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Dominique Ponton[1], Bernard De Mérona

Fish life-history tactics in a neotropical river with a highly stochastic hydrological regime: the Sinnamary River, French Guiana, South America

Orstom, Bp 165, 97323 Cayenne Cedex, French Guiana, France

[1]Present address: Orstom, Univ. Montpellier II, Laboratoire d'Hydrobiologie Marine et Continentale, UMR-CNRS 5556, Case 093, 34095 Montpellier Cedex 5, France

Abstract

Data on maximal length, minimal length at first maturity, relative length at first maturity, length of the reproductive period, percentage of mature oocytes in gonads, mean diameter of mature oocytes in gonads, and mean number of oocytes potentially laid per clutch were obtained for 87 of the 126 freshwater and 18 euryhaline fish taxa of the Sinnamary River in French Guiana, South America. These data were compared with those of Venezuelan fish obtained by Winemiller (1989) in order to obtain some insight on life-history patterns of fish assemblages living in habitats that differ in flow predictability. In the Sinnamary River, the duration of the reproduction period was found to be about twice that observed in Venezuelan Llanos but the length of the reproductive period was not negatively correlated with the proportion of mature oocytes. Independently of the size of the fishes, oocytes of Guianese Characiformes were smaller than those of their Venezuelan counterparts yet no significant difference in fecundity was observed. Globally, the reproductive patterns of fish species caught in the Sinnamary River did not correspond exactly to the three end points pattern emphasized by Winemiller (1989); however, some patterns of life history tactics were outlined.
Key words: freshwater fish, neotropics, reproductive strategies, river flow predictability

1. Introduction

There are more than 20 thousand fish species already described in the world (Nelson 1984) exhibiting a huge diversity of morphological, biological (Bone *et al.* 1995), ecological (Wootton 1990), and reproductive traits (Breder, Rosen 1966). Among them, tropical freshwater fish present the highest diversity of reproductive patterns (Lowe-McConnell 1987). A classification of the life-history pattern of fish species was

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recently proposed by Winemiller (1989). This classification was based on age at maturity, fecundity and juvenile survivorship of different neotropical fish species found in the Venezuelan Llanos. Winemiller, Rose (1992) went on to propose this grouping as a framework for studying relationships between habitat and life-history strategies. Indeed, habitat is generally considered as the templet in which life-history strategies evolve under the pressure of different selective forces (Southwood 1988, but see Persat *et al.* 1994).

This theoretical background is of particular importance when considering the fish assemblages whose habitats undergo drastic modifications following the damming of a river. Long term consequences of a dam on the fish in a given river are difficult to predict from other studies because of different characteristics between locations. This is especially true in tropical areas where fish assemblages vary greatly from basin to basin. Therefore the life-history studies carried out in these latitudes should provide a useful framework for understanding why some species persist and even develop in perturbed environments and why others vanish. Although the diversity of reproductive behavior of fish species in the neotropics has been regularly emphasized (Lowe-McConnell 1987; Val, Almeida-Val 1995), very few accurate data are available to test hypotheses in the framework of life-history strategy theories (Vazzoler 1992). This is particularly true for Guianese fish fauna for which very few data exist in the scientific literature even at the genus level (Ponton, Tito de Morais 1994). This paucity of information is of particular concern when regarding the fish assemblages of the Sinnamary River, French Guiana, South America. Before 1994, this river presented important stochastic water level fluctuations related to local and sporadic rains. This flow variability might have shaped some life history traits of its fish species, especially short-lived ones (Benton, Grant 1996). In 1994, an hydroelectric dam was completed in the river's lower reaches and had an immediate and profound impact on the assemblages of juveniles that showed an important decrease of the relative abundance of Characiformes (Ponton, Copp 1997).

Given this theoretical background, our aims were (1) to collect data on reproductive traits of the most abundant fish species present anywhere in the Sinnamary River, (2) to study the covariations of these variables and detect any effect of systematic position on them, (3) to use these variables to group fish species presenting general common patterns, and (4) to compare some traits of Guianese fish species with those found in the Venezuelan Llanos.

2. Material and methods

The Sinnamary River and its flow regime

The Sinnamary River is approximately 260 km in length (Fig. 1) and drains an area of 6565 km^2 that receives a mean annual precipitation of 3000 mm (for a description of the entire river system, see Boujard 1992 and Tito de Morais *et al.* 1995). Discharge averages 230 $m^3 s^{-1}$ per year and presents important variations between days, weeks, months and years (Fig. 2). Indeed, small tropical rivers like those of French Guiana are subjected to extreme short-term variability in discharge (Westby 1988) in relation to local and sporadic rain (Vauchel unpublished).

Fish sampling and identification

Fish were caught with different sampling gears both in the main channel of the Sinnamary River and in some of its tributaries (Fig. 1). Large fish species were collected in the main channel with gill nets of mesh size 10, 15, 20, 25, 30, 35, 40, 50, 60 and 70 mm between knots. All nets were set at about 5 p.m. and removed between 7 a.m. and 10 a.m. Small and miniature fish species were collected in the river's tributaries and adjacent flooded areas with light traps and Rotenone (see Ponton 1994 and Ponton, Copp 1997, respectively for a complete description of both sampling methods). Fish caught with gill nets were sorted, identified, and measured in the field. Smaller fish caught with light-traps or Rotenone were preserved in 90% alcohol in the field and then transferred to 75% alcohol in the laboratory where they were processed.

All specimens were sorted and identified by using keys for adults (Géry 1977; LeBail *et al.* 1983, 1984; Rojas-Beltran 1984; Lauzanne, unpubl.; Planquette *et al.* 1996). The specimens were measured for standard length (SL) to the nearest 1 mm. Fish species were classified by order and family as proposed by Nelson (1984).

