Journal of Tropical Ecology (2008) **24**:505–515. Copyright © 2008 Cambridge University Press
doi:10.1017/S0266467408005294 Printed in the United Kingdom

Geological differentiation explains diversity and composition of fish communities in upland streams in the southern Amazon of Colombia

Fernando Arbeláez, Joost F. Duivenvoorden[1] and Javier A. Maldonado-Ocampo

Institute for Biodiversity and Ecosystem Dynamics (IBED), Universiteit van Amsterdam, Kruislaan 318, 1098 SM Amsterdam, The Netherlands
Programa Inventarios de Biodiversidad, Instituto Alexander von Humboldt, Villa de Leyva, Boyacá, Colombia

(*Accepted 22 July 2008*)

Abstract: Fish biomass, species richness and composition were compared between upland streams draining two contrasting geological units (Pebas and Tsa) in Colombian Amazonia. Because Pebas sediments reportedly show higher levels of base concentrations than Tsa sediments, we expected that the fish communities from the Pebas streams would show highest biomass and species richness, and that the species composition would vary between the two upland systems. Eight forest streams were sampled in four locations, applying four daily sampling events. Tsa soil samples were comparatively sandy, whereas Pebas soil samples tended to be siltier, with higher levels of exchangeable acidity, Ca, Mg and total bases. Conductivity, concentrations of bases (Ca, Mg, K and Na), bicarbonates and temperature showed higher values in Pebas stream-water samples than in Tsa. In total, 7696 fish individuals were captured, belonging to eight orders, 28 families and 122 species. Pebas streams had 1.3 times more species than Tsa streams, and more than twice the total biomass. Species richness and biomass were highly correlated with conductivity and water concentrations of Mg and Na, and biomass alone with dissolved oxygen. Fish species composition differed significantly between the geological units. Species turnover was not related to distance between sampling locations.

Key Words: ichthyology, Pebas formation, rain forest, soil, Tertiary, water chemistry

INTRODUCTION

The Amazon Basin holds the world's most diverse freshwater fish fauna (Henderson & Crampton 1997, Saul 1975), with probably more than 2500 species (Junk & Soares 2001). About half of these species are restricted to small tributaries of large rivers, many of which dissect the upland or *terra firme* interfluves in a vast and dense hydrological network (Junk *et al.* 2007). These upland streams usually drain heavily leached soils. Their waters are poor in nutrients and dissolved solids, and are characterized by a low primary productivity and a low biomass of aquatic macrophytes (Lowe-McConnell 1987, Mendonça *et al.* 2005, Walker 1995). Yet, the surrounding forests provide a mix of food resources (arthropods, leaves, flowers, fruits, seeds and pollen) in support of the fish communities, which generally show a high species diversity (dos Anjos & Zuanon 2007, Goulding *et al.* 1988, Knöppel 1970, Lowe-McConnell 1987).

Most ecological studies of upland-stream fish communities have focused on habitat use, feeding habits, spatial and temporal distribution, and community structure (Arbeláez *et al.* 2004, Bührnheim & Cox-Fernandes 2001, 2003, dos Anjos & Zuanon 2007, Henderson & Walker 1986, 1990; Knöppel 1970, Sabino & Zuanon 1998, Silva 1993). Fish catches per unit of effort were almost five times higher in floodplains of the Amazon River than in floodplains of the Rio Negro River (Saint-Paul *et al.* 2000). Low concentrations of dissolved mineral salts in water bodies might restrict certain fish species by affecting their ionic and acid-basic regulation (Mendonça *et al.* 2005). Although some ecological studies included tributaries at wide spatial scales (Crampton 1999, Galacatos *et al.* 1996, Galvis *et al.* 2006, Saul 1975, Silvano *et al.* 2000), few specifically addressed fish community turnovers between geological units in upland forests.

In Colombian Amazonia, two geological units are widely found: the Pebas formation and the Terciario

---

[1] Corresponding author, at IBED. Email: j.f.duivenvoorden@.uva.nl

Superior Amazónico (Tsa) unit (PAT 1997, Proradam 1979). Deposits of the Pebas formation are generally fine-textured (Hoorn 1994). They are known for their comparatively high base concentrations (Kalliola & Flores Paitan 1998), and are presumably of Andean origin (Hoorn 1994, Lips & Duivenvoorden 1996, Vonhof *et al.* 1998). In contrast, geostratigraphic studies in the middle and lower Caquetá basin, about 200 km north of Leticia, suggested that sediments of the Tsa unit originated from the Guiana Shield (Hoorn 1994, 2006). Duivenvoorden & Lips (1993, 1995) associated this unit to soils that were more leached and showed coarser textures than soils developed in Pebas sediments, and to forests which differed in tree species composition compared to forests found on Pebas sediments.

This study aimed to compare fish communities in upland streams draining the Pebas or Tsa units, in the southernmost part of Colombian Amazonia. Soil and water samples were taken to corroborate our assumptions that the Pebas streams would show higher levels of conductivity and elemental concentrations than the Tsa streams. We expected to find that the fish communities from the Pebas streams would show the highest biomass and species richness, and that the species composition would vary significantly between the two upland systems.

METHODS

Study area and sampling locations

Fieldwork took place between November 2005 and March 2006 in the southern part of Colombian Amazonia (Figure 1). This area is characterised by a humid and hot equatorial climate. The annual rainfall at Leticia averages 3400 mm (over 1973–2004). Mean annual temperature is 25.7 °C, and mean annual relative humidity 86% (Galvis *et al.* 2006, Rudas-Lleras & Prieto-Cruz 2005).

Sampling was performed in forest streams draining uplands belonging to either the Tsa unit or the Pebas formation. Based on geological maps (PAT 1997, Proradam 1979) (Figure 1), two locations were chosen in each geological unit. The two Pebas locations included forest streams near the village of Santa Sofia (03°58′44″S, 70°06′58″W; 03°58′58″S, 70°07′38″W) and near the Mata-matá River biological station (03°48′23″S, 70°15′58″W; S03°47′53″S, 70°15′58″W), whereas the two Tsa locations included forest streams near the El Zafire Biological Station (04°00′26″S, 69°53′47″W; 03°59′5″S, 69°53′24″W) and the headwaters of the Purité River (03°41′54″S, 70°12′24″W; 03°41′38″S, 70°12′27″W). Both Mata-matá and Purité sampling locations were within the Amacayacu National Park.

