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Fish richness and species-habitat relationships in two coastal streams of French Guiana, South America

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Synopsis

We examined the factors controlling fish species richness and taxa-habitat relationships in the Malmanoury and Karouabo coastal streams in French Guiana between the short and long rainy seasons. The aims were to evaluate the environmental factors that describe species richness on different scales and to define the ecological requirements of fish taxa in the two streams at that period of the year. We sampled ten regularly spaced freshwater sites in each stream with rotenone. We caught a total of 7725 individuals representing 52 taxa from 21 families and 6 orders. More taxa were caught in the Malmanoury (n = 46) than in the Karouabo stream (n = 37). These values augmented by the number of fish taxa caught only by gill nets in a parallel survey fitted very well to a log-log model of fish richness versus catchment area in Guianese rivers. Most of the fish taxa encountered in the Malmanoury and Karouabo streams were of freshwater origin and nearly all the fish species caught in these two small coastal streams were also found in the nearby Sinnamary River with the exceptions of the cichlid *Heros severus* and the characid *Crenuchus spirulus*. Moreover, no significant relationship was found between a size-independent estimate of fish richness and distance from the Ocean. Thus, despite their coastal position, the Malmanoury and Karouabo streams contained fish assemblages with strong continental affinities. At a local scale, independently of site size, those with relatively more habitat types harbored a relatively greater number of fish taxa. Canopy cover, water conductivity and bank length were the most important environmental variables for fish assemblage composition at that period of the year. Oxygen and vegetation participated also in defining fish habitat requirements but to a lesser extent.

Introduction

One approach in evaluating the impacts of human disturbances on streams and rivers is to understand the relationship between their organisms and the environment. As the complexity of lotic systems implies different functional scales, such studies must be carried out on different levels of observation that depend on the questions to be answered (Wiens et al. 1986, Minshall 1988, Bayley & Li 1992, Hildrew & Giller 1994).

On very large scales, such as zoogeographical areas (sensu Bayley & Li 1992), fish species richness is usually considered to be mainly determined by climatic and/or geological events (Mahon 1984, Moyle & Herbold 1987, Hugueny & Lévêque 1994). The number of fish species in a specific drainage basin is generally mainly explained by catchment area (Livingstone et al. 1982, Hugueny 1989, Welcomme 1990) and river discharge (Oberdorff et al. 1995). On more local scales such as pool/riffle sections or reaches (sensu Frissel et al. 1986), the physical factors useful to predict the number of species are usually: (i) habitat size or volume (Angermeier & Schlosser 1989, Hugueny 1990), (ii) habitat diversity expressed by an index that incorporates either depth, current velocity and substrate (Gorman & Karr 1978; Angermeier & Schlosser 1989), (iii) diversity of current velocities (Hugueny 1990), and (iv) distance from the ocean and/or channel width and depth (Angermeier & Karr 1983, Hugueny 1990, Lyons & Schneider 1990).

Fish species-habitat associations are generally established by studying ecological preferences of the taxa. Such studies are usually undertaken on small spatial scales such as microhabitats, pool/riffle sections and reaches (sensu Frissel et al. 1986). On these scales, current velocity, water depth and substrate proved to be good predictors of fish assemblage characteristics (e.g. Pouilly 1993), fish densities (e.g. Bain et al. 1988), and fish richness and diversity (e.g. Schlosser 1982). However, fish species can also be associated with other environmental parameters such as vegetation (Lobb & Orth 1991, Copp 1991), low oxygen conditions prevailing in leaf litter (Henderson & Walker 1990), water conductivity (Taylor et al. 1993) or temperature (Baltz et al. 1987).

In general, most of the knowledge concerning the relationships between lotic fishes and their environment relates to temperate climates and very little is known of factors structuring fish species richness and taxa-habitat relationships in neotropical rivers. In French Guiana, South America, such studies are even scarcer. Those performed on a biogeographical scale have addressed only certain taxonomic groups (see Boujard 1992 for cichlids) and the only study on the scale of a drainage basin considered longitudinal distributions of fish taxa in the Sinnamary River (Boujard & Rojas-Beltran 1988). On a more local scale such as reaches, Rojas-Beltran (1986) described the temporal variations of a fish assemblage in a small tributary of the Kourou River. In addition, Boujard et al. (1990a, b, c) studied the association between fish species and different types of habitats in the Arataye River but the use of gill nets limited the study to large species. All these studies were undertaken in large rivers or in their tributaries and no data have yet been published on fish-habitat relationships in the numerous small streams that drain the French Guiana Atlantic coast.

In this context, the aim of our study on fish assemblages in the Malmanoury and Karouabo coastal streams was to evaluate the environmental factors that describe species richness on different scales and to define the ecological requirements of the different fish taxa encountered in the two streams. This information is of particular concern with respect to these two streams as they border the European Space Center from where the toxic product emitting Ariane 5 rocket will be launched.

Study sites

The Malmanoury and Karouabo streams drain the Atlantic coastal plain of French Guiana to the north-east (Figure 1). These streams are 21 and 26 km long and drain areas of approximately 93 km^2 and 98 km^2, respectively. The mean annual discharge of the Karouabo Stream has been estimated at ca. 5.0 m^3 s^{-1} with maximal instantaneous values > 60 m^3 s^{-1} (Lointier unpublished). Its flow regime depends on the alternation of the short-, November to February, and long-, April to July, rainy season, with May and June being the wettest months, and the dry season (August to November), which is typical of the Guianese climate. Almost nothing is known about the flow characteristics of the Malmanoury Stream. Given its slightly larger drainage area, its mean annual discharge can be estimated to be somewhat above 5.0 m^3 s^{-1}, and its flow regime should be comparable to the Karouabo.

