



## Body shape, diet and ontogenetic diet shifts in young fish of the Sinnamary River, French Guiana, South America

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A total of 1468 young fish representing 66 taxa from the Sinnamary River, French Guiana was classified by complete cluster analysis of mean relative body width and mean relative body height into four groups. These had anguilliform, disciform, flat or intermediate body shapes and belonged chiefly to Gymnotiformes, Perciformes, Siluriformes and Characiformes, respectively. Several of the taxa shifted from one to another body shape during ontogenesis. Seven diet groups were defined by complete cluster analysis. Among these, six groups were represented by carnivorous fish. The three most frequent groups had diets of (1) mainly insect larvae and small crustaceans, (2) insect larvae, and (3) predominantly terrestrial insects. The majority of the fish taxa showed ontogenetic diet shifts. Carnivorous fish usually switched from small-size prey, such as small crustaceans, to intermediate-size prey, such as insect larvae and/or to large-size prey, such as insects and/or fish. However, taxa differed in their capacities to switch from small prey to intermediate and/or to large prey. Taxa of different body shapes had significantly different diets. Disciform fish fed mainly on aquatic insect larvae and terrestrial insects but also, in small amounts, on small crustaceans. Most anguilliform taxa ate insect larvae. Individuals belonging to the depressiform or intermediate morphotype had varied diets ranging from plant debris and substratum to fish.

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Key words: neotropical fish; young stages; morphology; food regime; ontogenetic diet shifts; French Guiana.

### INTRODUCTION

Studying the early life stages of fish is of major importance for understanding the structure of fish communities, as events that occur during this crucial period determine year-class strength (Snyder, 1983; Balon, 1984; Houde, 1987; Grosberg & Levitan, 1992). Among the different factors influencing survival of young fish, the availability of suitable prey (Hartmann, 1983), feeding efficiency (locating and catching prey) and capabilities of avoiding predators (Webb & Weihs, 1986) are of central importance. These factors are linked strongly to body shape and morphological features that constrain swimming capabilities (Webb, 1984), and thus resource use (Gatz, 1979), or predator avoidance (Keast, 1978; Webb & Weihs, 1986; Bone *et al.*, 1996).

Tropical freshwater fish species exhibit a great diversity of biological and ecological attributes (Lowe-McConnell, 1987). In South America, only Winemiller (1991) has studied freshwater fish morphology while most studies on

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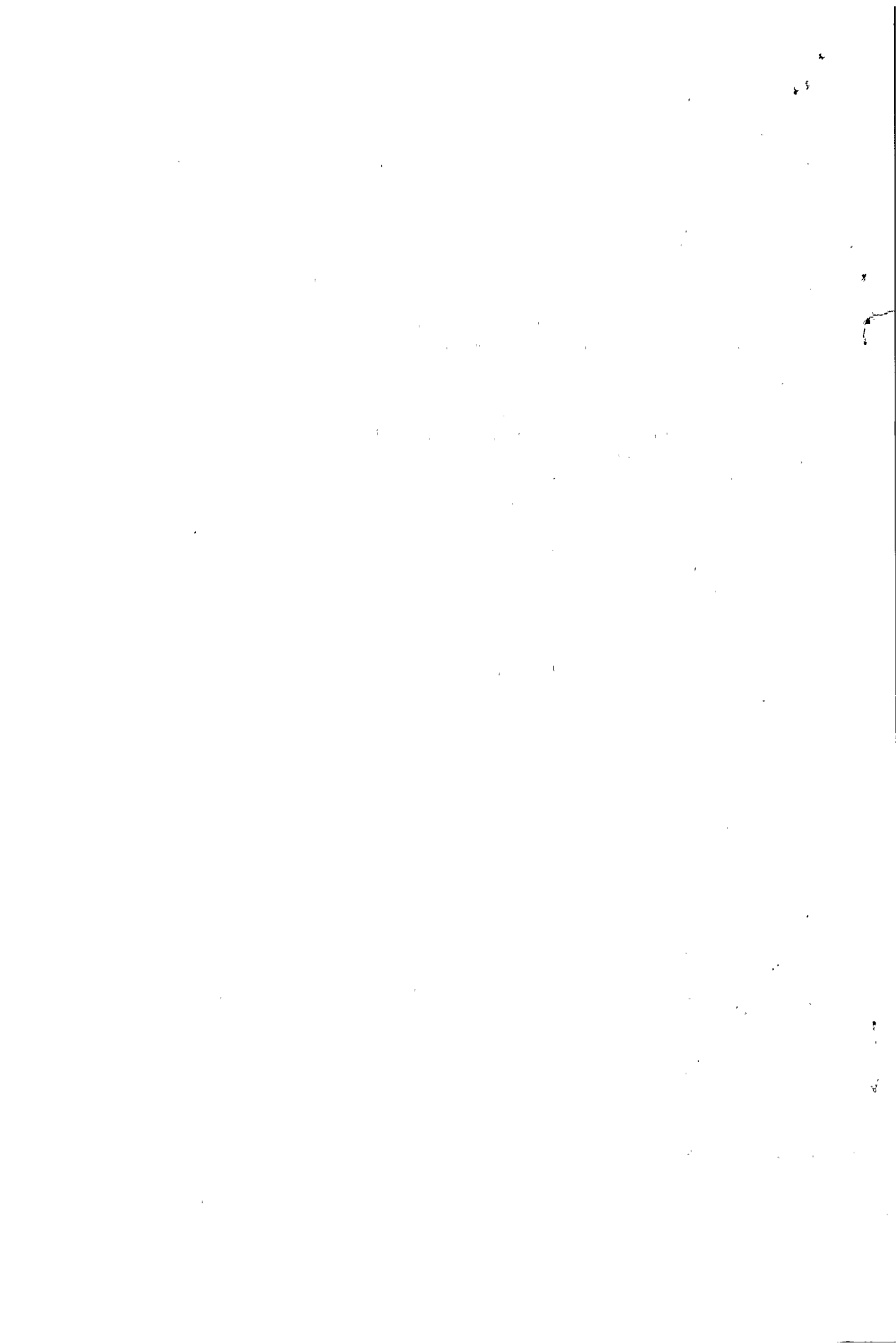
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fish diets focus only on the adult stages (Knöppel, 1970; Zaret & Rand, 1971; Lowe-McConnell, 1979; Goulding, 1980; Power, 1983, 1984; Carvalho, 1984; Flecker, 1992). Thus, very few detailed studies are available on the food habits of young tropical fish (piscivores: Winemiller, 1989; armoured catfish: Mol, 1995). Consequently, while ontogenetic diet shifts have been studied well in temperate freshwater fish (Keast, 1978, 1980; Hartmann, 1983; Ponton & Müller, 1988; Copp & Mann, 1993; Garner, 1996), few studies exist on ontogenetic diet shifts in neotropical freshwater fish (Angermeier & Karr, 1983; Winemiller, 1989; Mol, 1995). For French Guiana, the area of our study, the few data that have been published on fish diet focused only on a limited number of adult taxa (Boujard *et al.*, 1988, 1990; Rojas-Beltran, 1989; Horeau *et al.*, 1996).