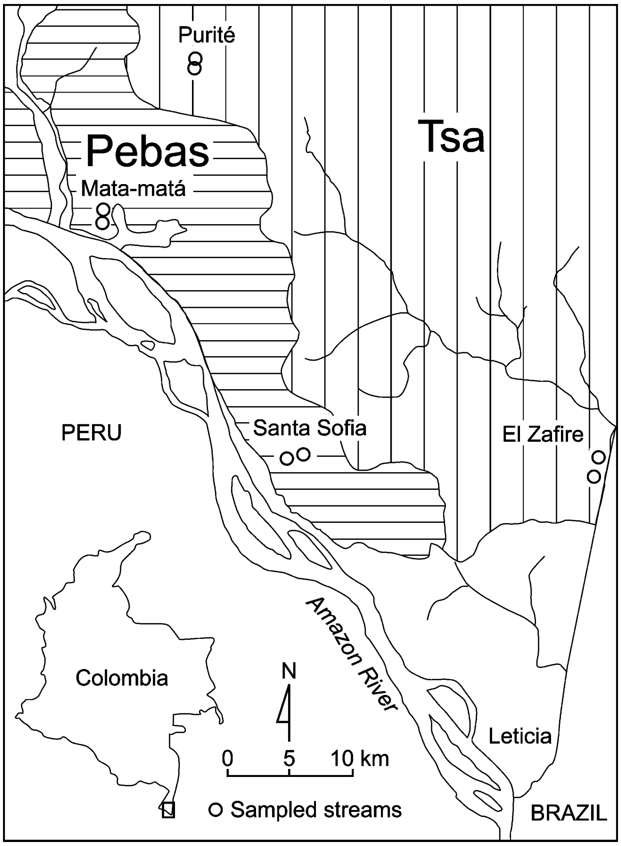

Figure 1. Location of the study area in southern Colombia, showing geological units (Pebas and Tsa) and sampling locations. Map sources are Proradam (1979) and PAT (1997).

At each sampling location, two upland streams were chosen based on advice from local people. The lack of detailed cartography precluded stream pre-selection. Sampling was probably in second-order or third-order streams. Criteria for stream choice were: (1) the stream source must be inside a well-developed forest (with a dense canopy cover) that lacked signs of recent human disturbance; (2) the stream channel must be located above the floodplains of the main rivers (Purité, Mata-matá and Amazon rivers), implying that the stream water level was not affected by the hydric pulse of these rivers; (3) the stream should not dry up at any time; and (4) the stream channel should not be wider than 6 m.

Soil and water sampling

Along each stream, between three and five 700-cm^3 superficial soil samples (A horizon, 0–5 cm depth) were collected in the floodplain forest surrounding the streams. They were taken at distances of 3–5 m from the stream channel and 10–15 m apart. Three 500-ml water samples from the middle part of the stream were taken on sampling days 0, 2 and 4. Water samples were put in plastic bottles, which were submerged in running water for cooling, and afterwards stored in a refrigerator. Also, pH, conductivity, dissolved oxygen and temperature were measured in each stream on sampling days 0, 2 and 4, using a portable multiparameter HACH Sension TM156 meter. Soil and water samples were analysed at the IGAC (Instituto Geográfico "Agustín Codazzi") soil laboratory in Bogotá, Colombia. Soil analyses comprised: granulometry with a Boyoucous hydrometer, after dispersion with $Na_2P_2O_7$; pH (H_2O) in a volumetric 1:1 soil:water solution; exchangeable acidity (meq per 100 g) by extraction in 1 N KCl and titration with 0.1 N NaOH in the presence of phenolphthalein; percentage of organic C, according to the Walkley–Black method; exchangeable bases (meq per 100 g) after extraction with 1 N NH_4 OAc (pH = 7) with Ca and Mg complexed with EDTA, and Na and K measured by flame photometry; cation exchange capacity (CEC; meq per 100 g) using the 1 N NH_4OAc (pH = 7) method; and available P (ppm) by extraction with 0.1 N HCl and 0.13 N NH_4F, according to BrayII (IGAC 1990). Water analyses comprised: pH by potentiometry; conductivity (μS cm^{-1}); calcium and magnesium (meq L^{-1}) by atomic absorption; potassium and sodium (meq L^{-1}) by atomic emission; total bases (meq L^{-1}); sulphates (meq L^{-1}) by turbidimetry; and chlorides, carbonates and bicarbonates (meq L^{-1}) by potentiometric titulation (IGAC 1990).

Fish sampling

In each stream, four daily sampling events took place. Each sampling day consisted of a 5-h routine from 14h30 to 19h30, covering afternoon, dusk and night hours, during which three fishing methods were used: one cast net (multifilament, 1.8 m radius, 1.5 cm^2 mesh) for 5 h, two dip nets (50 cm diameter, 0.5 mm mesh) for 2 h (14h30–16h30) and one seine net (2 × 3.5 m, 0.5 mm mesh) for 3 h (16h30–19h30). The sampling started at a fixed position, alternating each day between upstream and downstream transects of 100 m, and attempting to cover every fish microhabitat within the transect. All captured individuals were preserved in formalin (10%). At the Humboldt Institute (IAvH) in Villa de Leyva, Colombia, fish were preserved in ethanol (70%), identified, and counted. All individuals of a species captured on each sampling day were weighed together using an electronic balance. Weights were approximated to the nearest gram and only measurements higher than 10 g were recorded; for those lower than 10 g, a uniform value of 5 g was assigned. Samples were deposited in the fish collection of the IAvH (IAvHP 8220 to 8425 and IAvHP 8647 to 9459).

Data analyses

In order to identify the main patterns in the soil and water physicochemical variables, Principal Components Analysis (PCA) was applied. Averages for each stream were used as input values for each PCA. In the water analyses, three variables (sulphate, chloride and carbonate concentrations) were discarded for having too many undetected values (i.e. below the detection threshold of the analytical method). Four samples showed undetected values for calcium and/or magnesium concentrations; for the averages used in the PCA, those values were changed to 0.1 of the smallest detected amount for that particular variable. Field pH and conductivity were not used in the PCA, but served to identify outliers from the laboratory analyses of the water samples. Based on that criterion, two samples from Tsa-El Zafire were removed for showing highly elevated values of conductivity (46.9 and 55.6 μS cm^{-1}) compared with the field measurements (average = 12.4, max = 23.8 μS cm^{-1}) and to the other samples. All variables used in PCA were inspected for normality using a Kolmogorov–Smirnov test with Lilliefors significance correction. Calcium concentration was ln-transformed to achieve normality following Zar (1996). Samples scores along the main PCA axes were tested for differences between geological units and between sampling locations using one-way ANOVA. When the variances among sampling locations were significantly different, a Tukey's honest significant difference post hoc test was computed to compare location means. In all ANOVA analyses, residuals showed normal distributions.

In order to get an overall estimate of the fish species richness in the area, species accumulation tables and richness estimators were computed for all sampling days using EstimateS 8.0.0 (http://www.purl.oclc.org/estimates) with 1000 randomizations without replacement and shuffling of individuals among samples within species. The index used for actual richness was Species Observed (Mau Tao), with its 95% confidence intervals, as computed by the software. Two abundance-based richness estimators were used: Chao1 with bias correction and its 95% confidence intervals, and Abundance-based Coverage Estimator (ACE) and its standard deviation, with 10 individuals as the upper abundance limit for infrequent species.

Correlations between species richness, biomass and numbers of individuals, with stream averages of the water variables were examined by means of Pearson correlation coefficients. Differences in fish species richness, numbers of individuals and total biomass were examined between geological units and between sampling locations. For this purpose, ANOVA with repeated measures was performed, using streams as replicates and the four sampling days as four levels of variation of the within-stream sampling

Table 1. Physicochemical data of soil samples (mean ± SD) taken in floodplain forests along eight upland streams, arranged over two geological units (Pebas and Tsa) and four sampling locations.