The upstream parts of both streams drain a dense forest dominated by *Parinari campestris* (Granville 1992). In its intermediate part the Karouabo Stream flows through a savannah and then loses its way in swamps with herbaceous plants such as *Eleocharis interstincta* alternated with subcoastal remnants of

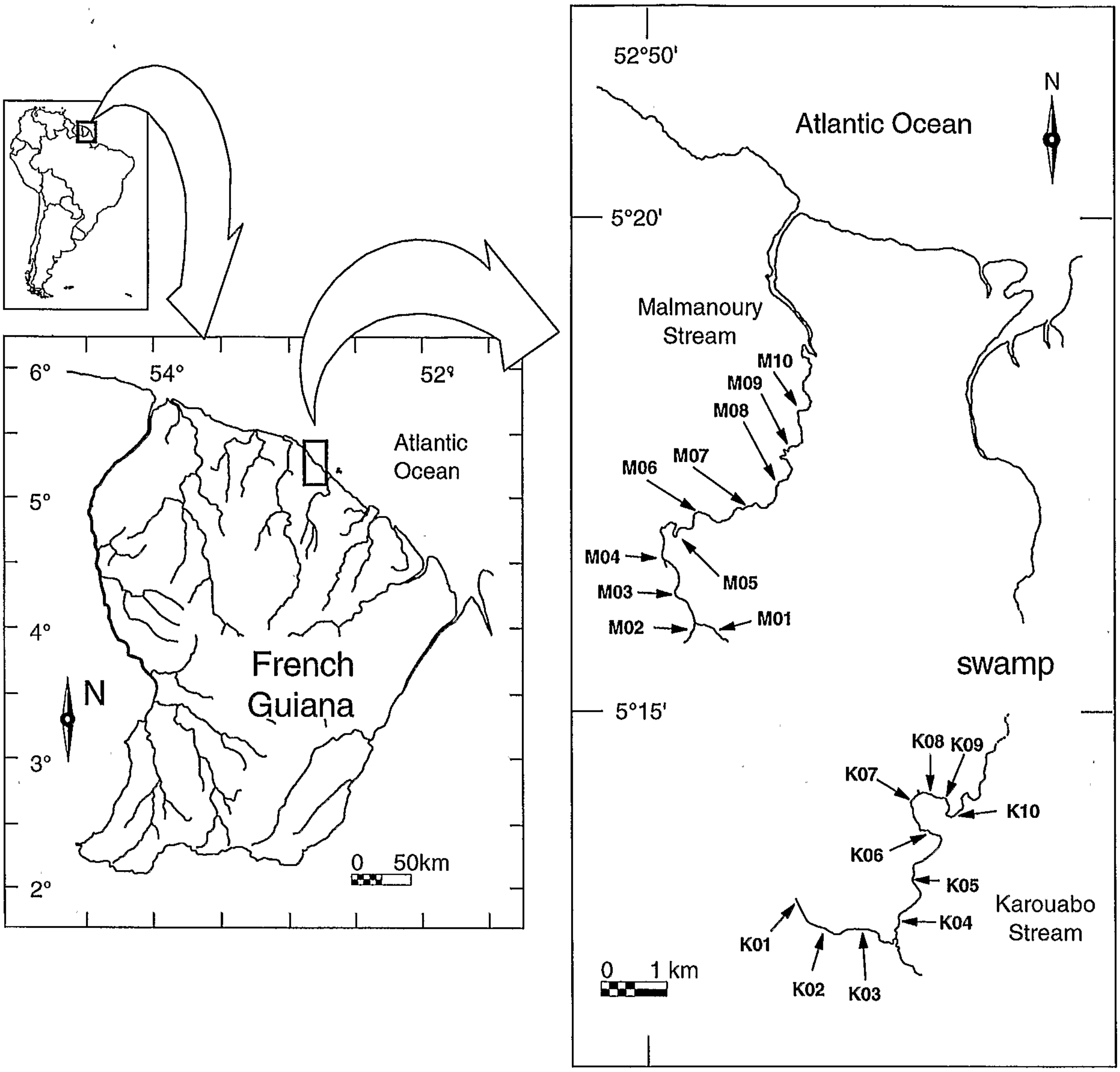

Figure 1. Map of the Malmanoury and Karouabo streams (French Guiana, South America) showing sampling sites (M01 to M10: Malmanoury Stream and K01 to K10: Karouabo Stream).

sandy shorelines where *Hymenaea courbaril* dominates (Loubry unpublished). The lower reaches of the Malmanoury stream meander through an hydromorphic forest of *Pterocarpus officinalis* and *Rhizophora racemosa*, the later being increasingly dominant near the estuary. Large herbaceous swamp areas occur on each bank of the main channel.

Material and methods

Fish sampling and habitat descriptions

We sampled ten regularly spaced sites (Figure 1) at random, i.e. without knowing whether fish were present or not, between the short and long rainy seasons (Malmanoury: 30 January – 3 February, 1995; Karouabo: 6 – 9 April 1995). At each site we measured water temperature, pH, oxygen and conductivity with a ICM 51000 multiparameter before we enclosed an area (varying from 20 to 131 m^2 among sites) with two or three 1 mm mesh stop nets. Per enclosed area we applied at least two successive doses of PREDATOX (6.6% emulsifiable solution of rotenone extracted from *Derris elliptica* by Saphyr, Antibes, France) well mixed with water (for a complete description of the sampling method see Ponton & Copp 1997). We collected fish with 1 mm mesh dip nets and immediately preserved them in 95% alcohol. All individuals were identified later in the laboratory using keys for adults by Géry (1977), Le Bail et al. (1983, 1984), Rojas-Beltran (1984), Planquette et al. (1996), Lauzanne (unpublished) and keys for juveniles by Ponton (unpublished).

At the end of fish sampling, we recorded habitat characteristics following a method modified from Gorman & Karr (1978). At each point sample of a 1 × 1 m grid we measured depth with a graduated stick and then recorded the occurrences of different categories of organic litter, vegetation and substrate (see Table 1). Then we measured water current velocity at 0.2 and 0.8 water depth and at 1-m intervals along three transects with a C2 OTT flowmeter. Finally, we visually estimated percentage canopy cover and measured total bank length and total area.

In a parallel survey gill nets (2.5 x 25 m, mesh size 10, 15, 20, 25, 30, 35, 40, 50 mm knot to knot) were also set in four sampling sites of the Malmanoury Stream and three other in the Karouabo Stream between 17:00 and 8:00 h.