Therefore, from young fish caught regularly in six tributaries of the Sinnamary River, the objectives of this paper were: (1) to identify groups homogeneous by their body form and to document changes in their shape during ontogeny; (2) to describe their food regimes and to detect ontogenetic diet shifts; and (3) to evaluate the relationships between body form and diet. Thereby, the present study is the first step of a larger project aiming to understand the relationships between habitat and life-history strategies of neotropical fish species during their early life. Beyond this fundamental aspect, the present investigations have an applied aspect concerning river regulation in the neotropics, as the Sinnamary River has been subjected to strong hydrological disturbance (Ponton & Copp, 1997) since the construction of the Petit Saut hydroelectric dam in 1994.

## MATERIALS AND METHODS

### SAMPLING

From January 1995 to October 1996, six tributaries of the Sinnamary River (Fig. 1) were sampled regularly with rotenone (for a complete description of the sampling method see Mérigoux *et al.*, 1998). For each of the 200 samples, all fish were preserved in 90% alcohol in the field and then transferred to 75% alcohol in the laboratory where they were processed later. All specimens were sorted and identified using keys for adults by Géry (1977); Rojas-Beltran (1984); Kullander & Nijssen (1989); Planquette *et al.* (1996), and keys for juveniles by Ponton (unpublished) and measured for standard length ( $L_s$ ) to the nearest 1 mm. Keys for juveniles are based on series of drawn specimens of variable size and on meristic parameters such as number of rays on the anal fin or position of fins. Juveniles were retained for analysis by separating them from adults according to the minimal size at first maturity observed for each species in the Sinnamary River (Ponton & Mérona, 1998). Depending on the number of individuals available, up to three size classes were separated for each taxon. Size limits were chosen in order to separate roughly early life stages (about 4 to 15–20 mm, depending on species) from young (about 15–20 to 30–50 mm) and older juveniles (about >30–50 mm). Within each of these size classes, three to 10 specimens (depending on their availability) were chosen randomly for analysis without any consideration of the time and place of sampling (Table I).

### BODY SHAPE AND DIET

For the description of body shape, three variables were measured on each individual: standard length, maximum height and maximum width. For smaller individuals measurements were taken on fish outlines drawn with the help of a camera lucida set up on a dissecting microscope. Calipers were used for larger individuals. With both techniques measurements were made to the nearest 0.1 mm.

Stomach contents (or contents of the anterior part of the digestive tract for stomachless species) were removed carefully under a dissecting microscope. Fish with an empty

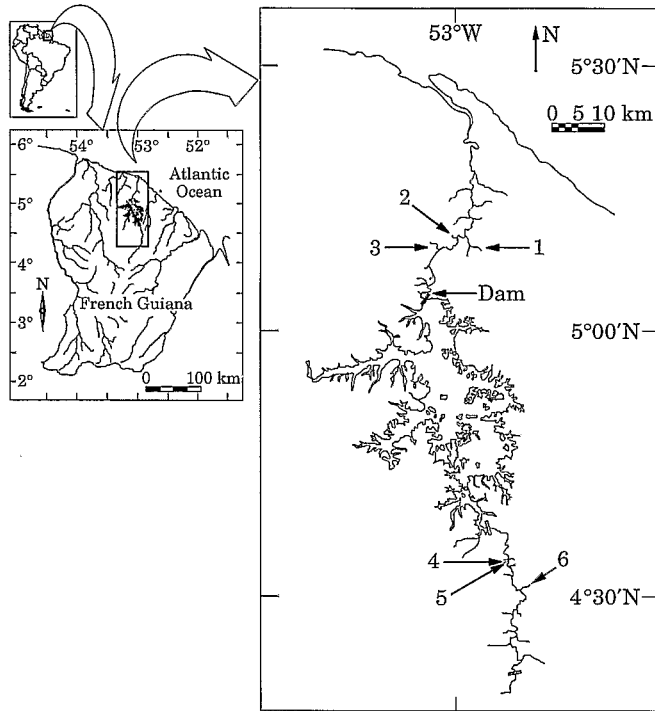


FIG. 1. Map of the Sinnamary River (French Guiana, South America) with the six tributaries sampled.

stomach were replaced randomly by other individuals, if sufficient material was available. Diet items were identified under a dissecting microscope (up to  $50\times$  magnification) or a microscope ( $100\text{--}400\times$  magnification) and assigned to 10 categories: fish (Fi), molluscs (snails) (Mo), large crustaceans (shrimps) (Cr), small crustaceans (Copepoda, Cladocera and Ostracoda) (sCr), terrestrial insects (TeIn), insect larvae (InLa), water mites (WaMi), rotifers (Ro), vegetative debris (VeDe), and substratum (Su). The relative volumes of each category were estimated following the method of Sheldon & Meffe (1993). For each fish, the most abundant food category was assigned rank 1, the second most abundant rank 2, and so on.