	Pebas				Tsa			
	Santa Sofía 1 (n = 5)	Santa Sofía 2 (n = 5)	Mata-matá 1 (n = 3)	Mata-matá 2 (n = 3)	El Zafire 1 (n = 5)	El Zafire 2 (n = 5)	Purité 1 (n = 3)	Purité 2 (n = 3)
Sand (%)	41.0 ± 10.0	55.0 ± 22.0	21.0 ± 3.0	31.0 ± 3.0	66.0 ± 18.0	63.0 ± 10.0	58.0 ± 3.0	52.0 ± 9.0
Silt (%)	38.0 ± 7.0	30.0 ± 14.0	52.0 ± 3.0	46.0 ± 2.0	21.0 ± 11.0	22.0 ± 6.0	25.0 ± 3.0	24.0 ± 4.0
Clay (%)	21.0 ± 4.0	16.0 ± 8.0	27.0 ± 3.0	23.0 ± 1.0	13.0 ± 7.0	15.0 ± 5.0	17.0 ± 3.0	24.0 ± 5.0
pH	3.4 ± 0.2	3.5 ± 0.1	3.7 ± 0.2	3.6 ± 0.2	3.7 ± 0.1	3.5 ± 0.1	4.0 ± 0.1	3.7 ± 0.1
Exchangeable acidity (meq per 100 g)	6.0 ± 1.2	5.7 ± 3.0	8.0 ± 0.6	9.0 ± 0.6	3.3 ± 1.3	4.9 ± 1.7	3.5 ± 0.3	5.6 ± 0.5
Exchangeable acidity saturation (%)	82.0 ± 7.0	91.0 ± 1.0	88.0 ± 3.0	92.0 ± 2.0	84.0 ± 6.0	88.0 ± 2.0	90.0 ± 1.0	94.0 ± 0.0
Organic carbon (%)	2.3 ± 0.7	1.5 ± 0.7	1.7 ± 0.4	2.3 ± 0.7	3.2 ± 1.4	3.6 ± 1.6	1.6 ± 0.5	1.7 ± 0.3
Cation exchange capacity (meq per 100 g)	13.1 ± 2.2	10.3 ± 6.5	16.5 ± 1.4	19.9 ± 1.3	15.1 ± 7.2	16.5 ± 6.9	11.3 ± 1.9	15.1 ± 3.1
Ca concentration (meq per 100 g)	0.5 ± 0.3	0.2 ± 0.1	0.5 ± 0.1	0.2 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0
Mg concentration (meq per 100 g)	0.5 ± 0.1	0.2 ± 0.1	0.4 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.0	0.1 ± 0.0
K concentration (meq per 100 g)	0.2 ± 0.0	0.1 ± 0.1	0.2 ± 0.1	0.3 ± 0.0	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.0
Na concentration (meq per 100 g)	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.2	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.0
Total bases concentration (meq per 100 g)	1.3 ± 0.3	0.6 ± 0.3	1.1 ± 0.3	0.7 ± 0.2	0.6 ± 0.3	0.7 ± 0.2	0.4 ± 0.1	0.4 ± 0.1
Base saturation (%)	10.0 ± 4.0	5.8 ± 1.1	6.7 ± 1.3	3.7 ± 0.7	4.6 ± 2.6	4.4 ± 0.8	3.4 ± 0.4	2.5 ± 0.4
P concentration (ppm)	8.6 ± 2.2	6.1 ± 1.7	3.4 ± 1.9	3.7 ± 1.3	6.1 ± 6.8	2.7 ± 0.7	4.1 ± 2.1	0.6 ± 0.0

factor. ANOVA, Pearson correlation and PCA analyses were performed in SPSS 11.5.

Patterns of fish species composition were studied by means of detrended correspondence analysis (DCA) on the basis of numbers of individuals per species for each sampling day. Detrended correspondence analysis was performed using CANOCO for Windows (Version 4.51), with detrending by second-order polynomials, scaling on inter-sample distances, biplot scaling and down-weighting of rare species. The DCA scores were used for a hierarchical cluster classification with the nearest neighbour method, measuring the squared Euclidian distance between sampling days, using SPSS 11.5.

RESULTS

Soil and water analyses

The first axis of the PCA of the soil variables (Table 1, Figure 2) explained 43% of the variance and significantly separated Pebas and Tsa samples (ANOVA F = 13.0, P = 0.01). As shown by the loadings, Tsa samples tended to be comparatively sandy, whereas Pebas samples tended to be siltier, with higher levels of exchangeable acidity, Ca, Mg and total bases. The sampling locations did not differ significantly along the first or second PCA axis (ANOVA, P > 0.05).

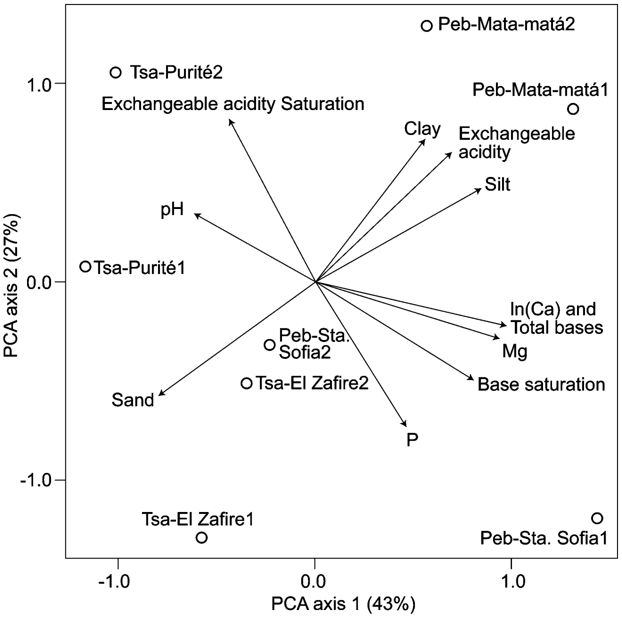

Figure 2. Results of a PCA based on soil sample averages of 15 physicochemical variables recorded in floodplains along eight upland streams. The scatter plot shows the scores along the first and second PCA axis for each stream, labelled according to geological unit, sampling location and stream number. The arrows denote the variable loadings on the axes (only variable loadings > 0.6 along PCA axis 1 or 2 are depicted).

In the PCA of the water analytical variables (Table 2, Figure 3), the first axis, which explained 67% of the variation, yielded a significant separation of the Pebas and

Table 2. Physicochemical data of water samples (mean ± SD) taken in eight upland streams, arranged over two geological units (Pebas and Tsa) and four sampling locations (ND = undetected values; # field measurements).