Data analysis

Habitat and fish taxa richness of each site. – At each point sample, we first merged the occurrences of the categories of depth, type of substrate, organic litter and vegetation coded 0 = absence or 1 = presence (see Table 1 for the different categories). Thus each point sample could be assigned to one of the different types of habitat each corresponding to a given chain of 0 and 1. In order to obtain size-independent estimates of habitat richness of each site, we then used the residuals of the regression of the total number of habitat types against the total number of point samples per site. Similarly, we regressed the total number of fish taxa caught per site against the total number of fish caught at that site in order to obtain size-independent (i.e. residuals) estimates of fish richness at each site.

Fish–habitat relationships and ecological requirements of taxa. – We first arranged habitat characteristics and fish densities in two data matrices: 'sites-by-environmental variables' and 'sites-by-fish taxa' (both rows-by-columns). Only the eight environmental variables in Table 1 were retained in the 'sites-by-environmental variables' matrix. Water temperature (mean = 26.3, SD = 1.24) and pH (mean = 4.8, SD = 0.25) varied little and were excluded. We also rejected water velocity as only three sites presented detectable current. Then we grouped data of canopy cover, conductivity, oxygen, bank length and depth in categories of equal

Table 1. Categories and codes of the environmental variables used to describe the habitat of each sampling site.

Variables	Categories	Codes
Disjunctive variables (1 category per site)		
Canopy cover (%)	< 75	1
	≥75	2
Conductivity (μs cm^{-1})	0–29	1
	30–36	2
	37–130	3
Oxygen (mg l^{-1})	1.2–2.9	1
	3–3.9	2
	4–6.8	3
Bank length (m)	0–10	1
	11–100	2
Fuzzy coded variable (> 1 category per site)		
Depth (cm)	0–27	1
	28–55	2
	56–82	3
	83–138	4
Litter	leaves	1
	wood diameter > 5 cm	2
	wood diameter < 5 cm	3
	roots diameter > 5 cm	4
	roots diameter < 5 cm	5
Vegetation	aquatic	1
	terrestrial herbaceous	2
	terrestrial shrubs or trees	3
Substrate	mud	1
	clay	2
	sand, gravels, stones, blocs	3

frequencies. The first four variables were disjunctive; i.e. they were represented by only one category per site (Table 1). Their codes were thus directly included in the 'sites-by-environmental variables' matrix. Water depth, litter, vegetation and substrate were described by using several categories per site (Table 1). We first submitted the frequencies of these different categories to fuzzy coding (Van Rijckevorsel 1987) in order to obtain only one positive score at each site (see Chevenet et al. 1994). These scores, or fuzzy-coded values, were then included in the 'sites-by-environmental variables' matrix. The 'samples-by-fish taxa' matrix contained $\log(x+1)$ transformed densities of the different fish taxa, except those occurring at only one site that have been excluded.

We submitted each matrix to correspondence analysis. This ordination technique first elucidated separately the typology of environmental variables and the relationships among taxa (Escofier & Pagès 1990, Chevenet et al. 1994). We then subjected the results from these two correspondence analyses to co-inertia analysis, a way to examine species-environment relationships when many species and several environmental variables are sampled in few sites (Dolédec & Chessel 1994). This technique is used to demonstrate whether a co-structure exists between environmental and faunistic data sets. The co-structure is determined by the maximization of the square-rooted projected inertia (which defines the structure of each table separately) and of the correlation between the two new sets of projected coordinates (Dolédec & Chessel 1994). We tested the significance of the resulting correlation by a Monte-Carlo method with 1000 random permutations of the rows of the environmental and faunistic data sets. All analyses and graphics were performed with ADE software (Thioulouse et al. 1995).

Results

A total of 7725 individuals representing 52 taxa from 21 families and 6 orders were collected at the 20 sampling sites (Table 2). More taxa were caught in the Malmanoury ($n = 46$) than in the Karouabo Stream ($n = 37$). Including additional taxa caught only by gill nets in a parallel survey ($n = 6$ and $n = 4$ respectively, Table 3), fish species richness in both streams fitted very well to a log-log model of fish richness versus catchment area in Guianese rivers (Figure 2).

In both Malmanoury and Karouabo streams, the Characiformes and the Perciformes accounted for 57% and 36% of the total individuals, respectively. The Siluriformes were poorly represented in the Karouabo Stream where only three taxa out of the ten encountered were found (Table 2). A total of 13 taxa collected in the Malmanoury Stream were not found in the Karouabo Stream and only five taxa encountered in the Karouabo Stream were not caught in the Malmanoury Stream (Table 2).

A total of 495 and 293 point samples allowed us to differentiate 164 and 134 different types of habitat in the Malmanoury and the Karouabo streams, respectively (Table 4). The mean relative number of habitat types per square meter was significantly higher in the Karouabo than in Malmanoury Stream. Identically, the mean relative richness of fish taxa was significantly greater in the Karouabo than in Malmanoury (Table 4).

A significant linear relationship was found between the number of habitat types and the total number of point samples per site (Figure 3a). In addition, the relationship between the number of fish taxa and the total number of fish individuals caught per site could also be expressed by a linear relationship (Figure 3b). Finally, a significant linear relationship was found between the residuals of these two regressions, i.e. between size-independent estimates of fish richness and habitat richness (Figure 3c). Thus, independently of site size, the higher the relative richness of habitat, the higher was the relative richness of fish.

The two matrices, Samples-by-Fish Taxa and Samples-by-Environmental Variables were significantly linked ($p < 0.001$, Monte-Carlo method with 1000 permutations). The first two axes of the analysis explained together 78% of the total co-inertia (Figure 4a). When examining the correlation ratios (Table 5), these axes separated taxa and sampling sites mainly according to canopy cover, conductivity and bank length, and to a lesser extend to oxygen contents and vegetation (Figure 4c). Co-inertia

Table 2. List of fish taxa, authority, abbreviated species code, number of fish (N) and range of standard length (SL in mm) in ten sampling sites of the Malmanoury Stream and ten other in the Karouabo Stream.