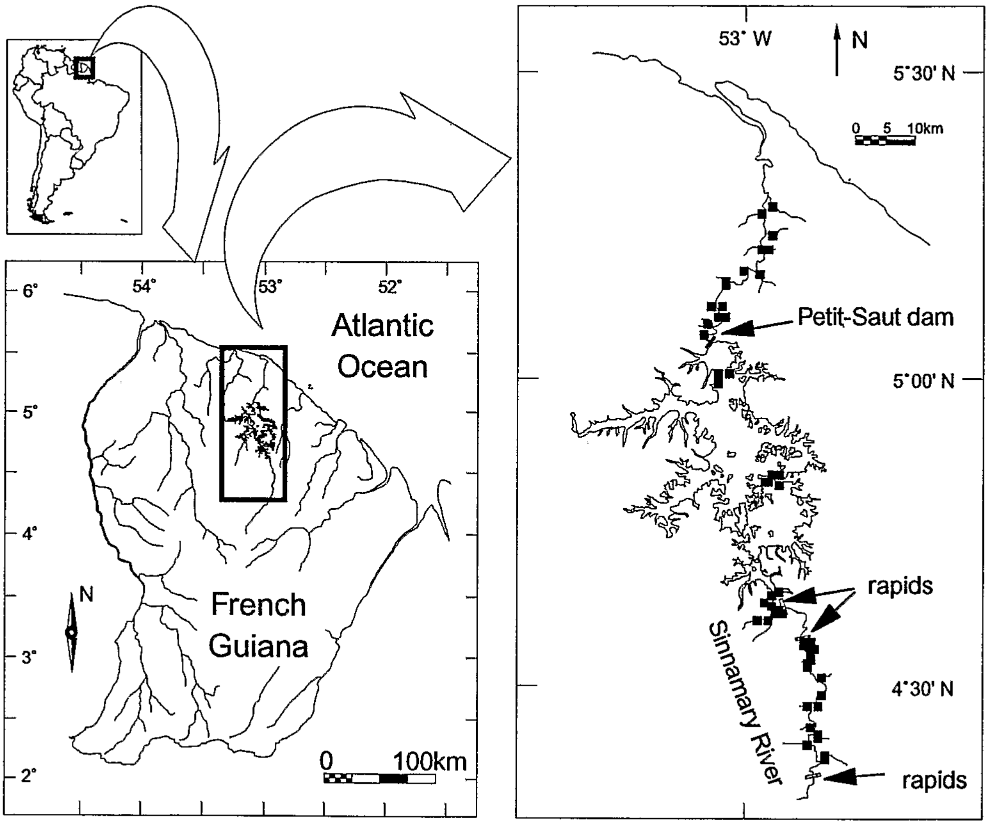

Fig. 1. Location of the Sinnamary River and the different sampling sites

Gonad sampling and analysis

A subset of large fish species caught by gill nets were dissected in the field for maturation examination. A five-point scale based on external appearance was used to classify the maturity stage of the ovaries: 1) immature; 2) start of maturation; 3) intermediate maturity; 4) full maturity; 5) active breeding. The features used to categorize the gonads were: size, shape, volume, degree of vascularization and opacity and the size and appearance of the oocytes in the ovaries. Stage 4 ovaries were extracted and put in Gilson fluid. After a minimal period of two months, oocytes were transferred to clear water and separated from remaining tissues. The diameters of at least 100 wet oocytes were measured by using a dissecting microscope and an ocular micrometer. The total number of oocytes per female was obtained either by using a dry gravimetric method and counting all the oocytes of two subsamples (minimum number of 100 oocytes per subsample), or by counting all the oocytes when their number was less than 300. The imprecision due to this method was < 5%.

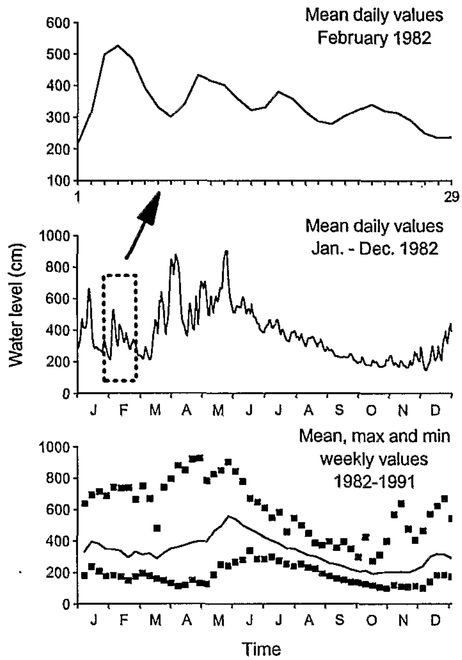

Fig. 2. Water level fluctuations recorded with a ELSYDE Model CHLOE-E gauging station set in the Sinnamary River, French Guiana, upstream from Petit-Saut rapids where Petit-Saut dam has been built (Fig. 1). Water levels were recorded at this station five to seven times per day from 1982 to 1992, i.e. before dam's doors were shut

Small and miniature species were carefully dissected in the laboratory for gonad examinations. The gonads of randomly chosen females were then transferred to Gilson fluid. After a minimal period of one month, the diameter of at least 30 wet oocytes per female were measured under a dissecting microscope equipped with an ocular micrometer. Females presenting the largest oocytes, i.e. corresponding to stage 4 of maturity used for large species, were kept for further analysis. For each mature female, the total number of oocytes was obtained either by suspending them in water and counting those of two 1/10 volume pipette subsamples, or by counting all of them when their total number was less than 300. The imprecision due to this method was < 5%.

Life history traits

Seven variables related to life history were retained for each fish species: maximal length, female minimal length at first maturity, female relative length at first maturity, length of the reproductive period, percentage of mature oocytes in gonads, mean diameter of mature oocytes in gonads, and mean number of oocytes potentially laid per clutch. The maximal standard length (MSL in mm) and minimal standard length at first maturity (SL1M in mm) were determined by measuring the largest individual and the shortest mature female caught in the Sinnamary River during the 1990–1996 sampling period, respectively. The relative size at first maturity (RSL1M) was calculated using the ratio SL1M to MSL. The length of the reproductive period (LRP in months) was estimated from the occurrence of stage 5 females and/or very young stages of their progeny (reservoir excepted), in periods of two months from the beginning of the rainy season (November) on. The relative abundance of mature oocytes (%MO in percentage) was calculated using the ratio: number of oocytes of the largest mode to total number of oocytes. %MO was used as a rough estimate of the number of reproductive bouts per year, hypothesizing that the larger the %MO is, the fewer the number of bouts in the year would be. The diameters of oocytes of the largest mode were averaged in order to obtain the mean diameter of mature oocytes (MDO in mm). Finally, an estimate of the mean number of oocytes potentially laid per clutch was calculated by multiplying the total number of oocytes in each fully mature female by %MO. This mean value, called mean fecundity (MF), will be referred to throughout the report. We thus adopt Bagenals (1978) statement that *"in tropical species where batches follow each other continuously ... the fecundity must only include one batch"*.

Data analysis

Data were first square root – (MSL and SL1M), arsin – (%MO), and log – (MDO and MF) transformed for normality. Effects of size were studied by regressing normalized SL1M, RSL1M, LPR, %MO, MDO, and MF on normalized MSL. Then, Pearson's coefficient of correlation was calculated among the normalized life history variables SL1M, RSL1M, LPR, %MO, MDO, and MF and among the last six variables corrected for SL (residuals from square root transformed MSL linear regression). For both analyses, weighting by the number of individuals modified only slightly p values. As a consequence, results of unweighted analyses will be presented throughout. Afterwards, a principal components analysis was computed from the correlation matrix derived from the 87 species and 6 variables (MSL, RSL1M, LPR, %MO, MDO, and MF). In order to obtain a simple structure, i.e. to identify components sharing more similar explained variance, axes were rotated by the Varimax procedure (Legendre, Legendre 1984). This method distributes the primary loadings of the different variables across more different components and thus offers a clearer identification of components (Wilkinson *et al.* 1996). Then, a cluster analysis was performed by the average linkage method by using Euclidean distances based on the standardized values of MSL, RSL1M, LPR, %MO, MDO, and MF of the 87 species. Finally, length of reproduction, mean diameter of mature oocytes and mean fecundity were compared to the values obtained by Winemiller (1989) in Venezuelan Llanos. Comparisons were performed only for Characiformes and Siluriformes (Winemiller's suborder Gymnotoidei excluded). These orders represent the majority of fish species in both studies. All data analysis were performed with Systat® 6.01 for Windows (Wilkinson *et al.* 1996).