	Pebas				Tsa			
	Santa Sofía 1 (n = 2)	Santa Sofía 2 (n = 3)	Mata-matá 1 (n = 3)	Mata-matá 2 (n = 3)	El Zafire 1 (n = 2)	El Zafire 2 (n = 2)	Purité 1 (n = 3)	Purité 2 (n = 3)
pH	6.7 ± 0.3	6.5 ± 0.5	5.9 ± 0.1	5.7 ± 0.1	6.8 ± 0.0	6.9 ± 0.3	5.0 ± 0.2	5.1 ± 0.1
Conductivity (μS cm^{-1})	22.5 ± 3.7	23.8 ± 8.9	15.3 ± 1.4	13.5 ± 0.1	6.5 ± 1.1	5.9 ± 0.4	6.1 ± 2.8	5.3 ± 1.2
Ca (meq L^{-1})	0.07 ± 0.02	0.07 ± 0.03	0.05 ± 0.01	0.03 ± 0.00	ND	ND	0.03 ± 0.03	0.03 ± 0.02
Mg (meq L^{-1})	0.04 ± 0.01	0.04 ± 0.02	0.02 ± 0.0	0.03 ± 0.01	ND	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.00
K (meq L^{-1})	0.04 ± 0.00	0.03 ± 0.01	0.02 ± 0.01	0.02 ± 0.00	0.02 ± 0.01	0.01 ± 0.00	0.00 ± 0.00	0.01 ± 0.00
Na (meq L^{-1})	0.06 ± 0.01	0.07 ± 0.02	0.06 ± 0.01	0.05 ± 0.01	0.02 ± 0.00	0.02 ± 0.00	0.01 ± 0.00	0.01 ± 0.00
Total bases (meq L^{-1})	0.23 ± 0.01	0.25 ± 0.10	0.15 ± 0.01	0.13 ± 0.00	0.14 ± 0.01	0.13 ± 0.00	0.07 ± 0.03	0.05 ± 0.01
Sulphates (meq L^{-1})	ND	0.01 ± 0.02	0.08 ± 0.01	0.08 ± 0.01	ND	ND	0.02 ± 0.01	ND
Chlorides (meq L^{-1})	0.02 ± 0.01	0.01 ± 0.01	ND	ND	0.01 ± 0.01	ND	ND	ND
Carbonates (meq L^{-1})	ND	ND	ND	ND	ND	ND	ND	ND
Bicarbonates (meq L^{-1})	0.22 ± 0.02	0.23 ± 0.11	0.07 ± 0.00	0.05 ± 0.01	0.13 ± 0.00	0.13 ± 0.00	0.05 ± 0.03	0.05 ± 0.01
Dissolved oxygen (mg L^{-1})#	5.0 ± 0.3	4.0 ± 0.2	4.0 ± 0.4	3.7 ± 0.0	5.3 ± 0.4	5.4 ± 0.0	4.4 ± 0.1	3.7 ± 1.7
Temperature (°C)#	25.7 ± 0.4	26.1 ± 0.0	24.7 ± 0.2	24.9 ± 0.3	25.4 ± 0.2	24.4 ± 0.2	24.6 ± 0.1	24.5 ± 0.1

Tsa samples (ANOVA F = 12.0, P = 0.01). Regarding sampling locations, there was a segregation between the two Pebas locations (Peb-Santa Sofía and Peb-Mata-matá; ANOVA F = 128, P < 0.01, Tukey's HSD test). Conductivity, concentrations of bases (Ca, Mg, K and Na), bicarbonates, and temperature, showed higher values in Pebas samples, especially in Peb-Santa Sofía, than in Tsa samples. Along the second PCA axis, which explained 26% of the variance, the geological units did not differ (ANOVA F = 0.7, P = 0.4), but the samples from Tsa-El Zafire had significantly higher scores than the other locations (ANOVA F = 24.5, P < 0.01, Tukey's HSD test) due to their higher pH and dissolved oxygen.

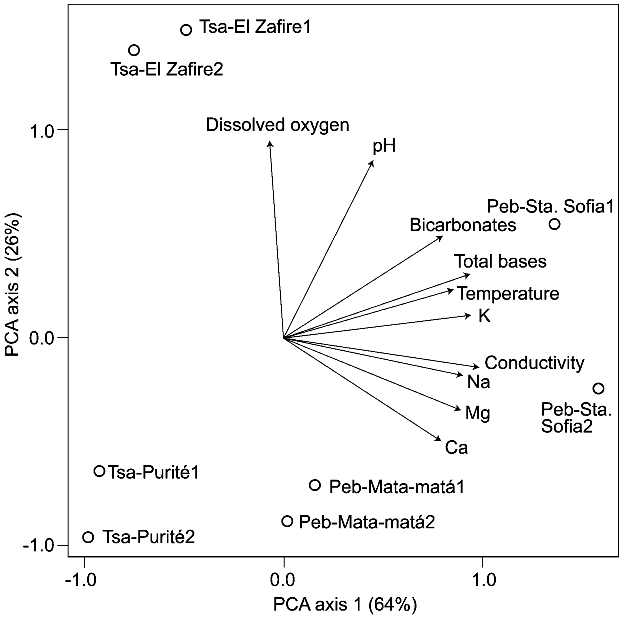

Figure 3. Results of a PCA based on sample averages of ten water physicochemical variables recorded in eight upland streams. The scatter plot shows the scores along the first and second PCA axis for each stream, labelled according to geological unit, sampling location and stream number. The arrows denote the variable loadings on the axes.

Ichthyofauna

In total, 7696 fish individuals were captured, belonging to eight orders, 28 families and 122 species (Appendix 1). The orders Characiformes and Siluriformes comprised 83% of the total species. These orders were also the most abundant, in particular Characiformes, which accounted for 81% of the captured individuals. The family Characidae showed the highest species richness (32%), followed by Loricariidae (9%) and Auchenipteridae (7%). The most abundant family was Characidae (74%), followed by Cichlidae (6%) and Loricariidae (3%). According to the Chao1 richness estimator, all samples contained 173 species (139–272 as 95% confidence interval). The ACE predicted 140 species (SD = 2.5), whereas the observed richness was 122 species (109–135 as Mao Tau 95% confidence interval). Thus, the observed richness accounted for 71% to 87% of the average estimated species number in the entire area.

The average richness per stream was 43 species, ranging from 35 species in stream Tsa-Purité1, to 54 in stream Peb-Santa Sofía1. Pebas streams had 1.3 times more species than Tsa streams, and more than twice the total biomass (Table 3). The number of individuals did not differ between geological units or sampling locations.

Species richness was highly correlated with conductivity (r = 0.96, N = 8, P < 0.01), and water concentrations of Mg (r = 0.84, N = 8, P < 0.01), K (r = 0.88, N = 8, P < 0.01) and Na (r = 0.93, N = 8, P < 0.01). Biomass was strongly correlated with conductivity (r = 0.94, N = 8, P < 0.01), and water

Table 3. Number of species, number of individuals, and total biomass (mean ± SD, cumulative totals in parentheses) in eight upland streams, arranged by geological unit and sampling location. F ratio and P are ANOVA results; ^{a,b} indicate results of Tukey's HSD test ($P < 0.05$).