Order family sub-family species	Authority	CODE	Malmanoury		Karouabo	
			N	SL min-max	N	SL min-max
Characiformes						
Curimatidae						
Cyphocharax spilurus	Günther, 1864	CYSP	1	34–34	93	14–45
Curimatidae unidentified juveniles		CUSP	-	-	53	7–22
Anostomidae						
Leporinus gossei	Géry, Planquette & LeBail, 1991	LGOS	–	–	1	66–66
Erythrinidae						
Erythrinus erythrinus	(Schneider, 1801)	EERY	2	70–85	1	58–58
Hoplerythrinus unitaeniatus	(Spix, 1829)	HOUN	4	170–200	–	–
Hoplias aimara	(Valenciennes, 1840)	HAIM	–	–	1	20–20
Hoplias malabaricus	(Bloch, 1794)	HMAL	33	15–220	7	17–231
Hoplias unidentified juveniles		HOPL	1	9–9	–	–
Lebiasinidae						
Pyrrhulininae						
Copella carsevennensis	(Regan, 1912)	CCAR	90	10–38	230	7–38
Nannostomus beckfordi	Günther, 1872	NBEC	84	10–30	105	11–30
Pyrrhulina filamentosa	Val. in Cuv. & Val., 1846	PFIL	536	9–75	45	8–65
Gasteropelecidae						
Gasteropelecus sternicla	(Linnaeus, 1758)	GSTE	391	10–42	12	9–13
Characidae						
Characidiinae						
Microcharacidium eleotrioides	(Géry, 1960)	MELE	31	7–21	4	17–19
Characinae						
Acestrorhynchus falcatus	(Bloch, 1794)	AFAL	17	31–155	–	–
Acestrorhynchus unidentified juveniles		ACSP	5	20–30	–	–
Cheirodontinae						
Pristella maxillaris	(Ulrey, 1894)	PMAX	71	6–26	11	18–28
Pseudopristella simulata	Géry, 1960	PSIM	501	8–30	298	14–30
Crenuchinae						
Crenuchus spirulus	Günther, 1863	CRES	2	35–35	–	–
Serrasalminae						
Metynnis cf. *lippincottianus*	(Cope, 1870)	MLIP	–	–	1	33–33
Tetragonopterinae						
Astyanax bimaculatus	(Linnaeus, 1758)	ABIM	7	22–86	1	93–93
Astyanax cf. *keithi*	(Géry et al., 1996)	AKEI	1	39–39	2	6–14
Hemigrammus boesemani	(Géry, 1959)	HBOE	1	28–28	–	–
Hemigrammus ocellifer	(Steindachner, 1882)	HOCE	389	10–36	33	11–32
Hemigrammus unilineatus	(Gill, 1858)	HUNI	30	12–37	–	–
Hyphessobrycon aff. *sovichtys*	Schultz, 1944	HSOV	21	18–25	29	14–30
Moenkhausia chrysargyrea	(Günther, 1864)	MCHR	151	11–66	18	21–92
Moenkhausia collettii	(Steindachner, 1882)	MCOL	891	9–53	20	20–45
Moenkhausia hemigrammoides	Géry, 1966	MHEM	182	12–37	–	–
Moenkhausia oligolepis	(Günther, 1864)	MOLI	–	–	6	8–10
Characidae unidentified juveniles		CHSP	25	9–18	–	–
Siluriformes						
Auchenipteridae						
Tatia intermedia	(Steindachner, 1876)	TINT	10	46–65	–	–
Auchenipteridae unidentified juveniles		AUCH	2	8–10	–	–
Pimelodidae						
Pimelodella cristata	(Müller & Troschel, 1848)	PCRI	5	58–112	–	–
Pseudopimelodus raninus	(Valenciennes, 1840)	PRAN	34	14–73	–	–
Rhamdia quelen	(Quoy & Gaimard, 1824)	RQUE	8	38–293	–	–
Pimelodidae unidentified juveniles		PIME	1	17–17	–	–

Table 2. Continued.

Order family sub-family species	Authority	CODE	Malmanoury		Karouabo	
			N	SL min-max	N	SL min-max
Siluriformes						
Helogenidae						
Helogenes marmoratus	(Günther, 1863)	HMAR	1	53–53	–	–
Aspredinidae						
Bunocephalinae						
Bunocephalus sp.		BUNO	16	50–84	–	–
Trichomycteridae						
Trichomycterus guianense	(Eigenmann, 1909)	TGUI	22	17–70	1	40–40
Callichthyidae						
Hoplosternum thoracatum	(Val. in Cuv. & Val., 1840)	HTHO	11	17–135	4	14–26
Loricariidae						
Ancistrus aff. *hoplogenys*	(Günther, 1864)	AHOP	23	17–106	3	40–83
Rhineloricaria stewarti	(Eigenmann, 1909)	RSTE	1	31–31	–	–
Gymnotiformes						
Sternopygidae						
Eigenmannia virescens	(Valenciennes, 1847)	EVIR	8	83–110	1	90–90
Hypopomidae						
Brachyhypopomus beebei	(Schultz, 1944)	BBEE	18	15–165	14	22–85
Gymnotidae						
Gymnotus anguillaris	Hoedeman, 1962	GANG	8	76–268	5	82–138
Gymnotus carapo	Linnaeus, 1758	GCAR	13	20–57	16	55–180
Gymnotus unidentified juveniles		GYSP	7	13–21	–	–
Electrophoridae						
Electrophorus electricus	Gill, 1864	ELEL	1	709–709	–	–
Cyprinodontiformes						
Aplocheilidae						
Rivulus agilae	Hoedeman, 1954	RAGI	136	8–30	76	12–30
Rivulus igneus	Huber, 1991	RIGN	–	–	1	22–22
Rivulus xiphidius	Huber, 1979	RXIP	–	–	13	9–24
Synbranchiformes						
Synbranchidae						
Synbranchus marmoratus	Bloch, 1795	SMAR	40	30–140	12	40–130
Perciformes						
Nandidae						
Nandinae						
Polycentrus schomburgkii	Müller & Troschel, 1848	PSCH	7	23–43	134	7–57
Cichlidae						
Cleithracara maronii	(Steindachner, 1882)	CMAR	73	13–75	41	9–70
Crenicichla saxatilis	(Linnaeus, 1758)	CSAX	141	8–185	18	25–152
Heros severus	Heckel, 1840	HSEV	86	7–65	29	9–70
Krobia guianensis	(Regan, 1905)	KGUI	1671	7–132	67	13–125
Nannacara anomala	Regan, 1905	NANO	119	8–50	168	7–50
Cichlidae unidentified juveniles		CICH	2	11–13	–	–
Eleotrididae						
Eleotris amblyopsis	(Cope, 1870)	EAMB	214	7–50	–	–
Others						
Unidentified		INDE	3	7–11	3	7–10
Total number of orders			6		6	
Total number of families			21		16	
Total number of taxa*			46		37	
Total number of individuals			6148		1577	