3. Results

Data available

We obtained data on MSL, SL1M, RSL1M, LPR, %MO, MDO, and MF for 87 fish species of the Sinnamary River (Appendix 1). These taxa belonged to 6 orders and 22 families from which Characiformes were the best represented with 49 species (56.3% of the total). Among them, Characidae were the most abundant, with a total of 29 species (33.3% of the total). For 26 species (29.9% of the cases), data were acquired by analyzing more than 10 individuals. Oppositely, for 21 species (24.1% of the total), values of MDO and MF were obtained from the examination of only one specimen. Most of the individuals were caught downstream from the dam (44.4%) and in the reservoir (44.7%). Most of them were caught before (1993: 23.2%), or during (1994: 23.2%, 1995: 47.5%) impoundment.

Period of reproduction

Most fish species presented extended periods of reproduction (Fig. 3). Stage 5 females and/or their progeny at early stages were even found over the entire year for 13 species, a large majority of them (61.5%) being Characiformes. The highest number of reproductive species were found from May to August, i.e. in the last part of the rainy season, when water levels usually are highest (Fig. 2).

Size effect in life history traits

Normalized SL1M, MDO, and MF presented significant positive linear relationships with normalized MSL and only RSL1M decreased significantly with MSL (Fig. 4). Significant correlations were positive for MDO with SL1M, MF with SL1M and %MO; they were negative for MDO with %MO and MF with MDO (Table I). When using the residuals of the square root transformed maximal length regressions, LRP became negatively, although marginally significantly, correlated to SL1M and RSL1M.

Life history traits and systematic position

Only relative size at maturity (RSL1M) and length of reproductive period (LRP) did not vary significantly among orders (Fig. 5 and Table II). Cypriniformes presented the lowest maximal size and lowest SL1M and Clupeiformes had the lowest mean diameter of mature oocytes (MDO) and the highest mean fecundity (MF) when compared to the other orders ($p < 0.05$ and $p < 0.001$ for all pairwise comparisons with Bonferroni post-hoc test, respectively). Adjustments of traits for square root transformed MSL as a covariate did not change the significative differences of MDO and MF among orders (Table II). Hence, independently of their size, fish species of the Sinnamary River present some reproductive traits strongly linked to their systematic position.

Multivariate and cluster analysis

The first three rotated axis of the principal components analysis from the correlation matrix derived from the 87 species and 6 variables explained 74.13% of total variance (Table III). The first axis was mainly influenced by MDO, MF, and %MO, the second axis by MSL, and the third axis by LRP. Plots of species by their scores on the first two principal components axis were performed separately for each order (Fig. 6). Many species presented low scores on PC1 or PC2 especially among Characiformes, Siluriformes and Perciformes. PC analysis separated clearly Clupeiformes (small MDO and high MF) from Gymnotiformes (large MDO and MSL) and from Cyprinodontiformes (large MDO, low MF and

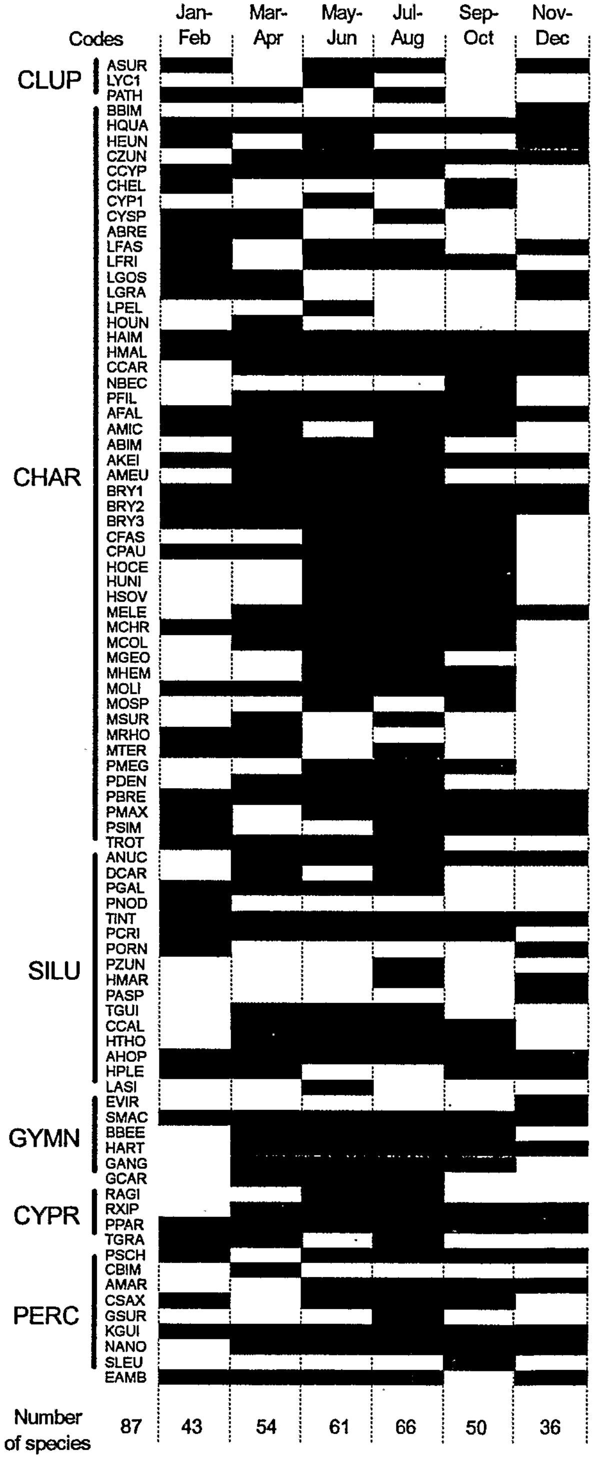

Fig. 3. Reproductive periods of 87 species of the Sinnamary River. Horizontal black bars indicate the occurrence of stage 5 females and/or very young stages of their progeny. See Appendix 1 for codes

MSL). The Characiform, Erythrinidae *Hoplias aimara* differed strongly from all the other taxa by its large size (Fig. 6).

Clustering of 87 species based on Euclidean distances on standardized values of the 6 variables resulted in 9 groups (Fig. 7) differentiating fish species by MDO, MSL and LRP values (Table IV). A total of 51 species, 40 of them being Characiformes, presented very large range of values for the three retained traits.