	Geological units				Sampling locations					
	Pebas (n = 4)	Tsa (n = 4)	F ratio	P	Santa Sofía (n = 2)	Mata-matá (n = 2)	El Zafire (n = 2)	Purité (n = 2)	F ratio	P
Number of species	48 ± 6 (95)	38 ± 2 (69)	14.4	0.01	53 ± 1^{a} (69)	44 ± 4^{a} (53)	40 ± 1^{a,b} (54)	36 ± 1^{b} (47)	13.9	0.01
Number of individuals	1004 ± 105 (4014)	921 ± 283 (3682)	0.3	0.60	973 ± 112 (1946)	1034 ± 129 (2068)	977 ± 323 (1955)	864 ± 350 (1727)	0.2	0.92
Total biomass (g)	847 ± 437 (13048)	412 ± 243 (6419)	10.4	0.02	4012 ± 746^{a} (8023)	2512 ± 400^{a,b} (5025)	1736 ± 205^{b} (3471)	1474 ± 291^{b} (2948)	12.3	0.02

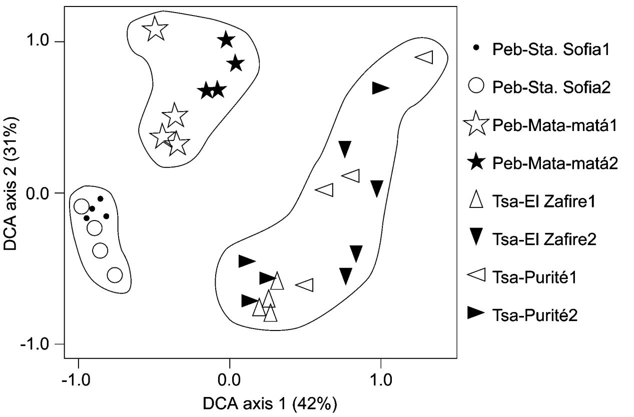

Figure 4. Results of a DCA based on the number of individuals per species for each sampling day in eight upland streams. The scatter plot shows the scores along the first and second DCA axis for 32 daily samples, labelled according to geological unit, sampling location, and stream number. Delineations illustrate the main groups formed by Hierarchical Cluster Analysis (Figure 5).

concentrations of Mg ($r = 0.90$, $N = 8$, $P < 0.01$), Na ($r = 0.87$, $N = 8$, $P < 0.01$) and dissolved oxygen ($r = 0.88$, $N = 8$, $P < 0.01$). The number of individuals, however, was not correlated with any water analytical variable. Biomass and species richness were significantly correlated ($r = 0.90$, $N = 8$, $P < 0.01$).

The graphic representation of the DCA (Figure 4) clearly grouped the daily samples by geological unit. The subsequent cluster analysis (Figure 5) confirmed that the Pebas sampling locations were well separated in the ordination diagram of the first and second DCA axes. However, the Tsa samples failed to separate according to sampling location.

DISCUSSION

Fish biomass, species richness and composition between geological units and sampling locations

The topsoil samples of the Tsa unit were sandier, had a lower CEC and lower exchangeable cation concentrations. Water samples from streams draining this unit had distinctly lower base concentrations compared with samples from the Pebas Formation. The Pebas streams supported more than twice the fish biomass found in Tsa streams. Total fish biomass was highly correlated with conductivity, and Mg and Ca concentrations. These results are in line with the positive correlations between fish biomass and water nutrient concentration documented elsewhere in Amazonia (Galacatos *et al.* 1996, Galvis *et al.* 2006, Ibarra & Stewart 1989, Saint-Paul *et al.* 2000).

Tsa streams supported a lower fish species richness than Pebas streams. Since the number of individuals captured was not significantly different, this difference was probably not due to undersampling. A high correlation was found between stream species richness and conductivity. Conductivity values (mean = 6.0 μS cm^{-1}, range = 5.3–6.5 μS cm^{-1}) and total species richness (69 species) of Tsa streams were quite similar to values reported from Manaus, Brazil (mean = 3.7 μS cm^{-1}, range = 3.0–8.0 μS cm^{-1}, 49 species; Mendonça *et al.* 2005). Pebas streams showed conductivity and species richness values (mean = 18.8 μS cm^{-1}, range = 13.5–23.8 μS cm^{-1}, 95 species) similar to an upland stream draining fluvial terraces of the Amazon River near Leticia, Colombia (mean = 30.6 μS cm^{-1}, range = 18.0–38.0 μS cm^{-1}, 120 species in Arbeláez *et al.* (2004), which increased to 137 following more recent surveys by Galvis *et al.* (2006)).

Fish species composition differed significantly between geological units. Species turnover was not related to distance between sampling locations, since streams 14 km away from each other had highly differentiated faunas (Peb-Mata-matá and Tsa-Purité), whereas the two samples from Tsa, 50 km apart from each other, had quite similar faunas. In upland streams, some fish taxa may not tolerate extremely low levels of elemental concentrations. This could explain the divergence of species assemblages in a mosaic of physical-chemical conditions (Mendonça *et al.* 2005). Possibly, differences in forest plant composition between the two geological units contributed to the divergent patterns in fish composition, as well. A differential distribution of stream fish species was also observed between two drainage basins that

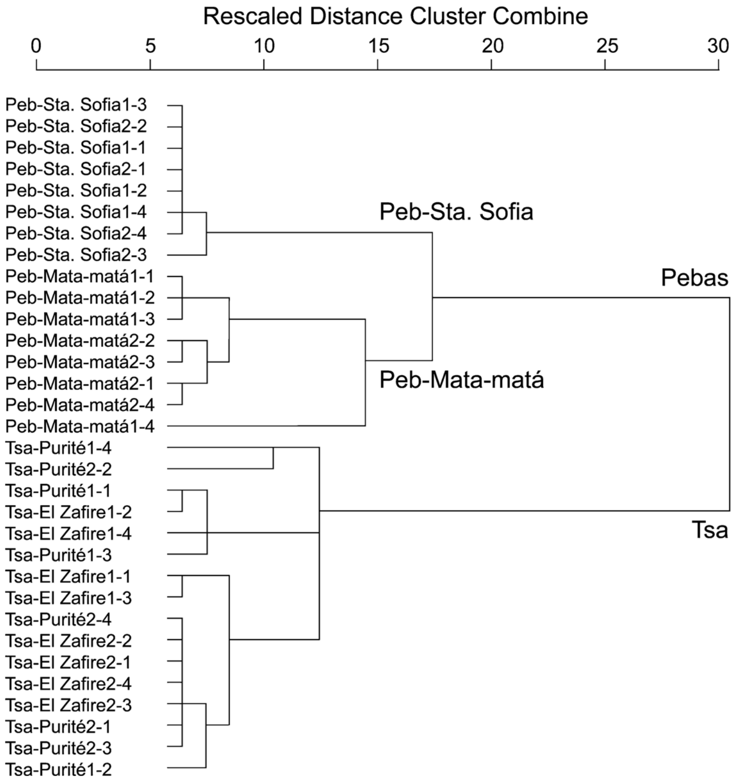

Figure 5. Dendrogram of a Hierarchical Cluster classification based on square Euclidean distances between the daily sample scores along DCA axis 1 and 2, shown in Figure 4. Each daily sample is labelled according to geological unit, sampling location, stream number and day number.

differed in soil texture and water properties (average conductivity and suspended particles) in the Reserva Florestal Adolfo Ducke, Central Amazonia (Mendonça *et al.* 2005). Faunal distribution patterns can be due to biogeographic history or to ecological requirements of species relative to habitat conditions related to soil geochemistry (Tuomisto 2007). Because of the short distances along which the species turnover occurred in the present study, the latter seems more probable.