* Number calculated without taxa corresponding to the codes HOPL, CHSP, AUCH, PIME, GYSP, CICH, INDE and with pooling CYSP-CUSP and ACSP-AFAL.

analysis allowed us to distinguish five groups of fish (Figure 4d) that correspond to four groups of stations (Figure 4b). These taxa were characterized by specific habitat requirements (Figure 4c). Sites with low bank length (0-10m) and < 75% canopy cover harbored characteristic taxa like Curimatidae, *Rivulus xiphidus*, and *Polycentrus schomburcki* when conductivity was medium (30 to 36 μs cm^{-1}) or *Hyphessobrycon* aff. *sovichtys* and *Heros severus* when aquatic vegetation was abundant (Figures 4, 5). *Nannostomus beckfordi* was typical of sites where both aquatic vegetation and medium conductivity were encountered. Sites with > 75% canopy cover and banks from 10 to 100 meters long presented fish assemblages whose composition depended on water characteristics. In these sites *Hoplerythrinus unitaeniatus* and *Hemigrammus unilineatus* were typical of waters with high conductivity

Table 3. List of fish taxa, authority, number of fish (N) in four sampling sites of the Malmanoury Stream and three other in the Karouabo Stream sampled with gill nets (mesh size 10, 15, 20, 25, 30, 35, 40, 50 mm knot to knot) during one night in a parallel survey. * = taxa caught only by gill nets.

order family sub-family species	Authority	Malmanoury N	Karouabo N
Elopiformes			
Megalopidae			
Megalops atlanticus	Valenciennes, 1846	4 *	2 *
Characiformes			
Anostomidae			
Leporinus friderici	(Bloch, 1794)	–	8*
Leporinus gossei	Géry, Planquette & LeBail, 1991	15*	1
Erythrinidae			
Hoplerythrinus unitaeniatus	(Schneider, 1801)	4	2
Hoplias malabaricus	(Bloch, 1794)	38	8
Characinae			
Acestrorhynchus falcatus	(Bloch, 1794)	242	63
Tetragonopterinae			
Astyanax bimaculatus	(Linnaeus, 1758)	15	6
Moenkhausia chrysargyrea	(Günther, 1864)	3	1
Piabucus dentatus	(Köhlreuter, 1761)	2 *	–
Siluriformes			
Auchenipteridae			
Parauchenipterus galeatus	(Linnaeus, 1766)	82*	76*
Pseudauchenipterus nodosus	(Bloch, 1794)	7*	–
Tatia intermedia	(Steindachner, 1876)	1	–
Callichthyidae			
Hoplosternum thoracatum	(Valenciennes in Cuvier & Valenciennes, 1840)	7	2
Loricariidae			
Ancistrus aff. *hoplogenys*	(Günther, 1864)	6	–
Hypostomus ventromaculatus	Boeseman, 1968	1*	–
Rhineloricaria stewarti	(Eigenmann, 1909)	1	–
Gymnotiformes			
Sternopygidae			
Eigenmannia virescens	(Valenciennes, 1847)	1	–
Cichlidae			
Crenicichla saxatilis	(Linnaeus, 1758)	7	–
Heros severus	Heckel, 1840	11	2
Number of taxa caught only by gill nets		6	4

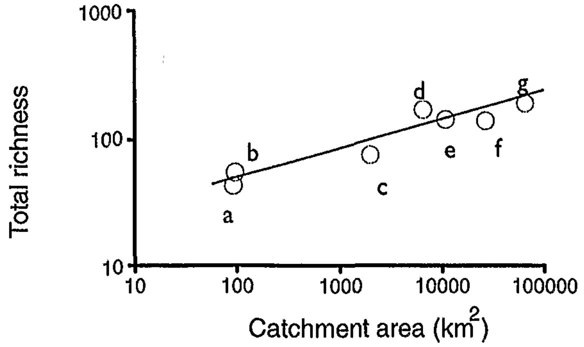

Figure 2. Relationship between total fish richness and catchment area for different Guianese rivers (log fish richness = 0.2154*log catchment area + 1.2471, F = 42.2009, df = 6, p = 0.0013). With a and b – Malmanoury and Karouabo streams respectively (this study), c – Kourou River (Planquette, INRA, Kourou unpublished data), d – Sinnamary River (Lauzanne & Tito de Morais, ORSTOM Cayenne unpublished data), e – Approuague River (Boujard et al. 1990 a, b), f – Oyapock River (Boujard et al. 1990 a, b), and g – Maroni River (Planquette, INRA, Kourou unpublished data). Data of catchment areas for c, d, e, f, and g are from Hiez & Dubreuil (1964).

($> 36 \mu s\ cm^{-1}$) and low oxygen concentrations ($< 3\ mg\ l^{-1}$). *Pimelodella cristata* and *Bunocephalus* sp. were more often caught when water conductivity was less than 30 $\mu s\ cm^{-1}$. *Pseudopimelodus raninus*, *Trichomycterus guianense*, and *Eleotris amblyopsis* were indifferent to water quality (Figures 4, 5). More than 50% of the fish taxa were classified as habitat generalists (Figure 4d). Among them *Nannacara anomala*, *Hoplosternum thoracatum*, *Cleithracara maroni*, *Pyrrhulina filamentosa*, and *Copella carsevennensis* were the most typical (Figures 4, 5).

Discussion

Fish richness in the Malmanoury and Karouabo streams

With total richness of 52 and 41 taxa respectively, the Malmanoury and Karouabo streams fit well to a log-log model linking fish richness to catchment area for different Guianese rivers (Figure 2). Our data confirm that catchment size is one of the main factors determining fish species richness in French Guiana as elsewhere (Livingstone et al. 1982, Hugueny 1989, Welcomme 1990, Oberdorff et al. 1995). Nearly all fish species caught in these two small coastal streams were also found in the nearby Sinnamary River (Boujard & Rojas-Beltran 1988, Lauzanne & Tito de Morais unpublished data). The only exceptions are the cichlid *Heros severus*, which was probably introduced accidentally into coastal

Table 4. Characteristics of sampling sites, point samples, habitat types and fish taxa in the Malmanoury and Karouabo streams. With SE = standard error, t = value of Student's t statistic when testing Ho = 'there is no difference between mean values observed in each stream', p = associated probability. Only probabilities for significant differences are given. Habitat types were obtained by merging the presence/absence data of each category of the four variables: depth, litter, vegetation, and substrate at each point sample (see explanation in text).