#### DATA ANALYSIS

Mean relative body width (ratio of maximum width to standard length) and mean relative body height of each size class were calculated. These ratios were treated with cluster analysis by the complete linkage method (Legendre & Legendre, 1979) using Euclidean distances.

For each individual, ranks of food categories were first converted into percentages by a modified version of the MacArthur broken stick model (Magurran, 1988). This model gives the expected percentage  $N_r$  of each food category when eaten randomly and simultaneously by a fish by:

$$N_r = \frac{100}{S} \sum_{n=r}^S \frac{1}{n}$$

with  $S$ =total number of food categories, and  $r$ =rank number of food category [ $r \in \{1, \dots, S\}$ ].

Thus, a fish feeding on two food categories would have  $100/2(1/1 + 1/2) = 75$  assigned to category ranked 1 and  $100/2(1/2) = 25$  to category ranked 2. Identically, an individual

TABLE I. Body shape and diet of fish taxa for different ontogenetical stages, with species authority and occurrences of switches between morphological or diet groups

Species	Authority	Early life stages				Young juveniles				Old juveniles				Body shape switch	Diet switch	
		$L_s$ (mm)	Body shape	Diet	$n$	$L_s$ (mm)	Body shape	Diet	$n$	$L_s$ (mm)	Body shape	Diet	$n$			
<b>Characiformes</b>																
<b>Hemiodontidae</b>																
<i>Hemiodopsis quadrimaculatus</i>	(Pellegriin, 1908)	10	9-14	Ang	sCr-InLa	10	15-24	Int	InLa							
<i>Parodon guyanensis</i>	Géry, 1959	10	7-16	Int	sCr-InLa											
<b>Curimatidae</b>																
<i>Chilodus zunevei</i>	Puyo, 1945	10	9-13	Int	InLa-sCr	10	14-30	Int	InLa-sCr	7	31-65	Int	InLa-sCr	No	No	No
Unidentified young Curimatidae		10	5-14	Int	InLa-sCr	10	15-30	Int	VeDe-Su	10	31-75	Int	VeDe-Su	No	Yes	Yes
<b>Anostomidae</b>																
<i>Leporinus despaxi</i>	Puyo, 1943	10	8-13	Int	sCr-InLa	10	14-45	Int	InLa-sCr	10	30-90	Int	VeDe-Su	—	—	—
Unidentified young Leporinus		10	7-16	Int	InLa-sCr	10	17-50	Int	InLa-sCr							
<b>Erythrinidae</b>																
<i>Erythrinus erythrinus</i>	(Schneider, 1801)	10	4-20	Int	InLa-sCr	10	21-50	Int	InLa-Fi							
Unidentified young <i>Hoplias</i>	(Valenciennes, 1840)	10	21-50	Int	InLa-Fi											
<i>Hoplias aimara</i>	(Bloch, 1794)	10	21-50	Int	InLa-Fi	10	51-160	Int	InLa-Fi	10	51-160	Int	InLa-Fi	No	Yes	Yes
<b>Lebiasnidae</b>																
<i>Copella carsevensensis</i>	(Regan, 1912)	10	6-12	Int	sCr-InLa	10	13-19	Int	InLa-sCr	10	20-24	Int	InLa	No	Yes	Yes
<i>Nannostomus beckfordi</i>	Günther, 1872	10	13-20	Int	InLa	10	21-25	Int	InLa	10	21-25	Int	InLa	—	—	—
<i>Pyrhulina filamentosa</i>	Val. in. Cuv., 1846	10	6-14	Int	InLa-sCr	10	15-30	Int	InLa-sCr	10	31-49	Int	Teln	No	Yes	Yes
<b>Gasteropelecidae</b>																
<i>Gasteropelecus sternicla</i>	(Linnaeus, 1758)	10	6-11	Int	Teln	10	12-15	Int	Teln							
<b>Characidae</b>																
<i>Asyanax bimaculatus</i>	(Linnaeus, 1758)	10	9-14	Int	InLa-sCr	10	15-30	Int	InLa-sCr							
<i>Asyanax cf. keithi</i>	Géry, Pianquette & LeBail, 1996	10	6-11	Int	sCr-InLa	10	12-25	Int	InLa-sCr	10	26-55	Disc	Teln	Yes	Yes	No