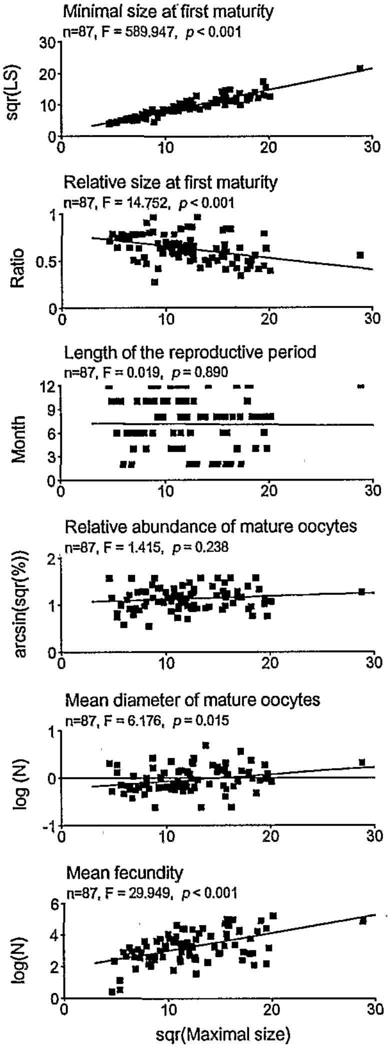

Fig. 4. Relationships of different life-history parameters (transformed values) with square root transformed maximal size. With n – number of observations, F – value of the F statistic and p – associated probability

Table I. Correlation matrix (Pearson's *r*) and significance of normalized life histories variables for 87 fish species of the Sinnamary River, French Guiana. Values in parentheses are for residuals of regressions with normalized maximal size. With ns: non significant, *: $0.01 < p \leq 0.05$, **: $0.001 < p \leq 0.01$, ***: $p \leq 0.001$

	Size at 1st maturity (SL1M)	Relative size at 1st maturity (RSL1M)	Length reproductive period (LRP)	Percentage mature oocytes (%MO)	Mean diameter of oocytes (MDO)	Mean fecundity (MF)
Size at 1st maturity	-	(0.937) ***	(-0.242) *	(-0.096) ns	(0.159) ns	(-0.006) ns
Relative size at 1st maturity	-0.052 ns	-	(-0.224) *	(-0.118) ns	(0.202) ns	(-0.027) ns
Length of reproductive period	-0.100 ns	-0.201 ns	-	(-0.096) ns	(0.072) ns	(-0.084) ns
Percentage mature oocytes	0.086 ns	-0.159 ns	-0.096 ns	-	(-0.287) **	(0.350) ***
Mean diameter of oocytes	0.298 **	0.080 ns	0.065 ns	-0.244 *	-	(-0.659) ***
Mean fecundity	0.475 ***	-0.218 *	-0.080 ns	0.366 ***	-0.414 ***	-

Comparison of some life history traits with venezuelian fishes

Both Guianese Characiformes and Siluriformes reached significantly larger maximal size than their Venezuelan counter parts (Table V). Moreover, the durations of their period of reproduction were about twice as long as those observed in Llanos. When comparing our findings with those of Winemiller (1989), an interesting difference was that the mean size of mature oocytes in Characiformes was significantly lower in our work despite the fact that fecundity did not significantly differ (Table V).

4. Discussion

Life-history tactics of fish species in the Sinnamary River

Examination of thousands of individuals provided data for 87 of the 126 freshwater and 18 euryhaline fish taxa recorded in the Sinnamary River (Lauzanne *et al.* 1995). Despite the huge sampling effort involved in this study, we were unable to obtain any data for Elopiformes Megalopidae (1 species), Gymnotiformes Electrophoridae (1 species), Siluriformes, Bunocephalidae and Doradidae (2 species), Cyprinodontiformes Anablepidae

(1 species), Syngnathiformes Syngnathidae (1 species), Perciformes Carangidae, Centropomidae, Gerridae, Gobioidae, Lutjanidae, Mugilidae, Pomadasydae, Scianidae, and Bothidae (16 species) and Synbranchiformes Synbranchidae (1 species). Except for the last one, all these families are geographically restricted to the lower reaches of the Sinnamary River (Lauzanne *et al.* 1993) where tide-induced variations of the river water levels surperimpose on hydrological

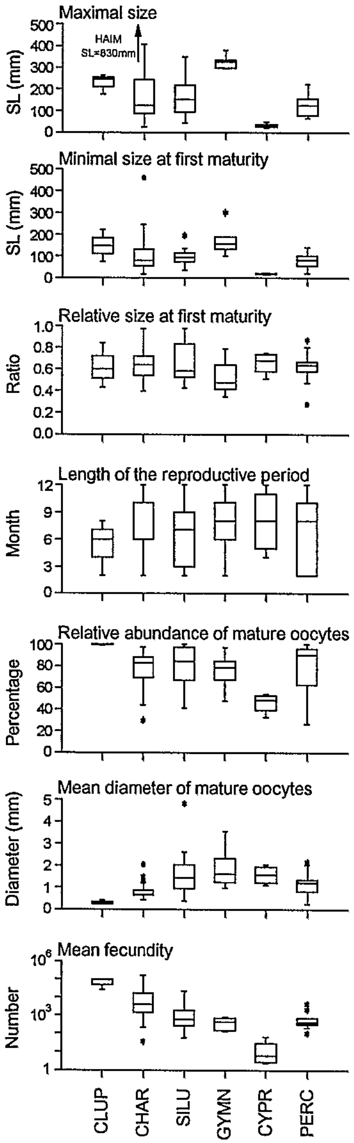

Fig. 5. Box and scatter plots of different life-history parameters of the 87 species grouped by order. Note the log scale for fecundity. With CLUP: Clupeiformes, CHAR: Characiformes, SILU: Siluriformes, GYMN: Gymnotiformes, CYPR: Cyprinodontiformes, and PERC: Perciformes

Table II. Results of ANOVA for order with and without normalized maximal length (square root transformed MSL) as a covariate. With F: value of the F statistic and p: associated probability

	With			Without		
	Class variable	F	p	Class variable	F	p
Maximal size (MSL)				Order	5.420	<0.001
Size at 1st maturity (SL1M)	Order	0.557	0.733	Order	4.816	0.001
	log MSL	426.710	<0.001			
Relative size at 1st maturity (RSL1M)	Order	0.570	0.723	Order	0.868	0.506
	log MSL	12.282	0.001			
Length of reproductive period (LRP)	Order	0.445	0.816	Order	0.454	0.809
	log MSL	0.001	0.976			
Percentage of mature oocytes (%MO)	Order	2.527	0.036	Order	2.732	0.025
	log MSL	0.585	0.447			
Mean diameter of oocytes (MDO)	Order	14.143	<0.001	Order	11.317	<0.001
	log MSL	15.178	<0.001			
Mean fecundity (MF)	Order	22.951	<0.001	Order	17.284	<0.001
	log MSL	47.423	<0.001			

Table III. Results of the principal components analysis using normalized data for the 87 fish species of the Sinnamary River

	Eigenvalues	Percent of total variance explained before components rotation	Percentage of total variance explained after components rotation
PC1	1.977	32.95	28.42
PC2	1.395	23.24	26.48
PC3	1.077	17.94	19.24

Variable	Components loadings PC1	PC2	PC3
MSL	0.644	-0.594	0.369
RSL1M	-0.564	0.437	0.364
LRP	-0.049	-0.431	-0.794
%MO	0.598	0.327	0.011
MDO	-0.390	-0.732	0.409
MF	0.856	0.149	0.095

Variable	Rotated Loading Matrix (VARIMAX, Gamma=1) PC1	PC2	PC3
MSL	0.028	0.950	-0.020
RSL1M	-0.220	-0.495	0.590
LRP	-0.143	-0.087	-0.889
%MO	0.651	0.188	0.078
MDO	-0.839	0.379	0.087
MF	0.713	0.504	0.040

events (Ponton, Copp 1997; Ponton, Vauchel, unpublished). As a result, it can be assumed that the 87 taxa for which data were obtained give a good picture of the life-history tactics developed by the whole fish assemblage of a large part of the Sinnamary River.