	Malmanoury	Karouabo	t	p
Sampling sites				
total number	10	10		
total sampling area (m^2)	638.9	278.2		
mean area (SE)	63.88 (2.92)	27.82 (3.24)	3.677	0.001
Point samples				
total number	495	293		
mean number per m^2 (SE)	0.88 (0.01)	1.09 (0.01)	1.812	–
Habitat types				
total number	164	134		
mean number per m^2 (SE)	0.358 (0.008)	0.619 (0.016)	3.753	0.001
Fish taxa				
total number	46	37		
mean number per m2 (SE)	0.386 (0.022)	0.659 (0.031)	3.520	0.001

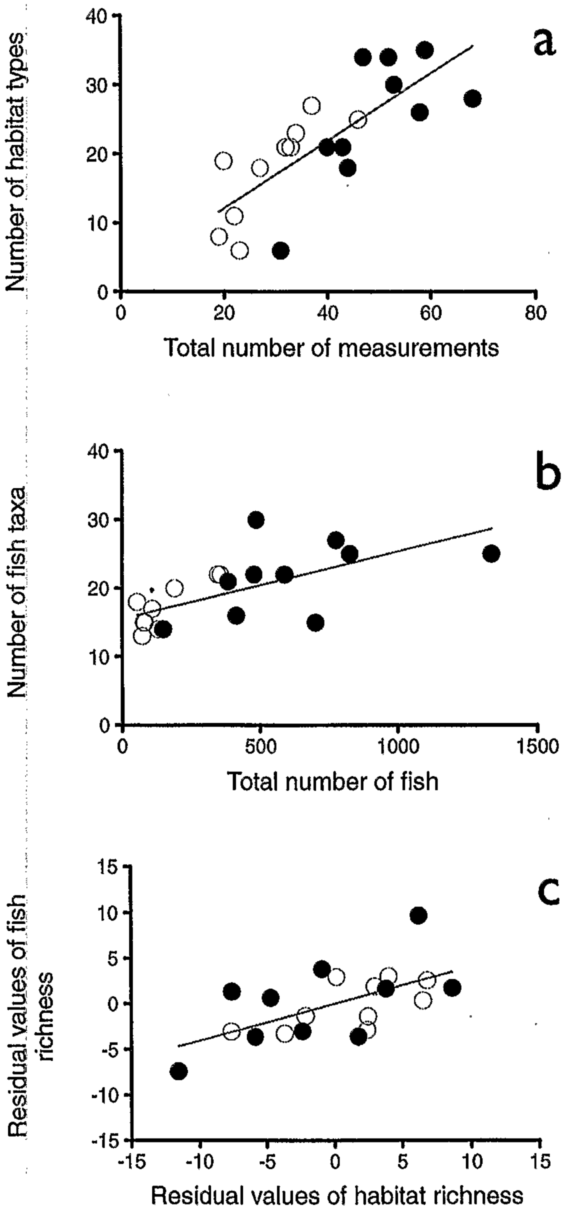

Figure 3. Relationships between (a) number of habitat types and total number of habitat measurements per site (number of habitat types = 0.488* number of point samples +2.386, F = 27.290, df = 19, p 0.001), (b) number of fish taxa and total number of fish caught per site (number of fish taxa = 0.010* number of individuals +15.534, F = 13.724, df = 19, p = 0.002), and (c) residuals of regression a and residuals of regression b (residuals regression figure 3b = 0.408* residuals regression figure 3a, F = 10.453, df = 19, p = 0.005). Closed circles = data from Malmanoury Stream and open circles = data from Karouabo Stream.

streams in the seventies,[1] and the characid *Crenuchus spirulus*, which is characteristic of coastal marshes in French Guiana (Planquette et al. 1996). The similarity of their fish fauna indicates that temporary connections between these three closely located river basins must have existed in the past (Sinnamary River) or must exist at present during periods of very high water levels (Malmanoury and Karouabo streams).

In contrast to Central American streams and rivers flowing into the Pacific where most fish species have marine affinities (Lyons & Schneider 1990), a large majority of the taxa caught in the Malmanoury and Karouabo streams are primary freshwater fish. Most of them belong to the Characiformes, as in larger Guianese rivers (Boujard et al. 1990a, Tito et al. 1995) and in Central Amazon rivers (Goulding 1980, Lowe-McConnell 1987). Nevertheless, some differences between the two streams could be explained by the free connection of the Malmanoury to the Ocean while the studied portion of the Karouabo is isolated from marine waters by a large swamp. Indeed, taxa supposed to have marine affinities like *Bunocephalus* sp. (Siluriformes, Aspredinidae) and *Eleotris amblyopsis* (Perciformes, Eleotrididae) were only found in the Malmanoury.

Table 5. Correlation ratios of the habitat variables on the first two axes F1 and F2 of the co-inertia analysis. These ratios represent proportions of the total variance explained by each axis to depict the separation among modalities of a variable.

Variables	Correlation ratios	
	F1	F2
Canopy cover	0.857	0.007
Conductivity	0.762	0.827
Oxygen	0.370	0.486
Bank length	0.637	0.026
Depth	0.219	0.033
Litter	0.028	0.008
Vegetation	0.218	0.181
Substrate	0.204	0.076

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[1] Our late colleague Dr Paul Planquette, INRA Kourou, French Guiana, personnal communication 1996d.