TABLE I. Continued

Species	Authority	Early life stages			Young juveniles			Old juveniles			Body shape switch	Diet switch			
		$L_s$ (mm)	Body shape	Diet	$n$	$L_s$ (mm)	Body shape	Diet	$n$	$L_s$ (mm)			Body shape	Diet	
Characidae (cont'd)															
<i>Bryconops</i> spp		10	8-15	Int	InLa	10	16-35	Int	Teln	10	36-80	Int	Teln	No	Yes
<i>Characidium fasciadorale</i>	Fowler, 1914	10	7-14	Int	InLa-sCr	10	15-30	Int	InLa	10	31-45	Int	InLa	No	Yes
<i>Charax pauciradiatus</i>	Günther, 1864	10	6-13	Int	sCr-InLa										
<i>Hemigrammus ocellifer</i>	(Steindachner, 1882)	10	7-12	Int	sCr-InLa	10	15-19	Int	InLa-sCr	10	20-25	Int	Teln	No	Yes
<i>Hemigrammus unilineatus</i>	(Gill, 1858)	10	9-12	Int	sCr-InLa	10	13-19	Int	InLa-sCr	10	20-29	Int	Teln	No	Yes
<i>Hypheobrycon</i> aff. <i>sovichthys</i>	Schultz, 1944	7	7-10	Int	InLa-sCr	10	11-15	Int	InLa-sCr	10	16-20	Int	InLa-sCr	No	No
<i>Melanocharacidium</i> sp.		10	5-13	Int	InLa-sCr										
<i>Microcharacidium electroides</i>	(Géry, 1960)	10	5-9	Int	InLa-sCr	10	10-14	Int	InLa						
<i>Moenkhausia chrysargyrea</i>	(Günther, 1864)	10	7-14	Int	InLa-sCr	10	15-30	Int	Teln	10	31-45	Disc	Teln	Yes	Yes
<i>Moenkhausia colletii</i>	(Steindachner, 1882)	10	5-12	Int	sCr-InLa	10	13-25	Int	InLa-sCr	10	26-35	Int	Teln	No	Yes
<i>Moenkhausia georgiae</i>	Géry, 1966	10	7-13	Int	sCr-InLa										
<i>Moenkhausia hemigrammoides</i>	Géry, 1966	10	7-13	Int	InLa-sCr	10	14-25	Int	Teln	10	26-35	Disc	Teln	Yes	Yes
<i>Moenkhausia oligolepis</i>	(Günther, 1864)	8	6-13	Int	InLa-sCr	10	14-30	Disc	Teln	10	31-65	Disc	Teln	Yes	Yes
<i>Moenkhausia surinamensis</i>	Géry, 1966					10	14-30	Int	Teln	10	31-60	Disc	Teln		
<i>Phenacogaster</i> aff. <i>megalostictus</i>	Eigenmann, 1909	10	5-12	Int	InLa-sCr	10	13-19	Int	InLa	10	20-29	Int	InLa	No	Yes
<i>Piabucus dentatus</i>	(Köhreuter, 1761)	10	9-14	Int	InLa-sCr	10	15-40	Int	Teln						
<i>Poptella brevispina</i>	(Reis, 1989)	10	5-13	Int	InLa-sCr	10	14-30	Disc	Teln						
<i>Pristella maxillaris</i>	(Ulrey, 1894)	10	7-10	Int	sCr-InLa	10	11-15	Int	InLa-sCr	10	16-19	Int	InLa-sCr	No	Yes
<i>Pseudopristella simulata</i>	Géry, 1960	10	6-11	Int	sCr-InLa	10	12-17	Int	InLa-sCr	9	18-22	Int	sCr-InLa	No	?
Unidentif. young <i>Acestrotrichynchus</i>		10	9-15	Int	InLa-sCr	10	16-40	Int	InLa-Fi	10	41-120	Int	Fi	No	Yes
Siluriformes															
Auchenipteridae															
<i>Tatia intermedia</i>	(Steindachner, 1876)	10	7-14	Int	Teln	10	14-25	Int	Teln	7	26-60	Int	Teln	No	No



TABLE I. *Continued*

Species	Authority	Early life stages			Young juveniles			Old juveniles			Body shape switch	Diet switch	
		<i>n</i>	<i>L<sub>s</sub></i> (mm)	Body shape	Diet	<i>n</i>	<i>L<sub>s</sub></i> (mm)	Body shape	Diet	<i>n</i>			<i>L<sub>s</sub></i> (mm)
Gymnotiformes (cont'd)													
Gymnotidae													
Unidentified young <i>Gymnotus</i>		10	9-19	Int	InLa								
<i>Gymnotus anguillar</i>	Hoedeman, 1962	10	20-50	Ang	InLa	10	51-185	Ang	InLa	10	51-185	Ang	InLa
<i>Gymnotus carapo</i>	Linnaeus, 1758	10	20-50	Ang	InLa	10	51-185	Ang	InLa-sCr	10	51-185	Ang	InLa-sCr
Cyprinodontiformes													
Aplocheilidae													
<i>Rivulus agilis</i>	Hoedeman, 1954	10	11-15	Int	InLa-sCr								
<i>Rivulus xiphidius</i>	Huber, 1979	10	5-10	Int	sCr-InLa	10	11-15	Int	InLa				
Poeciliidae													
<i>Poecilia parae</i>	(Eigenmann, 1894)	10	6-12	Int	InLa-sCr								
Synbranchiformes													
Synbranchidae													
<i>Synbranchus marmoratus</i>	Bloch, 1795	9	32-59	Ang	sCr-InLa	7	60-100	Ang	InLa	9	101-200	Ang	InLa
Perciformes													
Nandidae													
<i>Polycentrus schomburgkii</i>	Müller & Troschel, 1848	10	14-19	Disc	InLa-sCr	10	20-30	Disc	InLa-sCr				
Cichlidae													
<i>Cichlasoma bimaculatum</i>	(Linnaeus, 1758)	10	10-13	Disc	InLa-sCr	10	14-34	Disc	InLa	10	30-70	Disc	InLa-sCr
<i>Cleithracara maronii</i>	(Steindachner, 1882)	10	10-13	Disc	InLa-sCr	10	14-34	Disc	InLa	10	35-52	Disc	InLa-sCr
<i>Crenicichla saxatilis</i>	(Linnaeus, 1758)	10	8-20	Int	InLa-sCr	10	21-50	Int	InLa-sCr	10	51-140	Int	InLa-Fi
<i>Kribia guianensis</i>	(Regan, 1905)	10	4-13	Disc	InLa-sCr	10	14-29	Disc	InLa	10	30-75	Disc	InLa-sCr
<i>Nannacara anomala</i>	Regan, 1905	10	6-12	Disc	InLa	10	13-19	Disc	InLa	10	20-29	Disc	InLa
<i>Satanoperca aff. leucosticta</i>	(Müller & Troschel, 1848)	10	14-30	Int	sCr-InLa	10	31-70	Int	sCr-InLa				
Eleotridae													
<i>Eleotris amblyopsis</i>	(Cope, 1870)	10	10-15	Int	sCr-InLa	10	16-20	Int	InLa	10	21-25	Int	sCr-InLa

*n*, Number of individuals; *L<sub>s</sub>*, range of standard length; Disc, disciform body; Ang, anguilliform; Dep, depressiform; Int, intermediate body; Fi, fish; Tel; Terrestrial insects; InLa, insect larvae; sCr, small crustacean; VeDe, vegetative debris; Su, substratum. Body shape and diet shifts are presented only for species with data for the three stages.