Life-history traits in different environments

Comparisons of our data with those of Venezuelan fishes obtained by Winemiller (1989) bring some insight on life-history patterns of fish assemblages living in habitats whose patterns of flood during the rainy season differ strongly. As a matter of fact, flow regime over short periods of time is more variable, and thus less predictable, in the 250 km long Sinnamary River (Westby 1988) than in the Venezuelan Llanos (Welcomme 1979).

Both Characiformes and Siluriformes were larger in the Sinnamary River than in the Venezuelan Llanos (Table V). A total of 12 species of these two orders (35.3% of the total) presented maximum standard length 50 mm in Winemiller's work compared to only 7 taxa (14.3% of the total) in our study. Size is a central feature in life-history patterns (Barbault 1988) and it is well known that it is inversely correlated with interspecific mortality rates in fishes (Roff 1992). In the Sinnamary River, these larger Characiformes and Siluriformes might find some advantage when confronted with flow stochasticity. Indeed, larger animals live longer and tend to suffer a smaller reduction in fitness with increasing habitat variability than those with shorter life

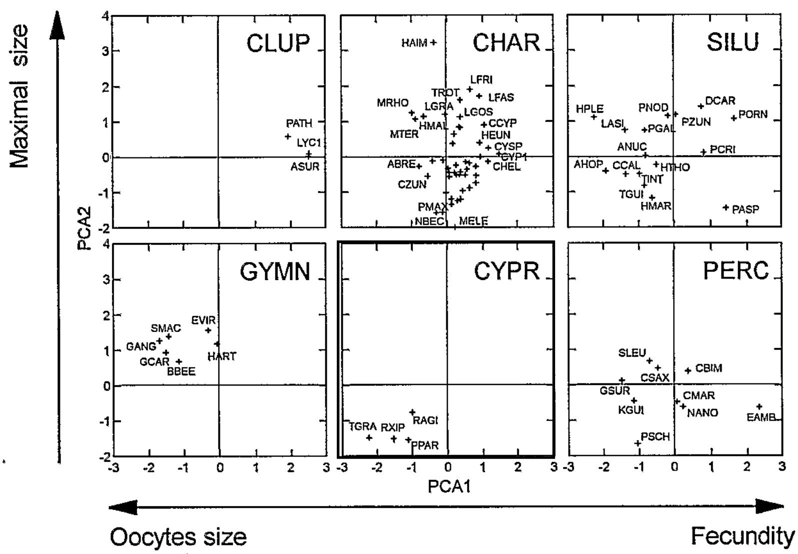

Fig. 6. PC1-by-PC2 plot of the principal components analysis of six life-history parameters by 87 species matrix presented by orders. See Appendix 1 for species codes. Note that some labels were removed for clarity. With CLUP: Clupeiformes, CHAR: Characiformes, SILU: Siluriformes, GYMN: Gymnotiformes, CYPR: Cyprinodontiformes, and PERC: Perciformes

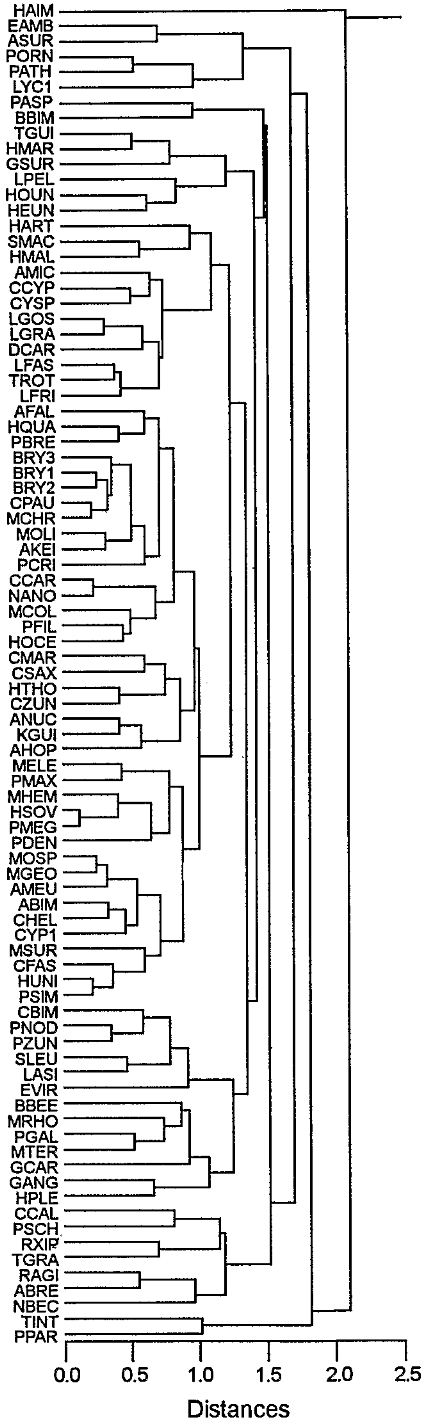

Fig. 7. Cluster diagram of the 87 fish species of the Sinnamary River based on Euclidean distances computed from six standardized life history variables. See Appendix 1 for species codes

Table IV. Groups of species found in the Sinnamary River according to the minimal and maximal values of their mean diameter of oocytes (MDO), maximal size (MSL), and length of reproductive period (LRP). With CLUP: Clupeiformes, CHAR: Characiformes, SILU: Siluriformes, GYMN: Gymnotiformes, CYPR: Cyprinodontiformes, and PERC: Perciformes. See Appendix 1 for species codes

Mean diameter of oocytes (MDO) in mm	Maximal size (MSL) in mm	Length of reproductive period (LRP) in month	Fish species by order					
			CLUP	CHAR	SILU	GYMN	CYPR	PERC
0.24-0.48	245-348	2-6	LYC1 PATH		PORN			
0.24	80-178	8-10	ASUR					EAMB
0.38-0.61	45-161	2		BBIM	PASP			
0.69-2.17	66-250	2-6		HEUN HOUN LPEL	HMAR TGUI			GSUR
0.45-2.32	23-405	4-12		ABIM AFAL AMEU AMIC AKEI BRY1 BRY2 BRY3 CCAR CCYP CFAS CHEL CPAU CYP1 CZUN CYSP HMAL HOCE HQUA HSOV HUNI LFAS LFRI LGOS LGRA MCHR MCOL MELE MGEO MHEM MOLI MOSP MSUR PDEN PFIL PHSP PBRE PMEG PSIM TROT	AHOP ANUC DCAR HTHO PCRI	HART SMAC		CMAR CSAX KGUI NANO
0.47-1.88	28-145	2-10		ABRE NBEC	CCAL		RAGI RXIP TGRA	PSCH
0.97-4.80	150-390	2-8		MRHO MTER	HPLE LASI PGAL PNOD PZUN	BBEE EVIR GANG GCAR		CBIM SLEU
2.03-2.61	21-76	12			TINT		PPAR	
2.05	830	12		HAIM				