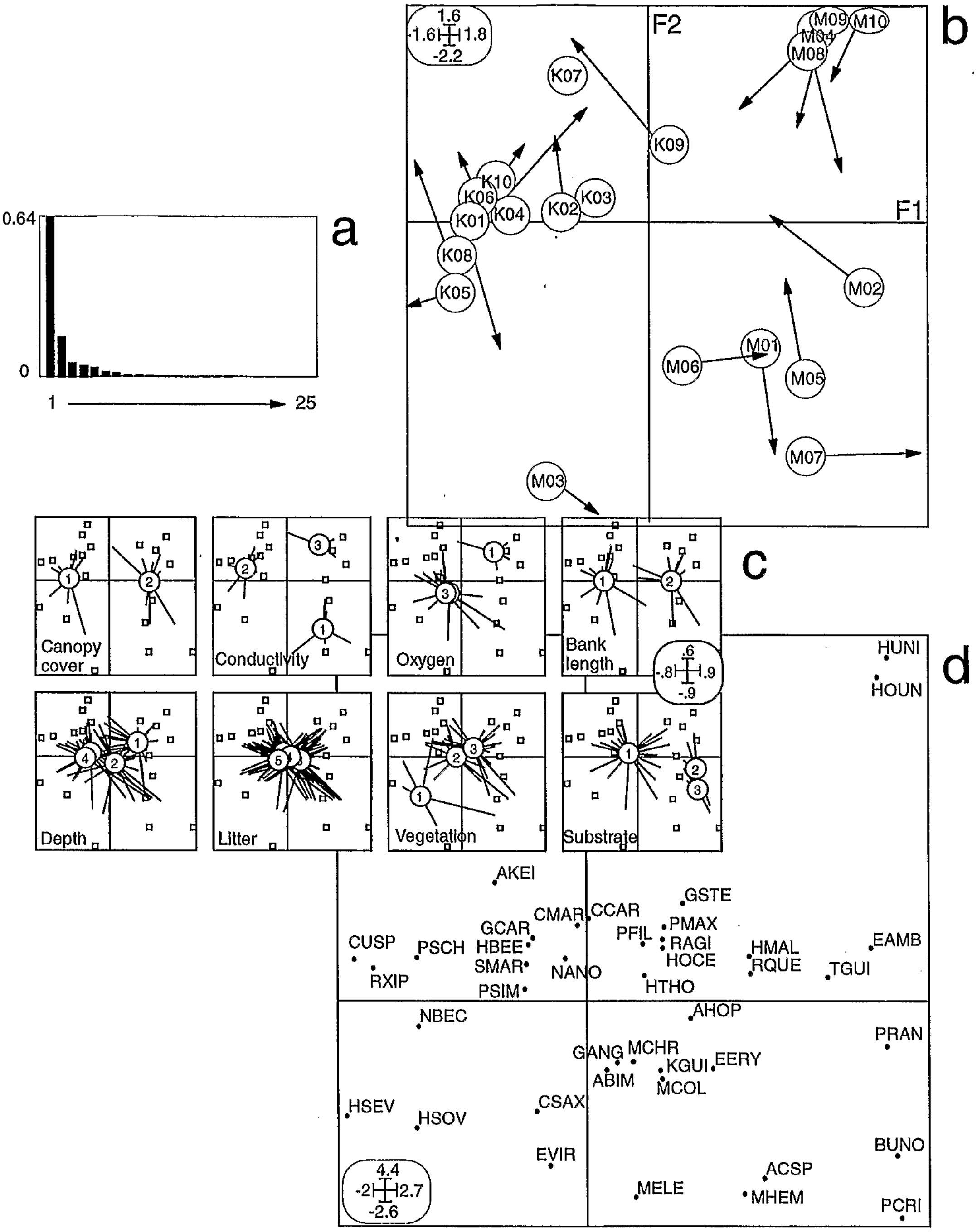

Figure 4. Results of co-inertia analysis expressing the relationships between fish taxa and habitat: a – histogram of the relative inertia of each axis, b – sampling site coordinates on the F1 × F2 plane of the co-inertia analysis. The arrows link the positions of sites obtained from habitat ordination to those given by faunistic ordination. c – Ordinations of the different modalities of habitat variables resulting from co-inertia analysis (see Table 5 for correlation ratios of each variable). Squares correspond to the positions of sampling sites determined by the faunistic table coordinates. Variable categories (codes in circles, see Table 1) are located at the weighted average of the coordinates of the sampling sites presenting that modality. Lines link sampling sites to their modalities but are only 60% of their total length for readability. They are omitted when a species contributed less than 1% to the modality distribution. d – Fish taxa coordinates on the F1 x F2 plane of the co-inertia analysis. See Table 2 for taxa codes.