Ichthyofauna and total species richness

The dominance in number of species and individuals of Characiformes, followed by Siluriformes, Perciformes (mainly Cichlidae) and Gymnotiformes, is commonly found in Amazonian fish communities (Galvis *et al.* 2006, Goulding *et al.* 1988, Lowe-McConnell 1987, Val & de Almeida-Val 1995). In north-west Amazonia upland streams, the genera *Moenkhausia* and *Hemigrammus* (Characidae) appear to be particularly diverse (Arbeláez *et al.* 2004, Galacatos *et al.* 1996), which was confirmed in this study (4 and 9 species, respectively; Appendix 1). Six species of *Tatia* (Auchenipteridae) were captured, which is a high number for upland streams. Three of these and one species of *Bunocephalus* (Aspredinidae) were sampled exclusively in Tsa locations and are probably new to science. With 122 species captured in eight streams, our study confirmed the high fish species richness in Amazonian upland streams (dos Anjos & Zuanon 2007, Knöppel 1970, Lowe-McConnell 1987, Mendonça *et al.* 2005). Totals of 137 and 143 species were captured in two streams near Leticia, Colombia (Arbeláez *et al.* 2004, Galvis *et al.* 2006). Three lowland tributaries of the Napo basin in Ecuador yielded 104 species (Galacatos *et al.* 1996). In contrast, surveys in Central Amazonia reported only 61 species in nine streams (dos Anjos & Zuanon 2007), 53 species in three streams (Knöppel 1970), or even fewer species in an unspecified number of streams (Bührnheim & Cox-Fernandes 2003, Henderson & Crampton 1997, Mendonça *et al.* 2005). Tributaries of the Juruá River in Brazilian Amazonia yielded 35 species in four streams (Silvano *et al.* 2000). The above comparisons are hazardous because different fish sampling protocols were applied, which influence species richness estimates (dos Anjos & Zuanon 2007).

The Chao1 estimator predicts richness based on the number of singletons (species with only one individual) and doubletons (species with two individuals) in each step of the sample accumulation procedure. In contrast, ACE uses a subjective number of individuals (10 in this case) to distinguish between infrequent and abundant species, and estimates species richness based on the occurrence of these infrequent species (Chao 2005). Because many species occurred with only one individual (19%), the Chao1 estimator predicted a larger richness (173 species) than ACE (140 ± 2.5 species), particularly in its upper 95% confidence interval (272 species). Even though the observed richness (122 species) was significantly lower than the estimated richness, it accounted for more than 71% of the latter. Its upper 95% confidence interval (135 species) was not very different from the estimated lower confidence intervals (139 and 137.5 species), implying that the data probably represented adequate approximations of the regional species richness.

ACKNOWLEDGEMENTS

Financial and logistical support was given by Tropenbos-Colombia, WWF-Education for Nature- Russel E. Train Fellowship programme, Institute for Biodiversity and Ecosystem Dynamics (IBED), Idea Wild, Instituto Alexander von Humboldt and Fundación BioDiversa Colombia. María Cristina Peñuela, Iván Arce, Juan David Bogotá, Donald Taphorn (Characiformes taxonomy), Alexandro Banda (map of Colombia), staff from the El Zafire field station and the Amacayacu National Park, and the communities of Santa Sofía, Mocagua and San Martín helped substantially. This study was part of the MSc in Tropical Ecology at the Universiteit van Amsterdam.

LITERATURE CITED

ARBELÁEZ, F., GÁLVIS, G., MOJICA, J. I. & DUQUE, S. R. 2004. Composition and richnes of the ichthyofauna in a *terra firme* forest stream of the Colombian Amazonia. *Amazoniana* 18:109–123.

BÜHRNHEIM, C. M. & COX-FERNANDES, C. 2001. Low seasonal variation of fish assemblages in Amazonian rain forest streams. *Ichthyological Exploration of Freshwaters* 12:65–78.

BÜHRNHEIM, C. M. & COX-FERNANDES, C. 2003. Structure of fish assemblages in Amazonian rain-forest streams: effects of habitats and locality. *Copeia* 2:255–262.

CHAO, A. 2005. Species richness estimation. Pp. 7909–7916 in Balakrishnan N., Read C. B. & Vidakovic B. (eds.). *Encyclopedia of statistical sciences*. Wiley, New York.

CRAMPTON, W. G. R. 1999. Os peixes da Reserva Mamirauá: diversidade e história natural na planície alagável da Amazônia. Pp. 10–36 in Queiroz H. L. & Crampton W. G. R. (eds.). *Estratégias para manejo de recursos pesqueiros em Mamirauá*. Sociedade Civil Mamirauá/CNPq, Brasília.

DOS ANJOS, M. B. & ZUANON, J. 2007. Sampling effort and fish species richness in small terra firme forest streams of central Amazonia, Brazil. *Neotropical Ichthyology* 5:45–52.

DUIVENVOORDEN, J. F. & LIPS, J. M. 1993. *Ecología del paisaje del Medio Caquetá: memoria explicativa de los mapas*. Tropenbos-Colombia, Bogotá. 301 pp.

DUIVENVOORDEN, J. F. & LIPS, J. M. 1995. *A land-ecological study of soils, vegetation, and plant diversity in Colombian Amazonia*. The Tropenbos Foundation, Wageningen. 438 pp.

GALACATOS, K., STEWART, D. J. & IBARRA, M. 1996. Fish community patterns of lagoons and associated tributaries in the Ecuadorian Amazon. *Copeia* 4:875–894.

GALVIS, G., MOJICA, J. I., DUQUE, S. R., CASTELLANOS, C., SÁNCHEZ-DUARTE, P., ARCE, M., GUTIÉRREZ, Á., JIMÉNEZ, L. F., SANTOS, M., VEJARANO, S., ARBELÁEZ, F., PRIETO, E. & LEIVA, M. 2006. *Peces del medio Amazonas – Región de Leticia*. Conservación Internacional, Bogotá D. C. 548 pp.

GOULDING, M., LEAL-CARVALHO, M. & FERREIRA, E. G. 1988. *Rio Negro, rich life in poor water: Amazonian diversity and foodchain ecology as seen through fish communities*. SPB Academic Publishing, The Hague. 200 pp.

HENDERSON, P. A. & CRAMPTON, W. G. R. 1997. A comparison of fish diversity and density between nutrient-rich and nutrient-poor lakes in the Upper Amazon. *Journal of Tropical Ecology* 13:175–198.

HENDERSON, P. A. & WALKER, I. 1986. On the leaf-litter community of the Amazonian blackwater stream Tarumazinho. *Journal of Tropical Ecology* 2:1–17.

HENDERSON, P. A. & WALKER, I. 1990. Spatial organization and population density of the fish community of the litter banks within a central Amazonian blackwater stream. *Journal of Fish Biology* 37:401–411.

HOORN, C. 1994. An environmental reconstruction of the paleo-Amazon River system (Middle-Late Miocene, NW Amazonia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 112:187–238.

HOORN, C. 2006. Mangrove forests and marine incursions in Neogene Amazonia (Lower Apaporis River, Colombia). *Palaios* 21:197–209.

IBARRA, M. & STEWART, D. J. 1989. Longitudinal zonation of sandy beach fishes in the Napo River Basin, Eastern Ecuador. *Copeia* 2:364–381.

IGAC 1990. *Métodos analíticos del laboratorio de suelos*. Instituto Geográfico "Agustín Codazzi", Bogotá. 502 pp.

JUNK, W. J. & SOARES, M. G. M. 2001. Freshwater fish habitats in Amazonia: state of knowledge, management, and protection. *Aquatic Ecosystem Health & Management* 4:437–451.

JUNK, W. J., SOARES, M. G. M. & BALEY, P. B. 2007. Freshwater fishes of the Amazon River basin: their biodiversity, fisheries, and habitats. *Aquatic Ecosystem Health and Management* 10:153–173.