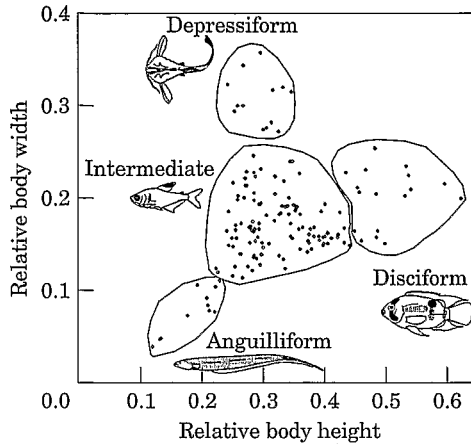


FIG. 2. Relative body width *v.* relative body height, indicating the four groups of body shapes resulting from complete cluster analysis of the 152 size classes of 66 taxa captured in the Sinnamary River (see Table I for the faunistic composition of the different groups).

feeding on three different categories would have 1100/18, 500/18, and 200/18 assigned for categories ranked 1, 2, and 3 respectively. Mean  $N_p$  values calculated for all the individuals of each size class were also treated with cluster analysis by the complete linkage method (Legendre & Legendre, 1979) using Euclidean distances. In order to provide a simpler index of prey use, the resulting diet groups were described by the prey items averaging >70% within the individuals of the group. Differences in diet among groups of fish with different body shapes were then tested by  $R^*C$  test of independence using  $G$ -test (Sokal & Rohlf, 1995).

## RESULTS

### MORPHOMETRY

The total of 1468 fish from 66 taxa grouped in 152 size classes (Table I) was separated by complete cluster analysis on mean relative body width and mean relative body height into four groups of different body shapes (Fig. 2). Disciform fish (*sensu* Holčík *et al.*, 1989) were characterized by high relative body height and medium relative body width values. This group included all stages of the Perciformes *Cleithracara maronii* (Steindachner), *Krobia guianensis* (Regan) and *Nannacara anomala* Regan, and juveniles of the Perciformes *Polycentrus schomburgki* Müller & Troschel and *Cichlasoma bimaculatum* L., and juveniles of the Characidae *Astyanax cf. keithi* Géry, Planquette & le Bail, *Moenkhausia chrysargyrea* (Günther), *M. hemigrammoides* Géry, *M. oligolepis* (Günther), *M. surinamensis* Géry and *Poptella brevispina* (Reis) (Table I). Anguilliform fish (*sensu* Holčík *et al.*, 1989) presented low relative body height and low relative body width values and included early life stages of *Hemiodopsis quadrimaculatus* (Pellegrin), juveniles of all Gymnotiformes, and all stages of *Synbranchus marmoratus* Bloch. Depressiform taxa (*sensu* Holčík *et al.*, 1989) were characterized by high relative body width and intermediate relative body height values. All stages of the Siluriformes *Pseudopimelodus raninus* (Valenciennes), *Bunocephalus coracoideus* Cope, *Callichthys callichthys* L.,

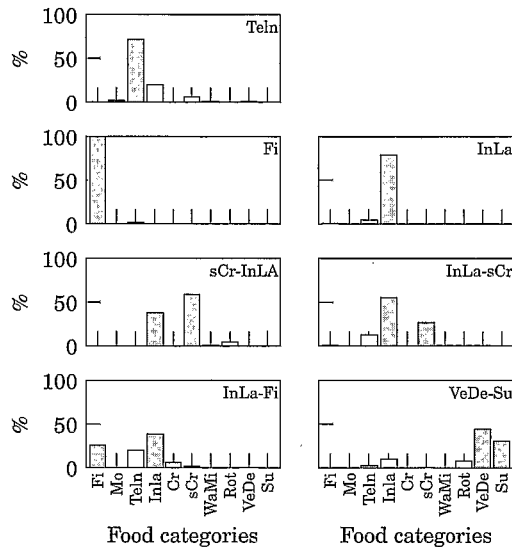


FIG. 3. Food spectra of each of the seven diet groups resulting from complete cluster analysis of Euclidean distances computed from percentages of food categories of the 152 size classes of 66 taxa captured in the Sinnamary River. Diet groups were defined by the categories representing  $\geq 70\%$  of the food items: Fi, fish; TeIn, terrestrial insects; InLa, insect larvae; sCr, small crustacean; VeDe, plant debris; Su, substratum (see Table I for faunistic composition of diet groups).

*Hoplosternum thoracatum* (Valenciennes) and *Ancistrus* aff. *hoplogenyis* (Günther) belonged to this group. The remaining taxa, mainly Characiformes, presented intermediate body shapes.

Only 11 taxa presented a body shape that switched from one group to another during their ontogeny (Table I). Most of these shifts were from an intermediate body shape during early life to an anguilliform shape (*Sternopygus macrurus* (Bloch & Schneider), *Brachyhyppopomus beebel* (Schultz), *Hypopomus artedi* (Kaup), *Gymnotus anguillaris* Hoedeman and *G. carapo* L., or a disciform shape (*A. cf. keithi*, *M. chrysargyrea*, *M. hemigrammoides* and *M. surinamensis*) during the juvenile period.