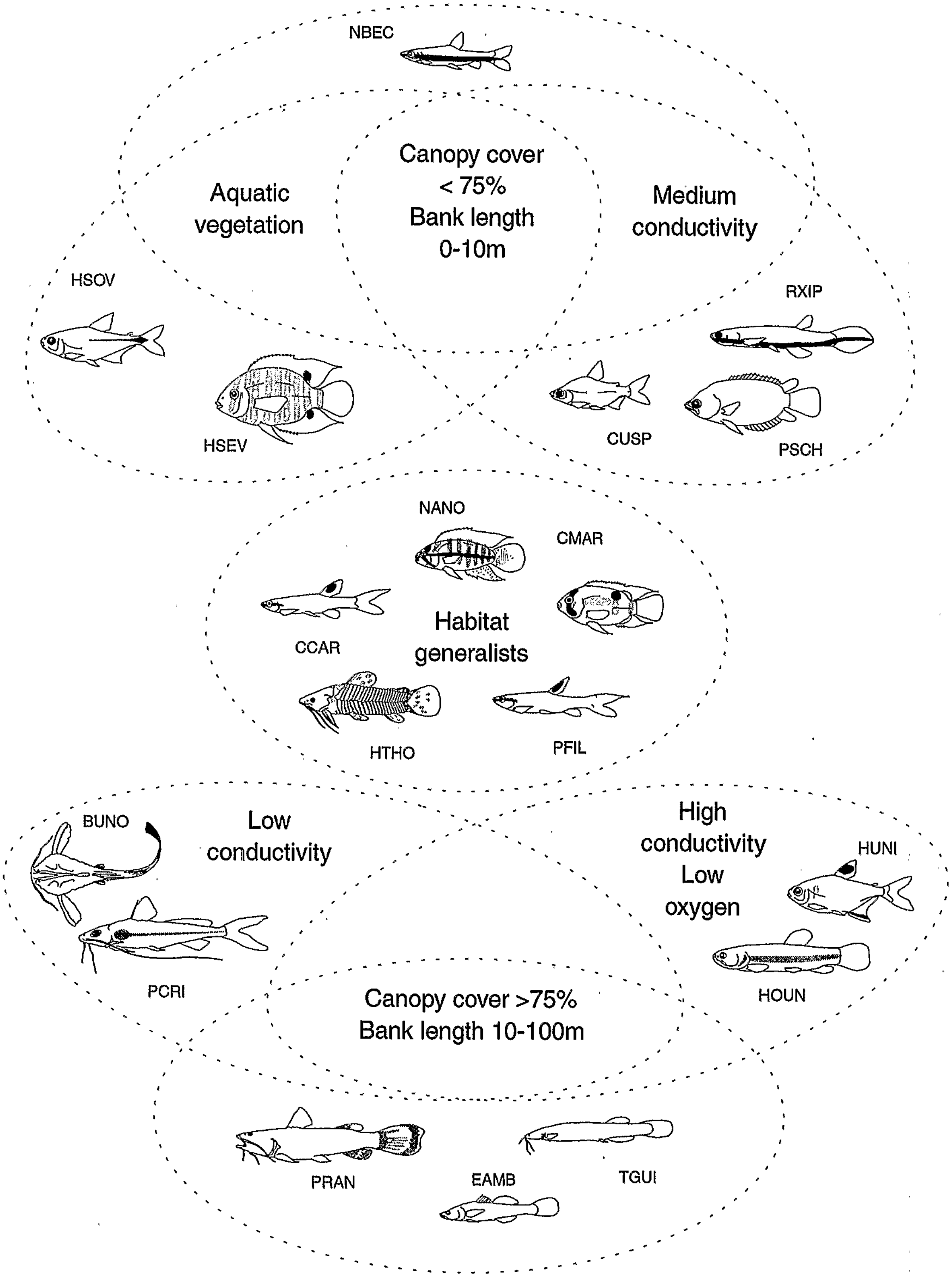

Figure 5. Schematic representation of fish assemblages that are most likely to be found in four types of habitat in the Malmanoury and Karouabo streams. Fish taxa considered as habitat generalists are also presented. Fish drawings, not to scale, after Lauzanne (unpublished) modified. See Table 2 for taxa codes.

Fish taxa richness at a local scale

At a local scale, the higher the relative richness of habitat, the higher was the relative richness of fishes (Figure 3c). This relationship agrees well with the hypothesis that interspecific competition and predation decrease in complex and/or highly diverse habitats (Hugueny 1990). It also confirms the positive relationship between fish species richness and habitat found in Panamanian streams by Gorman & Karr (1978) and Angermeier & Schlosser (1989). Contrary to Lyons & Schneider (1990) we found no significant relationship between size-independent estimates of fish richness and distance from the Ocean either in the Malmanoury (F = 0.756, df = 9, p = 0.400) or in the Karouabo Stream (F = 1.452, df = 9, p = 0.263). However, while fish assemblages in our streams were dominated by taxa of freshwater origin, those studied by Lyons & Schneider had predominantly marine affinities and thus taxa were colonizing the stream from the ocean.

Fish taxa and their habitat

The main environmental variables that define habitats of fish assemblages in the Malmanoury and Karouabo streams between the short and long rainy seasons were canopy cover, water conductivity and bank length. Oxygen and vegetation were also influential but to a lesser extent. Our results can be compared to those of Taylor et al. (1993) who found that conductivity was the strongest descriptor of site-specific assemblage structure in the upper Red River system, southwestern Oklahoma, U.S.A. However, type of substrate, depth and current velocity are usually stated as being the best environmental variables predicting fish assemblage composition at small scales (see for example Gorman & Karr 1978, Schlosser 1982, Hugueny 1990). These discrepancies may be due to the homogeneous bottom of most of our sampling sites consisting mainly of mud. Thus, we principally collected fish taxa either preferring muddy substrates or being neutral with respect to substrate. Moreover, for maximum efficiency, sampling with rotenone requires limited depths and current velocities reducing variability among the sites.

The habitat requirements of some fish taxa may be explained by their feeding and/or reproductive habits. For example *Hoplerythrinus unitaeniatus*, *Hemigrammus unilineatus, Pimelodella cristata, Pseudopimelodus raninus*, *Bunocephalus* sp., *Trichomycterus guianense* and *Eleotris amblyopsis* were more frequently caught in sites with significant bank length in dense forests (Figure 5). These taxa may have selected these riparian ecotones as they provide a diversified food source in Guianese rivers (Tito et al. 1995). Conversely, in open water sites with dense aquatic vegetation, fish species depend more on autochthonous food than on prey of terrestrial origin. Indeed, food items of *Heros severus* include large quantities of aquatic vegetation, at least in captivity (Ponton unpublished), while *Nannostomus beckfordi*, which is characteristic of coastal swamps in French Guiana (Planquette et al. 1996), may feed on microcrustaceans and insect larvae in aquatic vegetation. Moreover, some fish taxa may have used specific habitats because of their reproductive habits. For example, small-sized Characiformes of the genus *Hyphessobrycon* and *Nannostomus* are known to lay their adhesive eggs on plants during the rainy season (Breder & Rosen 1966, Burt et al. 1988).

Although descriptive, our work is a first step towards understanding fish richness and species-habitat relationships in Guianese coastal streams at different spatial scales. At a large scale, our results indicate that the total number of fish species in these streams is strongly dependent on their catchment area. At a local scale, we found that (1) the relative number of fish in a given site increases with its relative complexity, and (2) the composition of fish assemblages at each site depends to a large part on the type of habitats present. These last two patterns are based on observations made between the short and long rainy seasons and future investigations should include temporal variability. Indeed, Karr et al. (1983) pointed out that relationships between fish richness and habitat may vary seasonally due to migrations induced by changing flow conditions, food availability and the search for suitable spawning and nursery areas. Similarly, microhabitat use by fish species depends on environmental conditions, species interactions, food availability and threat of predation (Bain 1995). Finally, future studies will attempt to detail relationships between environmental parameters and the life styles (mainly feeding and reproductive ones) of the different fish taxa. Outgoing the systematic position of the different fish taxa, will give broad applicable insights on human impacts in neotropical areas and specifically on the effects of toxic products emitted during launchings of the Ariane 5 European rocket.

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