and pelagic (Copepoda and Caldocera) micro-crustaceans appeared (Horeau *et al.*, 1997). Such modifications in the food web in man-made lakes usually induce fishes to feed on prey that are different from those of the river (Lowe-McConnell, 1987). In the Petit-Saut reservoir, young cichlids (this study), as well as most adult fish species (Horeau *et al.*, 1997), consumed small prey intensively as a response to the great abundance of micro-crustaceans, and the absence of overhanging, insect-bearing, terrestrial vegetation. Among tropical freshwater fishes, only some African cichlids such as *Oreochromis leucostictus* (Trewavas) (Robotham, 1990), or the microphagous tilapias (Lazzaro, 1987), are adapted for exploiting small-bodied species of tropical zooplankton at the juvenile and adult stages. It is hypothesized that the energy expended by *K. guianensis* and *C. saxatilis* juveniles to capture small prey is high, and the net energy they gain is low. This may explain why the young of these two species were thinner in the lower reservoir sites than in the tributaries (Fig. 5). If this hypothesis is corroborated, theoretical works on size-structured population dynamics of species with a continuous recruitment (Werner & Gilliam, 1984) predict that Petit-Saut reservoir will harbour stunted populations of cichlids, i.e. populations consisting of many small individuals. Future studies should document how the food resources of young cichlids evolve in the reservoir under the influence of water level variations, with the establishment of a riparian vegetation and the colonization of decaying wood by new types of insect larvae. These studies should also check whether young cichlids in the reservoir present lower size-at-age than those in the natural habitats.

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