KALLIOLA, R. & FLORES PAITAN, S. (eds.) 1998. *Geoecología y desarollo Amazónico: estudio integrado en la zona de Iquitos, Perú*. Turun Yliopisto, Turku. 544 pp.

KNÖPPEL, H. A. 1970. Food of central Amazonian fishes: contribution to the nutrient-ecology of Amazonian rainforest-streams. *Amazoniana* 2:257–352.

LIPS, J. M. & DUIVENVOORDEN, J. F. 1996. Fine litter input to terrestrial humus forms in Colombian Amazonia. *Oecologia* 108:138–150.

LOWE-MCCONNELL, R. H. 1987. *Ecological studies in tropical fish communities*. Cambridge University Press, Cambridge. 382 pp.

MENDONÇA, F. P., MAGNUSSON, W. E. & ZUANON, J. 2005. Relationships between habitat characteristics and fish assemblages in small streams of Central Amazonia. *Copeia* 4:751–764.

PAT 1997. *Zonificación ambiental para el plan modelo Colombo-Brasilero (Eje Apaporis-Tabatinga: PAT)*. IGAC, Bogotá. 410 pp.

PRORADAM 1979. *La Amazonia Colombiana y sus recursos*. Proyecto radargramético del Amazonas, República de Colombia, Bogotá. 590 pp.

RUDAS-LLERAS, A. & PRIETO-CRUZ, A. 2005. *Flórula del Parque Nacional Natural Amacayacu, Amazonas, Colombia*. Missouri Botanical Garden, Saint Louis. 680 pp.

SABINO, J. & ZUANON, J. 1998. A stream fish assemblage in Central Amazonia: distribution, activity patterns and feeding behavior. *Ichthyological Exploration of Freshwaters* 8:201–210.

SAINT-PAUL, U., ZUANON, J., CORREA, M. A. V., GARCIA, M., FABRE, N. N., BERGER, U. & JUNK, W. J. 2000. Fish communities in central Amazonian white- and blackwater floodplains. *Environmental Biology of Fishes* 57:235–250.

SAUL, W. G. 1975. An ecological study of fishes at a site in upper Amazonian Ecuador. *Proceedings of the Academy of Natural Sciences of Philadelphia* 127:93–134.

SILVA, C. P. D. 1993. Feeding and spatial distribution of some species of fishes in Igarape do Candiru, Amazonia, Brazil. *Acta Amazonica* 23:271–285.

SILVANO, R. A. M., DO AMARAL, B. D. & OYAKAWA, O. T. 2000. Spatial and temporal patterns of diversity and distribution of the Upper Jurua River fish community (Brazilian Amazon). *Environmental Biology of Fishes* 57:25–35.

TUOMISTO, H. 2007. Interpreting the biogeography of South America. *Journal of Biogeography* 34:1294–1295.

VAL, A. L. & DE ALMEIDA-VAL, V. M. F. 1995. *The fishes of the Amazon and their environment: physiological and biochemical aspect*. Springer-Verlag, Berlin. 224 pp.

VONHOF, H. B., WESSELINGH, F. P. & GANSSEN, G. M. 1998. Reconstruction of the Miocene western Amazonian aquatic system using molluscan isotopic signatures. *Palaeogeography, Palaeoclimatology, Palaeoecology* 141:85–93.

WALKER, I. 1995. Amazonian streams and small rivers. Pp. 167–193 in Tundisi, J. G., Bicudo, C. E. M. & Matsumura-Tundisi, T. (eds.). *Limnology in Brazil*. Sociedade Brasileira de Limnologia/Academia Brasileira de Ciencias, Brazil.

ZAR, J. H. 1996. *Biostatistical analysis*. Prentice Hall, London. 662 pp.

Appendix 1. Number of individuals of fish taxa recorded in eight upland streams, arranged over two geological units (Peb = Pebas, Tsa = Terciario Superior Amazónico) and four sampling locations (SS = Santa Sofía; MA = Mata-Matá; PU = Purité; ZA = El Zafire).

Species	Peb-SS1	Peb-SS2	Peb-MA1	Peb-MA2	Tsa-ZA1	Tsa-ZA2	Tsa-PU1	Tsa-PU2	Total
Characiformes (60 spp.)	851	763	718	869	1000	550	518	972	6241
Curimatidae	12	47	1	12					72
Curimatella alburna Müller & Troschel, 1844		3							3
Cyphocharax pantostictos Vari & Barriga S., 1990			1	12					13
Cyphocharax spiluropsis Eigenmann & Eigenmann, 1889		38							38
Steindachnerina guentheri Eigenmann & Eigenmann, 1889	12	6							18
Prochilodontidae	1								1
Semaprochilodus insignis Müller & Troschel, 1844	1								1
Anostomidae	1	5	2				1		9
Leporinus cf. *friderici* Bloch, 1794	1	3	2				1		7
Leporinus agassizi Steindachner, 1876		1							1
Leporinus cf. *natereri* Steindachner, 1876		1							1
Chilodontidae	1	3							4
Chilodus punctatus Müller & Troschel, 1844	1	3							4
Crenuchidae	29	26	40	17	4	6	2	13	137
Characidium sp. 1	11	10	1		1	3			26
Characidium sp. 2	9	10	37	17	2	3		3	81
Characidium sp. 3							1		1
Crenuchus spilurus Günther, 1863							1	8	9
Melanocharacidium cf. *nigrum* Buckup, 1993	9	6	2					2	19
Odonthocharacidium aphanes Weitzman & Kanazawa, 1977					1				1
Gasteropelecidae			11	52	4		1	3	71
Carnegiella strigata Günther, 1864			8	2	4		1	3	18
Gasteropelecus maculatus Steindachner, 1879			3	50					53
Characidae	807	680	592	678	981	539	501	928	5706
Acestrorhynchus lacustris Lütken, 1875	1		1	1		1			4
Astyanax abramis Jenyns, 1842	6	3	9						18
Astyanax anterior Géry, 1965			2			1		2	5
Axelrodia stigmatias Fowler, 1913					5				5
Brachychalcinus cf. *nummus* Böhlke, 1958	8			1					9
Brycon melanopterus Cope, 1872	7	3							10
Bryconops inpai Knöppel, Junk & Géry, 1968	11		3	1	271	92	96	25	499
Charax leticiae Lucena, 1987		1							1

Appendix 1. Continued.