Table V. Comparisons of mean values of square root (MSL), LPR, log (MOD), and log (MF) for Guianese and Venezuelan Characiformes and Siluriformes. MOD and MF were corrected for size by using the residuals from square root transformed MSL linear regressions. With t: value of the t statistic and p: associated probability

	Sinnamary River	Venezuelan Llanos	t	p
Characiformes				
Nb of species	49	34		
MSL (mm)	168.3 (139.9)	114.5 (91.7)	2.373	0.020
LPR (month)	7.3 (3.1)	3.9 (3.0)	5.919	<0.001
MDO (mm)	0.8 (0.3)	1.1 (0.4)	-6.496	<0.001
MF (N/clutch)	15747 (28252)	9653 (29701)	0.771	0.443
Siluriformes				
Nb of species	16	22		
MSL (mm)	163.2 (83.4)	101.3 (69.5)	2.672	0.011
LPR (month)	6.4 (3.6)	2.7 (1.2)	4.226	<0.001
MDO (mm)	1.6 (1.1)	1.6 (1.0)	-0.745	0.461
MF (N/clutch)	3263 (6253)	1796 (3306)	-0.746	0.461

histories (Benton, Grant 1996). Moreover, unpredictable extreme hydrological events have a great impact on the survival of the progeny of some fish species in the Sinnamary River (Ponton, Vauchel 1998).

In the Sinnamary River, the duration of the reproductive period is about twice that observed in Venezuelan Llanos (Table 5). Most of the fish species had protracted periods of reproduction, a trait generally favored in an unpredictable environment (Winemiller, Rose 1992). The only total spawners were found to be mainly Clupeiformes, taxa restricted to the downstream reaches (Lauzanne *et al.* 1993). In the Venezuelan Llanos, 32 fish species out of a total of 72, 63% being Characiformes, appeared to exhibit one or two bouts of reproduction during the first weeks following the onset of rains (Winemiller 1989). Numerous fish species have been found to exhibit a total spawning strategy concomitant with the large rise in waters during the annual flood in the central Amazon (Araujo-Lima 1990, Zaniboni 1985). In these areas, total spawners consist mainly of large Characins (Schwassmann 1992) such as *Prochilodus* species (Lowe-McConnell 1987). This strategy is often associated with massive upstream migrations, a behavior which has never been observed in the Sinnamary River.

Interestingly, the length of the reproductive period was not negatively correlated with the proportion of mature oocytes (Table I). This lack of correlation may indicate that in some Guianese fish species not every female is necessarily involved in each reproduction event. For example, gonads of the medium-sized Characidae *Moenkhausia oligolepis* contain an average of 91% oocytes of large size (Appendix 1). However, semi-monthly samples of young fish in one of the main tributaries of the downstream reaches revealed regular outburst of this species progeny during the whole rainy season (Ponton, unpublished). Lastly, similar %MO may not necessary indicate identical number of potential reproductive bouts per year as temporal patterns of ovarian development take place at different speeds for different species (Wootton 1979).

Oocytes of Characiformes appear smaller in the Sinnamary River than in the Venezuelan Llanos independently of the size of the fish (Table V). Some methodological bias may explain these discrepancies. We used Gilson fluid to separate oocytes of ethanol-fixed and fresh samples and Winemiller (1989) fixed his specimens in formalin prior to examination in the laboratory. However, both Gilson (Albaret 1982) and formalin are known to shrink biological tissues and we thus assumed that no correction factor for shrinking was necessary. Lower mean size of Characiformes oocytes in the Sinnamary River suggests smaller sizes of their progeny, therefore a greater mortality among them (Bagarinao, Chua 1986). Indeed, larger eggs mean larger offspring (Ware 1975) that have the ability to ingest larger prey and that have greater swimming capabilities for avoiding predation. The smaller size of Characiformes progeny in the Sinnamary River and their potential lower survival rates may be a valuable trade-off with numerous reproductive bouts per year in a river presenting a low predictable flow regime.

The lack of significant difference in fecundity between the two systems is paradoxical given the statistically smaller size of eggs in the Sinnamary River. There are two reasons for a negative relationship between egg size and fecundity. Firstly, the total volume of oocytes is limited by the size of the fish. Wootton (1992) found a significant correlation between total egg volume and size for 238 teleost species. Secondly, a given species can only produce many small or few large eggs for a given amount of energy dedicated to reproduction (Duarte, Alcaraz 1989, Mann, Mills 1979, Elgar 1990). Testing the existence of such a trade-off and the potential effects of hydrological variability on reproductive investment by females would require an assessment of the total reproductive output per female and per year or fecundity sensu Wootton (1979). Unfortunately our sampling strategy did not allow us to estimate this parameter and Winemiller (1989) gave only estimates of the number of reproductive bouts per year per species, not per female.

In conclusion, the values of different life-history traits presented in this work (Appendix 1) form the largest database ever gathered and published for fish species in the Guianas. The reproductive tactics of fish species caught in the Sinnamary River do not correspond exactly to the pattern of three end points emphasized by Winemiller (1989) but some patterns of life history tactics can be outlined and compared to Winemiller's findings. Guianese fish species, characterized by small oocytes, large maximal size and short reproductive season, belong clearly to the "seasonal strategy" group of Winemiller (1989). As previously shown, large seasonal-strategists characids are absent and are replaced by Clupeiformes. At the opposite end of the spectrum of oocytes sizes, some fish species present large oocytes, medium to large maximal size, and no clear pattern in their reproductive period. Among them *Hypostomus plecostomus*, *Cichlasoma bimaculatum*, and *Satanoperca* sp. aff. *leucosticta* are known to provide parental care to their offspring (Ponton, Tito 1994). That being so, some species of this group possess the suite of characteristics forming the "equilibrium strategy" stressed by Winemiller (1989). Remarkably, numerous fish species, most of them Characiformes, presented traits with intermediate values that impeded any classification of their reproductive pattern (Fig. 6, Table IV). There is no doubt that with a more complete database, especially estimates of juvenile mortality, some of these species would group in the "opportunistic strategy". In future studies, our results will be used to detail relationships between reproductive strategies expressed by fish and the environmental parameters of the different habitats within the Sinnamary River. Grouping fish taxa by their common reproductive traits will allow us to get beyond the systematic of the different fish taxa and thus give broader applicable insights on the impacts of hydroelectric dams on neotropical fish assemblages.