#### DIET

Among the 1468 full fish stomachs analysed (Table I), seven groups of diet were obtained by complete cluster analysis (Fig. 3). All these groups were defined by one or two main sources of food: terrestrial insects (TeIn, 16.5% of the groups; Table I, Fig. 3), fish (Fi, 0.7% of the groups), mostly small crustaceans and also insect larvae (sCr-InLa, 12.5%), mostly insect larvae and also fishes (InLa-Fi, 5.9%), insect larvae only (InLa, 23.0%), and mostly insect larvae and also small crustaceans (InLa-sCr, 36.8%) for the carnivorous fish and mostly plant debris and also substratum (VeDe-Su, 4.6%) for the other fish.

Most taxa showed ontogenetic diet shifts (Table I). Carnivorous fish switched usually from small-size prey such as small crustaceans to intermediate-size prey such as insect larvae and/or to large-size prey such as insects and/or fish (Table I). However, taxa differed in their capacities to switch from small prey to intermediate and/or to large prey. Some fish even started feeding directly on

TABLE II. Relative dietary abundance (in %) for the different fish body shapes

Body shape	n	Diet groups						
		VeDe-Su	sCr-InLa	InLa-sCr	InLa	TeIn	InLa-Fi	Fi
Disciform	19	0.0	0.0	36.8	26.4	36.8	0.0	0.0
Aguilliform	13	0.0	7.7	15.4	76.9	0.0	0.0	0.0
Depressiform	13	23.1	15.4	7.6	15.4	23.1	15.4	0.0
Intermediate	107	3.7	14.0	42.1	16.8	15.9	6.6	0.9

n, Number of size groups of the 66 species; Fi, fish; TeIn, terrestrial insects; InLa, insect larvae; sCr, small crustacean; VeDe, vegetative debris; Su, substratum.

insect larvae and switched to insects and/or fish (Table I). Only seven taxa belonged to the same diet groups from early life stages to older juveniles: *Chilodus zunevei* Puyo and *Hypphessobrycon* sp. aff. *sovichthys* Schultz fed mainly on insect larvae and also on small crustaceans, *Tatia intermedia* (Steindachner) fed mainly on terrestrial insects, *Ancistrus* aff. *hoplogenyis* on plant debris and substratum, *Trichomycterus guianense* (Eigenmann), *G. anguillar* and *N. anomala* on insect larvae.

#### RELATIONSHIPS BETWEEN BODY SHAPE AND DIET

Taxa of different body shapes had significantly different diets (Table II; G-value=46.131, d.f.=18,  $P<0.001$ ). Disciform fish fed mainly on aquatic insect larvae and terrestrial insects but also, in small amounts, on small crustaceans. Most anguilliform taxa specialized on insect larvae. Individuals belonging to the depressiform or intermediate morphotype presented varied diets ranging from plant debris and substratum, to fish.

#### DISCUSSION

In a study based on 17 temperate fish species, Douglas & Matthews (1992) argued that interrelationships between body shape, diet, and taxonomic status are predictable. They demonstrated that often studies on eco-morphology reflect only taxonomic or phylogenetic aspects. Phylogenetic systematics is increasingly used to interpret morphological and ecological data in an evolutionary context (Westneat, 1995). Unfortunately, the systematic relationships between neotropical fish species of entire families are still largely unknown (see Montoya-Burgos *et al.*, 1997, for an example in Loricariidae). However, the importance of the systematic position of a fish species for the determination of its body shape is suggested in our study: 69.2% of taxa with an anguilliform body belonged to Gymnotiformes, 63.2% of the taxa with a disciform body were Perciformes, all flat fishes were Siluriformes and 71% of the taxa with an intermediate body shape belonged to Characiformes.

Independent of their systematic position, most of the young fish inhabiting the tributaries of the Sinnamary River feed mainly on small crustaceans, insect larvae, and terrestrial insects. For most fish taxa, the importance of small crustaceans in the diet decreased with increasing age and size and small

crustaceans were replaced progressively by terrestrial insects. These results correspond well to those of Horeau *et al.* (1996), who highlighted the importance of allochthonous inputs in the diets of several adult fish of the Sinnamary River. In rivers, flooding cycles modify on a regular basis food resource availability and thus feeding specializations of fish tend to appear poorly (Winemiller, 1990). However, two types of specialization were detected for early stages in Guianese fish: piscivory and use of plant debris and substratum (Table I). Indeed, several young taxa presented piscivorous feeding habits at a very small size: young of *Acestrorhynchus* spp. were able to ingest fish occasionally, and juveniles of *Hoplias aimara* (Valenciennes) and *H. malabaricus* (Bloch) preyed upon fish as soon as they had reached >20 mm (Table I). Thus, the young stages of these species have diet spectra identical to those of the adults (Planquette *et al.*, 1996). Piscivorous tendency during early life stages was also noted for other species known to eat fish later in their lives: *Pimelodella cristata* (Müller & Troschel) and *P. gracilis* (Valenciennes) (Planquette *et al.*, 1996), *Rhamdia* sp. and *Crenicichla saxatilis* (L.) (Knöppel, 1970; Angermeier & Karr, 1983; Winemiller, 1989), and *Synbranchus marmoratus* (Winemiller, 1989). The young of Curimatidae, *Leporinus despaxi* Puyo, *L.* spp. and *Ancistrus* aff. *hoplogenyis* ate mainly plant debris and substratum. The adults of several species of Curimatidae such as *Cyphocharax spilurus*, *C. helleri*, *Curimata cyprinoides* (Planquette *et al.*, 1996), *C. pristigaster* (Carvalho, 1984) are known to be detritivores and Angermeier & Karr (1983) found that adults of species of *Ancistrus* fed exclusively on algae in Panamanian streams. Similar to what has been demonstrated for the adults (Power, 1983, 1984), young *A.* aff. *hoplogenyis* might have ingested large amounts of substratum in order to ingest the algae it contains.