Species	Peb-SS1	Peb-SS2	Peb-MA1	Peb-MA2	Tsa-ZA1	Tsa-ZA2	Tsa-PU1	Tsa-PU2	Total
Charax tectifer Cope, 1870	3	14	29	82	3	4		7	142
Creagrutus cochui Géry, 1964	80	18							98
Ctenobrycon hauxwellianus Cope, 1870	5								5
Cynopotamus cf. *amazonus* Günther, 1868		1							1
Gephyrocharax sp.	44	37	65	40	50	16	43	80	375
Hemibrycon sp.	4								4
Hemigrammus analis Durbin, 1909			3		93		69	123	288
Hemigrammus cf. *gracilis* Lütken, 1875	28								28
Hemigrammus levis Durbin, 1908			2	54	23				79
Hemigrammus sp.				11					11
Hyphessobrycon cf. *agulha* Fowler, 1913	3	9	31	182	237	89	60	107	718
Hyphessobrycon cf. *serpae* Durbin, 1908	1								1
Knodus breviceps Eigenmann, 1908	397	206	369	205	31	160	105	273	1746
Microschemobrycon cf. *geisleri* Géry, 1973	1				2	1			4
Moenkhausia cf. *chrysargyrea* Günther, 1864	10	29							39
Moenkhausia cf. *collettii* Steindachner, 1882		2							2
Moenkhausia comma Eigenmann, 1908			43	55	6		1		105
Moenkhausia cf. *dichroura* Kner, 1858	20	35							55
Moenkhausia cf. *lepidura* Kner, 1858	42	92			31				165
Moenkhausia oligolepis Günther, 1864	21	6	4	7		2			40
Moenkhausia sp. 1	4								4
Moenkhausia sp. 2			1	15					16
Moenkhausia tridentata Holly, 1929					6		62	30	98
Phenacogaster cf. *pectinatus* Cope, 1870	20	58			8	19			105
Pristobrycon sp. 1	3	1							4
Pristobrycon sp. 2	2	1							3
Roeboides myersii Gill, 1870		1							1
Tetragonopterus argenteus Cuvier, 1816	1	4							5
Triportheus cf. *angulatus* Spix & Agassiz, 1829	3	20							23
Triportheus pictus Garman, 1890	1								1
Tyttocharax cochui Ladiges, 1950	81	139	30	24	215	154	65	281	989
Erythrinidae		2	33	17	3	3	3	3	64
Hoplias malabaricus Bloch, 1794		2	33	17	3	3	3	3	64
Lebiasinidae			39	93	8	2	10	25	177
Copeina guttata Steindachner, 1876							1		1
Nannostomus marginatus Eigenmann, 1909			34	78		2	1		115
Pyrrhulina laeta Cope, 1872			5	15	8		8	25	61
Siluriformes (41 spp.)	147	93	75	86	125	108	39	40	713
Cetopsidae	9	1	1		16	9	10	9	55
Denticetopsis praecox Ferraris & Brown, 1991	9	1	1		16	8	9	8	52
Helogenes marmoratus Günther, 1863						1	1	1	3
Aspredinidae	24	17			36	11	1	2	91
Bunocephalus coracoideus Cope, 1874					1				1
Bunocephalus sp.					35	11	1	2	49
Pterobunocephalus sp.	24	17							41
Trichomycteridae			10	2				6	18
Trichomycterus sp.			10	2					12
Vandellia cirrhosa Valenciennes, 1846								6	6
Callichthyidae	8	6	1	9		27		8	59
Corydoras elegans Steindachner, 1876								7	7
Corydoras rabauti La Monte, 1941			1	9					10
Corydoras semiaquilus Weitzman, 1964						27			27
Corydoras sp.	8	6							14
Megalechis thoracata Valenciennes, 1840								1	1
Loricariidae	58	50	13	5	54	42	10	7	239
Ancistrus sp.	27	22	8	4	23	24	3	2	113
Farlowella oxyrryncha Kner, 1853	2		1			5	1	3	12
Farlowella platoryncha Retzer & Page, 1997			1						1
Hypostomus oculeus Fowler, 1943		2	1	1					4
Limatulichthys griseus Eigenmann, 1909	29	22							51
Otocinclus sp. 1					12	9	6	2	29
Otocinclus sp. 2					1	1			2
Parotocinclus sp.					6				6
Rineloricaria castroi Isbrücker & Nijssen, 1984		3	2			3			8

Appendix 1. Continued.

Species	Peb-SS1	Peb-SS2	Peb-MA1	Peb-MA2	Tsa-ZA1	Tsa-ZA2	Tsa-PU1	Tsa-PU2	Total
Rineloricaria cf. *lanceolata* Günther, 1868		1							1
Spatuloricaria sp.					12				12
Heptapteridae	30	11	2		10	10	3	4	70
Heptapteridae sp.							2		2
Heptapterus sp. 1	4	2							6
Heptapterus sp. 2					4	3	1	1	9
Mastiglanis asopos Bockmann, 1994	14								14
Mastiglanis sp.		5			3	1			9
Pimelodella cf. *steindachneri* Eigenmann, 1917	5	3							8
Pimelodella geryi Hoedeman, 1961	7	1	2		3	6		3	22
Pimelodidae	3	6							9
Pimelodus sp.	3	6							9
Doradidae		1							1
Scorpiodoras heckelii Kner, 1855		1							1
Auchenipteridae	15	1	48	70	9	9	15	4	171
Glanidium cf. *riberoi* Haseman, 1911		1				3			4
Glanidium sp.							1		1
Tatia cf. *intermedia* Steindachner, 1877					6	4	9	3	22
Tatia aulopygia Kner, 1858					1				1
Tatia perugiae Steindachner, 1882	15				2	1	5	1	24
Tatia sp. 1			1						1
Tatia sp. 2			32	18					50
Tatia sp. 3			15	52					67
Tetranematichthys quadrifilis Kner, 1858						1			1
Gymnotiformes (9 spp.)	40	17	67	70	1	34	4	15	248
Gymnotidae			13	11			1		25
Gymnotus cf. *carapo* Linnaeus, 1758			8	9					17
Gymnotus javari Albert, Crampton & Hagedorn, 2003			5	2					7
Gymnotus sp.							1		1
Sternopygidae	23	5	8	23		22		5	86
Eigenmannia virescens Valenciennes, 1842	19	4	8	19		20			70
Sternopygus macrurus Bloch & Schneider, 1801	4	1		4		2		5	16
Rhamphichthyidae	17	12			1	12	1	4	47
Gymnorhamphichthys rondoni Miranda-Ribeiro, 1920	17	12			1	12	1	4	47
Hypopomidae			46	36			2	6	90
Brachyhypopomus sp. 1			40	22			2	5	69
Brachyhypopomus sp. 2				9					9
Steatogenys elegans Steindachner, 1880			6	5				1	12
Cyprinodontiformes (2 spp.)				14		1	2		17
Rivulidae				14		1	2		17
Rivulus sp. 1				12		1			13
Rivulus sp. 2				2			2		4
Beloniformes (1 sp.)		2							2
Belonidae		2							2
Potamorrhaphis guianensis Jardine, 1843		2							2
Synbranchiformes (1 sp.)	1		1	1					3
Synbranchidae	1		1	1					3
Synbranchus marmoratus Bloch, 1795	1		1	1					3
Perciformes (7 spp.)	13	19	82	85	80	55	53	84	471
Polycentridae							1		1
Monocirrhus polyacanthus Heckel, 1840							1		1
Cichlidae	13	19	82	85	80	55	52	84	470
Apistogramma sp. 1		1	10	10	3		4		28
Apistogramma sp. 2			1	9		8	20	47	85
Apistogramma sp. 3			1	3					4
Biotodoma sp.					2	3		1	6
Bujurquina mariae Eigenmann, 1922	10	17	27	60	72	43	28	34	291
Crenicichla cf. *alta* Eigenmann, 1912	3	1	43	3	3	1		2	56
Lepidosireniformes (1 sp.)						1			1
Lepidosirenidae						1			1
Lepidosiren paradoxa Fitzinger, 1837						1			1
Total	1052	894	943	1125	1206	749	616	1111	7696