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Appendix 1. Data of life-history traits of 87 species of the Sinnamary River, French Guiana. With Ntot: total number of fish analyzed, Nfem: number of stage 4 females analyzed, SLfem: range of size (standard length) of females, MSL: maximal standard length observed among all the individuals, SL1M: standard length at first maturity, RL1M: relative length at first maturity or SL1M/MSL, LRP: length of the reproductive period in months, %MO: percentage of mature oocytes in the gonads of stage 4 females, Noo: total number of oocytes measured, MDO: mean diameter of mature oocytes, Nfec: number of females analyzed for fecundity estimates, MF: mean fecundity or mean number of mature oocytes in stage 4 females or mean number of eggs laid per clutch

Order / Family / Species	Authority	Code	Ntot	Nfem	SLfem min-max (mm)	MSL (mm)	SL1M (mm)	RL1M	LRP (month)	%MO	Noo	MDMO (mm)	Nfec	MF
Clupeiformes														
Engraulididae														
Anchovia surinamensis	(Bleeker 1866)	ASUR	329	31	76-104	178	76	0.43	8	100	27	0.2	36	25644
Lycengraulis batesii	(Günther 1868)	LYC1	14	3	222-222	264	222	0.84	2	100	1	0.2	1	90176
Pterengraulis atherinoides	(Linnaeus 1766)	PATH	400	83	171-245	245	147	0.60	6	99	24	0.4	33	96066
Characiformes														
Hemiodontidae														
Bivibranchia bimaculata	Vari 1985	BBIM	110	4	106-106	161	106	0.66	2	92	1	0.6	1	36
Hemiodopsis quadrimaculatus	(Pellegrin 1908)	HQUA	1776	220	126-166	200	92	0.46	12	67	17	0.8	21	8748
Hemiodus unimaculatus	(Bloch 1794)	HEUN	244	11	190-237	240	200	0.83	6	92	7	0.7	7	54736
Curimatidae														
Chilodus zunevei	Puyo 1945	CZUN	173	12	76-92	96	75	0.78	10	75	3	1.3	12	1560
Curimata cyprinoides	(Linnaeus 1766)	CCYP	1709	74	110-258	254	102	0.40	8	84	28	0.6	41	43325
Cyphocharax helleri	Steindachner 1910	CHEL	422	43	100-117	117	81	0.69	4	87	8	0.6	9	41768
Cyphocharax sp1		CYP1	773	54	81-134	134	81	0.60	4	97	12	0.5	14	24540
Cyphocharax spilurus	Günther 1864	CYSP	2896	103	89-133	152	76	0.50	6	89	33	0.5	36	22084
Anostomidae														
Anostomus brevior	Géry 1960	ABRE	254	23	76-105	123	71	0.58	4	44	4	0.9	4	307
Leporinus fasciatus	(Bloch 1794)	LFAS	107	8	134-382	382	149	0.39	8	94	4	0.9	7	78557
Leporinus friderici	(Bloch 1794)	LFRI	1862	63	296-396	405	160	0.40	8	77	11	0.9	18	159627
Leporinus gossei	Géry, Planquette & LeBail 1991	LGOS	292	28	166-230	253	151	0.60	6	89	6	1.2	6	37822
Leporinus granti	Eigenmann 1912	LGRA	598	60	132-198	245	132	0.54	6	87	12	1.5	15	11862
Leporinus pellegrini	Steindachner 1910	LPEL	24	2	164-164	169	164	0.97	2	64	1	0.9	1	13275
Erythrinidae														
Hoplerythrinus unitaeniatus	(Spix 1829)	HOUN	51	7	212-240	250	212	0.85	2	88	3	1.2	3	43748
Hoplias aimara	(Valenciennes 1840)	HAIM	643	14	470-740	830	460	0.55	12	91	5	2.1	9	72868
Hoplias malabaricus	(Bloch 1794)	HMAL	729	13	205-334	334	160	0.48	12	63	9	1.3	11	5813
Lebiasinidae														
Copella carsevennensis	(Regan 1912)	CCAR	893	5	26-39	53	26	0.49	10	91	5	0.6	7	335
Nannostomus beckfordi	Günther, 1872	NBEC	975	1	26-26	35	26	0.74	2	30	1	0.5	1	425
Pyrrhulina filamentosa	Val. in Cuv. 1846	PFIL	1446	12	50-76	95	55	0.58	8	78	9	0.7	10	2207

Appendix 1 (continued)

Order Family Species	Authority	Code	Ntot	Nfem	SLfem min-max (mm)	MSL (mm)	SL1M (mm)	RL1M	LRP (month)	%MO	Noo	MDMO (mm)	Nfec	MF
Characiformes (cont'd)														
Characidae														
Acestrorhynchus falcatus	(Bloch 1794)	AFAL	2761	114	140-265	285	151	0.53	12	84	16	0.8	29	16459
Acestrorhynchus microlepis	(Schomburgk 1841)	AMIC	1810	89	158-211	271	127	0.47	8	74	9	0.7	26	2475
Astyanax bimaculatus	(Linnaeus 1758)	ABIM	1845	108	92-173	173	83	0.48	6	88	18	0.7	28	25398
Astyanax cf *keithi*	Géry, Planquette & LeBail 1996	AKEI	3335	43	60-105	105	59	0.59	12	95	14	0.7	23	5845
Astyanax meunieri	Géry, Planquette & LeBail 1996	AMEU	751	17	66-96	115	66	0.57	6	86	5	0.7	6	4521
Bryconops sp. 1		BRY1	1274	73	103-123	143	95	0.66	12	83	8	0.7	14	1770
Bryconops sp. 2		BRY2	6469	235	91-122	130	80	0.62	12	75	17	0.7	38	3082
Bryconops sp. 3		BRY3	904	50	92-110	127	87	0.69	10	83	9	0.7	10	851
Characidium fasciadorsale	Fowler 1914	CFAS	1018	3	47-54	60	47	0.78	6	92	3	0.7	3	3986
Charax pauciradiatus	Günther 1864	CPAU	836	57	106-150	150	88	0.59	10	80	10	0.7	29	3605
Hemigrammus ocellifer	(Steindachner 1882)	HOCE	5793	2	29-38	63	34	0.54	6	69	2	0.5	10	1930
Hemigrammus unilineatus	(Gill 1858)	HUNI	436	6	31-42	42	31	0.74	6	88	3	0.7	4	883
Hyphessobrycon aff. *sovichtys*	Schultz 1944	HSOV	9047	4	25-30	42	27	0.64	6	63	4	0.6	8	882
Microcharacidium eleotrioides	(Géry 1960)	MELE	497	12	17-23	23	18	0.78	10	83	12	0.5	35	209
Moenkhausia chrysargyrea	(Günther 1864)	MCHR	2586	67	69-87	103	67	0.65	10	83	25	0.7	22	5785
Moenkhausia collettii	(Steindachner 1882)	MCOL	11568	39	36-54	86	36	0.42	8	77	24	0.6	21	1031
Moenkhausia georgiae	Géry 1966	MGEO	140	22	67-88	113	67	0.59	4	84	8	0.7	10	3440
Moenkhausia hemigrammoides	Géry 1966	MHEM	3193	5	30-44	50	39	0.78	6	64	5	0.6	10	1130
Moenkhausia oligolepis	(Günther 1864)	MOLI	7400	198	75-97	100	70	0.70	10	91	31	0.6	28	11130
Moenkhausia sp.		MOSP	64	3	70-92	110	70	0.64	4	77	2	0.6	1	3862
Moenkhausia surinamensis	Géry 1966	MSUR	866	30	62-107	116	91	0.78	4	95	6	0.7	7	8412
Myleus rhomboidalis	(Cuvier 1818)	MRHO	35	1	245-245	390	245	0.63	4	47	1	1.2	1	1512
Myleus ternetzi	(Norman 1929)	MTER	918	32	180-231	247	165	0.67	6	69	10	2.1	12	6528
Phenacogaster aff. *megalostictus*	Eigenmann1909	PMEG	2512	1	30-36	55	35	0.64	6	60	1	0.6	3	857
Piabucus dentatus	(Köhlreuter 1761)	PDEN	71	13	110-149	153	110	0.72	6	65	3	1.0	10	1614
Poptella brevispina	Reis 1989	PBRE	2828	258	69-100	126	68	0.54	12	69	29	0.7	40	2507
Pristella maxillaris	(Ulrey 1894)	PMAX	6797	11	25-32	32	25	0.78	10	70	11	0.7	10	785
Pseudopristella simulata	Géry 1960	PSIM	8944	11	30-37	39	30	0.77	6	81	11	0.7	9	1476
Triportheus rotundatus	(Schomburgk 1841)	TROT	3257	289	194-260	381	170	0.45	8	83	37	0.9	58	26018