Wainwright & Richard (1995) argued that all fish species change prey use during ontogeny. In our study, the majority of the fish taxa showed ontogenetic diet shifts and young fish were usually able to feed on larger prey at a larger size (Table I). However, taxa differed in their capacities to switch from small prey to intermediate and/or to large prey. So far, evidence for diet changes with age for neotropical freshwater fishes are scarce in the scientific literature. Mol (1995) observed for the two armoured catfish *Callichthys callichthys* and *Hoplosternum thoracatum*, a diet shift from small crustaceans and rotifers to a mixed diet dominated by insect larvae when individuals reached 8.4 mm, a pattern that agrees well with our results. Identically to Winemiller's (1989) results in the Venezuelan Llanos, Guianese *G. carapo* of <50 mm preyed mainly upon insect larvae and switched later to a food regime composed of insect larvae and terrestrial insects. Dietary shifts are induced usually by changes with growth of morphological features correlated to body size (Wainwright & Richard, 1995). The enlargement of the mouth gape (Keast, 1978, 1985; Hartman, 1983; Dabrowski & Bardega, 1984), the development of fins, muscles and swimbladder (Bone *et al.*, 1996) and body shape (Keast, 1978) influence prey selection and catch efficiency.

With data for 66 of the 126 freshwater and 18 euryhaline fish taxa recorded in the Sinnamary River (Lauzanne *et al.*, 1995), our work forms the largest database ever gathered and published for body shape and diet of young neotropical Guianese fish. The large percentage of young fish with intermediate body shapes stresses the need for complementary morphological variables as

indicators of ecological fish groups. As the most useful morphological variables are those that affect behavioural performances (Wainwright, 1996), further investigations should relate size and position of fins, mouth gape, development of dentition, development of the digestive system, among other variables, to feeding habits during ontogeny. Moreover, future studies should also define if young fish exhibit seasonal variability in their diets as shown for adult fish in other freshwater tropical systems (Lowe-McConnell, 1979; Zaret & Rand, 1971; Goulding, 1980; Boujard *et al.*, 1990). Comparisons of seasonal variability of diets between sites situated downstream of the dam and upstream of the reservoir would allow evaluation of the impacts of flow disturbances on food resource use by fish during their early life. Beyond these topics, body shape and diet described in this work will be used together with other biological traits related to reproduction to define aspects of life history strategies of fishes in the Sinnamary River. The understanding of the relationships between these life history strategies and environmental parameters will enable us in future to link general community characteristics to the environment (Statzner *et al.*, 1994) beyond the systematic details of the different fish taxa. This approach should provide insights into the fundamental factors structuring fish communities as well as the broader applications of the impacts of hydroelectric dams on neotropical fish assemblages.

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### References

- Angermeier, P. L. & Karr, J. R. (1983). Fish communities along environmental gradients in a system of tropical streams. *Environmental Biology of Fishes* **9**, 116–135.
- Balon, E. K. (1984). Reflections on some decisive events in the early life of fishes. *Transactions of the American Fisheries Society* **113**, 178–185.
- Bone, Q., Marshall, N. B. & Blaxter, J. H. S. (1996). *Biology of Fishes*. London: Chapman & Hall.
- Boujard, T., Le Bail, P. Y. & Planquette, P. (1988). Données biologiques sur quelques espèces continentales de Guyane Française d'intérêt piscicole. *Aquatic Living Resources* **1**, 107–113.
- Boujard, T., Sabatier, D., Rojas-Beltran, R., Prevost, M. F. & Renno, J. F. (1990). The food habits of three allochthonous feeding Characoids in French Guiana. *Revue d'Ecologie (Terre Vie)* **45**, 247–258.
- Carvalho, F. M. (1984). Aspectos biológicos e ecofisiológicos de *Curimata (Potamorhina) pristigaster*, um Characoidei neotropical. *Amazoniana* **7**, 525–539.
- Copp, G. H. & Mann, R. H. K. (1993). Comparative growth and diet of tench *Tinca tinca* (L.) larvae and juveniles from river floodplain biotopes in France and England. *Ecology of Freshwater Fish* **2**, 58–66.
- Dabrowski, K. & Bardega, R. (1984). Mouth size and predicted food size preferences of larvae of three cyprinid fish species. *Aquaculture* **40**, 41–46.
- Douglas, M. E. & Matthews, W. J. (1992). Does morphology predict ecology? Hypothesis testing within freshwater stream fish assemblages. *Oikos* **65**, 213–224.
- Flecker, A. S. (1992). Fish trophic guilds and the structure of a tropical stream: weak vs. strong indirect effects. *Ecology* **73**, 927–940.