Appendix 1 (continued)

Order Family Species	Authority	Code	Ntot	Nfem	SLfem min-max (mm)	MSL (mm)	SL1M (mm)	RL1M	LRP (month)	%MO	Noo	MDMO (mm)	Nfec	MF
Siluriformes														
Doradidae														
Auchenipterus nuchalis	(Spix 1829)	ANUC	6275	346	86-197	197	85	0.43	10	69	28	1.4	93	687
Doras carinatus	(Linnaeus 1766)	DCAR	99	12	160-300	300	120	0.40	4	92	1	0.9	5	20513
Parauchenipterus galeatus	(Linnaeus 1766)	PGAL	189	45	136-214	238	136	0.57	8	61	21	1.4	31	2036
Pseudauchenipterus nodosus	(Bloch 1794)	PNOD	13	9	112-163	210	112	0.53	2	97	4	1.9	6	1644
Tatia intermedia	(Steindachner 1876)	TINT	790	4	59-90	90	62	0.69	12	98	1	2.6	6	264
Pimelodidae														
Pimelodella cristata	(Müller & Troschel 1848)	PCRI	1140	20	112-132	161	83	0.52	10	95	4	0.7	6	5323
Pimelodus ornatus	(Kner 1857)	PORN	41	3	285-285	348	195	0.56	4	100	1	0.5	1	17205
Pseudopimelodus zungaro	(Humboldt 1833)	PZUN	5	1	113-113	225	113	0.50	2	100	1	1.7	1	770
Helogenidae														
Helogenes marmoratus	(Günther 1863)	HMAR	28	6	60-76	76	60	0.79	4	77	3	1.0	2	146
Cetopsidae														
Paracetopsis sp.		PASP	3	1	35-35	45	35	0.78	2	100	1	0.4	1	380
Trichomycteridae														
Trichomycterus guianense	(Eigenmann 1909)	TGUI	131	2	75-77	77	75	0.97	6	83	2	1.6	2	452
Callichthyidae														
Callichthys callichthys	Linnaeus 1758	CCAL	30	1	126-126	145	126	0.87	8	41	1	1.3	1	519
Hoplosternum thoracatum	(Val. in Cuv. & Val. 1840)	HTHO	45	2	110-110	130	110	0.85	8	85	1	1.5	1	1753
Loricariidae														
Ancistrus aff. *hoplogenys*	(Günther 1864)	AHOP	264	7	65-82	110	75	0.68	12	58	3	2.2	6	58
Hypostomus plecostomus	(Linnaeus 1758)	HPLE	145	17	104-196	196	97	0.49	8	64	10	4.8	24	185
Lasiancistrus sp.		LASI	694	1	92-92	160	92	0.58	2	71	1	2.6	1	280
Gymnotiformes														
Sternopygidae														
Eigenmannia virescens	(Valenciennes 1847)	EVIR	117	8	134-257	298	102	0.34	2	84	5	1.4	10	819
Sternopygus macrurus	(Bloch & Schneider 1801)	SMAC	194	8	144-373	373	146	0.39	12	67	5	2.3	10	697
Hypopomidae														
Brachyhypopomus beebei	(Schultz 1944)	BBEE	509	2	170-170	335	170	0.51	8	48	1	1.0	1	125
Hypopomus artedi	(Kaup 1856)	HART	192	5	217-280	320	132	0.41	10	97	2	1.2	5	681
Gymnotidae														
Gymnotus anguillaris	Hoedeman 1962	GANG	301	4	188-225	295	188	0.64	8	84	1	3.5	3	260
Gymnotus carapo	Linnaeus 1758	GCAR	464	2	300-300	380	300	0.79	6	72	1	1.9	1	144

Appendix 1 (continued)

Order Family Species	Authority	Code	Ntot	Nfem	SLfem min-max (mm)	MSL (mm)	SL1M (mm)	RL1M	LRP (month)	%MO	Noo	MDMO (mm)	Nfec	MF
Cyprinodontiformes														
<u>Aplocheilidae</u>														
Rivulus agilae	Hoedeman 1954	RAGI	598	2	20-28	47	24	0.51	4	51	2	1.1	13	65
Rivulus xiphidius	Huber 1979	RXIP	1322	6	16-23	28	18	0.64	10	54	6	1.3	45	13
Poeciliidae														
Poecilia parae	(Eigenmann 1894)	PPAR	337	1	15-15	21	15	0.71	12	33	1	2.0	2	3
Tomeurus gracilis	Eigenmann 1909	TGRA	52	2	20-25	28	21	0.75	6	46	2	1.9	4	3
Perciformes														
Nandidae														
Polycentrus schomburgkii	Müller & Troschel 1848	PSCH	201	2	56-56	70	56	0.80	10	27	1	0.6	1	104
Cichlidae														
Cichlasoma bimaculatum	(Linnaeus 1758)	CBIM	176	15	98-137	150	100	0.67	2	99	5	1.2	8	2066
Cleithracara maronii	(Steindachner 1882)	CMAR	369	6	57-72	90	57	0.63	8	96	5	1.0	10	413
Crenicichla saxatilis	(Linnaeus 1758)	CSAX	2406	17	135-178	222	140	0.63	8	87	4	1.3	6	676
Geophagus surinamensis	(Bloch 1791)	GSUR	25	1	111-135	156	135	0.87	2	63	1	2.2	4	324
Krobia guianensis	(Regan 1905)	KGUI	7122	3	80-100	125	83	0.66	12	63	3	1.4	9	206
Nannacara anomala	Regan 1905	NANO	1708	8	21-45	66	31	0.47	10	92	8	0.8	19	416
Satanoperca aff. *leucosticta*	(Müller & Troschel 1848)	SLEU	176	1	91-132	158	91	0.58	2	90	1	2.0	2	389
Eleotridae														
Eleotris amblyopsis	(Cope 1870)	EAMB	9303	21	22-33	80	22	0.28	10	100	21	0.2	10	4217