- Garner, P. (1996). Microhabitat use and diet of 0+ cyprinid fishes in a lentic, regulated reach of the River Great Ouse, England. *Journal of Fish Biology* **48**, 367–382.
- Gatz, A. J. J. (1979). Community organization in fishes as indicated by morphological features. *Ecology* **60**, 711–718.
- Géry, J. (1977). *Characoids of the World*. Neptune City: T. F. H. Publications.
- Grosberg, R. K. & Levitan, D. R. (1992). For adults only? Supply-side ecology and the history of larval biology. *Trends in Ecology and Evolution* **7**, 130–133.
- Goulding, M. (1980). *The Fishes and the Forest: Explorations in Amazonian Natural History*. Berkeley: University of California Press.
- Hartmann, J. (1983). Two feeding strategies of young fishes. *Archiv für Hydrobiologie* **96**, 496–509.
- Holčík, J., Banarescu, P. & Evans, D. (1989). A general introduction to fishes. In *The Freshwater Fishes of Europe* (Holčík, J., ed.), pp. 18–147. Wiesbaden, Germany: AULA Verlag.
- Horeau, V., Cerdan, P., Champeau, A. & Richard, S. (1996). Importance des apports exogènes dans le régime alimentaire de quelques poissons de 'criques' du bassin versant du fleuve Sinnamary (Guyane Française). *Revue d'Ecologie (Terre Vie)* **51**, 29–41.
- Houde, E. D. (1987). Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium* **2**, 17–29.
- Keast, A. (1978). Trophic and spatial interrelationships in the fish species of Ontario temperate lake. *Environmental Biology of Fishes* **3**, 7–31.
- Keast, A. (1980). Food and feeding relationships of young fish in the first weeks after the beginning of exogenous feeding in Lake Opinicon, Ontario. *Environmental Biology of Fishes* **5**, 305–314.
- Keast, A. (1985). Development of dietary specializations in a summer community of juvenile fishes. *Environmental Biology of Fishes* **13**, 211–224.
- Knöppel, H. A. (1970). Food of central Amazonian fishes, contribution to the nutrient-ecology of Amazonian rain-forest-streams. *Amazoniana* **2**, 257–352.
- Kullander, S. O. & Nijssen, H. (1989). *The Cichlids of Surinam*. Leiden: E. J. Brill.
- Lauzanne, L., Tito de Morais, L., Ponton, D., Mérona, B. de, Bron, J. C., Raffray, J., Tarcy, M., Mallet, A., Brehm, N. & Besançon, A. (1995). *Structure et biologie des peuplements ichthyques du fleuve Sinnamary en Guyane Française*. Cayenne: ORSTOM, Lab. d'Hydrobiologie.
- Legendre, L. & Legendre, P. (1979). *Ecologie Numérique. La Structure des Données Écologiques*. Paris: Masson: Collection d'écologie.
- Lowe-McConnell, R. H. (1979). Ecological aspects of seasonality in fishes of tropical waters. *Symposium of the Zoological Society of London* **44**, 219–241.
- Lowe-McConnell, R. H. (1987). *Ecological Studies in Tropical Communities*. Cambridge: Cambridge University Press.
- Magurran, A. E. (1988). *Ecological Diversity and its Measurement*. Cambridge: Cambridge University Press.
- Mérigoux, S., Ponton, D. & De Merona, B. (1998). Fish richness and species-habitat relationships in two coastal streams of French Guiana, South America. *Environmental Biology of Fishes* **51**, 25–39.
- Mol, J. H. (1995). Ontogenetic diet shifts and diet overlap among three closely related neotropical armoured catfishes. *Journal of Fish Biology* **47**, 788–807.
- Montoya-Burgos, J. I., Müller, S., Weber, C. & Pawlowski, J. (1997). Phylogenetic relationships between Hypostominae and Ancistrinae (Siluroidei: Loricariidae): first results from mitochondrial 12S and 16S rRNA gene sequences. *Revue Suisse de Zoologie* **104**, 185–198.
- Planquette, P., Keith, P. & LeBail, P. Y. (1996). *Atlas des poissons d'eau douce de Guyane*. (tome 1). Collection du Patrimoine Naturel, vol. 22. IEGB-M.N.H.N. Paris: INRA.
- Ponton, D. & Copp, G. H. (1997). Early dry-season assemblage structure and habitat use of young fish in tributaries of the River Sinnamary (French Guiana, South

- America) before and after hydrodam operations. *Environmental Biology of Fishes*, in press.
- Ponton, D. & Müller, R. (1988). Distribution and food of larval and juvenile *Coregonus* sp. in Lake Sarnen, Switzerland. *Finnish Fisheries Research* **9**, 117–125.
- Ponton, D. & Mérona, B. de (1998). Fish life-history tactics in a neotropical river with a highly stochastic hydrological regime: the Sinnamary river, French Guiana, South America. *Polskie Archiwum Hydrobiologii*, in press.
- Power, M. E. (1983). Grazing responses of tropical freshwater fishes to different scales of variation in their food. *Environmental Biology of Fishes* **9**, 103–115.
- Power, M. E. (1984). Depth distributions of armored catfish: predator-induced resource avoidance? *Ecology* **65**, 523–528.
- Rojas-Beltran, R. (1984). Clé de détermination des poissons continentaux et côtiers de Guyane. *Bulletin de Liaison Groupe de Recherche Guyane* **7**, 97310 Kourou, French Guiana: INRA.
- Rojas-Beltran, R. (1989). Quelques aspects de l'écologie alimentaire de trois machoirans (Teleostei, Siluriformes, Ariidae) de la Guyane. *Cybium* **13**, 181–187.
- Sheldon, A. L. & Meffe, G. K. (1993). Multivariate analysis of feeding relationships of fishes in blackwater streams. *Environmental Biology of Fishes* **37**, 161–171.
- Snyder, D. E. (1983). Fish eggs and larvae. In *Fisheries Techniques* (Nielsen, L. A. & Johnson, D. L., eds), pp. 165–197. Bethesda, MD: The American Fisheries Society.
- Sokal, R. R. & Rohlf, F. J. (1995). *Biometry*, 3rd edn. New York: W. H. Freeman.
- Statzner, B., Resh, V. H. & Doledec, S. (1994). Ecology of the upper Rhône River: a test of habitat templet theories. *Freshwater Biology* **31** (Special Issue), 253–556.
- Wainwright, P. C. (1996). Ecological explanation through functional morphology: the feeding biology of sunfishes. *Ecology* **77**, 1336–1343.
- Wainwright, P. C. & Richard, B. A. (1995). Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes* **44**, 97–113.
- Webb, P. W. (1984). Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist* **24**, 107–120.
- Webb, P. W. & Weihs, D. (1986). Functional locomotor morphology of early life history stages of fishes. *Transactions of the American Fisheries Society* **115**, 115–127.
- Westneat, M. W. (1995). Phylogenetic systematics and biomechanics in ecomorphology. *Environmental Biology of Fishes* **44**, 263–283.
- Winemiller, K. O. (1989). Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan Ilanos. *Environmental Biology of Fishes* **26**, 177–199.
- Winemiller, K. O. (1990). Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs* **60**, 331–367.
- Winemiller, K. O. (1991). Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecological Monographs* **61**, 343–365.
- Zaret, T. M. & Rand, A. S. (1971). Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology* **52**, 336–342.

