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Compositional change in fish assemblages along the Andean piedmont – Llanos floodplain gradient of the río Portuguesa, Venezuela

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The Llanos is an extensive area of savannas and floodplains in central and western Venezuela that encompasses a gradual elevation gradient from the río Orinoco to the foothills of the Andean piedmont. The río Portuguesa is one of the major rivers in this region that until recently had escaped major anthropogenic impacts and still maintains substantial seasonal fish migrations. However, little work has been conducted on fish ecology in this river. The present study analyzes museum collections sampled at 28 locations along the longitudinal gradient of the río Portuguesa to assess similarity of species composition from the foothills of the Andean piedmont to the lowland llanos floodplain. The standardized samples used in this analysis contained greater than 133 species representing 6 orders and 27 families, dominated by characiforms (61 species) and siluriforms (52 species). Detrended correspondence analysis (DCA) ordination of samples revealed a continual pattern of compositional change, and species are added at a faster rate than they are lost as one moves from the foothills of the piedmont to the low llanos. Based on DCA, samples from three elevational segments were found to significantly differ in fish species composition. Assemblages in the upper reaches contained unique species of loricariid catfishes, small pimelodid and trichomycterid catfishes, and small characiforms not observed at lower elevations. The lowland reach contained species of cichlids, large catfishes and characids not collected from the other two regions. Samples from the middle region revealed transitional species composition. Longitudinal species turnover probably reflects differences in environmental characteristics such as a water velocity, substrate composition and disturbance regime. Findings from this broad-scale analysis contribute to a baseline for future studies of fish ecology in this region.

Llanos corresponde a uma área extensa de savanas e planícies de inundação situadas no centro e no oeste da Venezuela, abrangendo um gradiente de elevação desde o rio Orinoco até a região montanhosa na base da cordilheira dos Andes. O rio Portuguesa é um dos principais rios desta região, até recentemente livre de maiores impactos antropogênicos, mantendo relevantes migrações sazonais de peixes. Apesar disto, poucos estudos sobre ecologia de peixes têm sido conduzidos neste ambiente. O presente estudo analisa coleções de museus amostradas em 28 locais ao longo do gradiente longitudinal do rio Portuguesa, avaliando a similaridade na composição das espécies desde a região montanhosa na base da cordilheira dos Andes até as terras baixas da planície de inundação do *Llanos*. As amostras padronizadas utilizadas nesta análise continham mais de 133 espécies, representando 6 ordens e 27 famílias, dominadas por caraciformes (61 espécies) e siluriformes (52 espécies). A ordenação das amostras através da análise de correspondência com remoção do efeito do arco (DCA) revelou um padrão contínuo de mudança na composição, com taxa de adição de espécies superior a de perda no sentido base da cordilheira ao baixo Llanos. Com base na DCA, as amostras dos três segmentos com distintas altitudes apresentaram diferenças significativas na composição das espécies de peixes. Assembéias do trecho superior contiveram unicamente espécies de loricarídeos, pimelodídeos de pequeno porte e tricomicterídeos, além de caraciformes de pequeno porte não observados nos segmentos inferiores. O trecho inferior apresentou espécies de ciclídeos, bagres de grande porte e caracídeos não coletados nas outras duas regiões. Amostras do trecho intermediário revelaram uma composição transicional de espécies. A alteração longitudinal na composição de espécies reflete, provavelmente, diferenças nas características ambientais, como: velocidade da água, composição do substrato e regime de distúrbio. Os achados desta análise de ampla-escala podem contribuir como ponto de partida para futuros estudos de ecologia de peixes nesta região.

Key words: longitudinal gradient, migration, ribazón, seasonality, turnover.

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Introduction

The Llanos is an extensive floodplain savanna in central and western Venezuela bordered by the Andes Mountains in the northwest, the Coastal Range (Cordillera de la Costa) to the north, and the Guiana Shield to the southeast. The region encompasses a gradual elevation gradient, from approximately 30 m above sea level at the río Orinoco to 150 m above sea level at the foothills of the Andean piedmont. The eastern flank of the Andes and the llanos are drained by left bank tributaries of the río Orinoco, which flows northeast through the center of Venezuela along the edge of the Guiana Shield. Lotic habitats vary across the elevational gradient, with piedmont segments characterized by steeper slopes, faster water velocity, and coarser substrates than low-gradient channels in the llanos (Baskin *et al*., 1980; Winemiller, 1989c).

The regional climate exhibits strong annual wet (late May to August) and dry (January to early May) seasonality. Average yearly rainfall is 1300 mm, with approximately 850 mm occurring between June and September (Winemiller, 1989a, 1989b). During the dry season, aquatic habitats of the llanos are largely restricted to creek channels, lagoons and remnant floodplain pools. Piedmont streams have reduced discharge during the dry season, and streams in areas of extensive deforestation may dry completely [see Lilyestrom & Taphorn (1983), Winemiller *et al*. (1996), and Allan *et al*. (2002)]. During the wet season, broad expanses of the llanos are inundated, and piedmont streams experience flash floods of short duration (Winemiller, 1989c). White-water tributaries draining the Andes (*e.g.* río Guanare, río Portuguesa) deposit nutrient-rich alluvial sediments in the llanos during flood periods. During the rainy season, many fishes migrate into lowland rivers, creeks and seasonally flooded terrain where they spawn (Winemiller, 1996). Other species spawn in the main river channel with eggs and larvae passively transported into marginal floodplain habitats.

During the falling-water period, large mixed-species schools called “ribazónes” ascend rivers of western Venezuela from the río Orinoco floodplain and río Apure delta and support an important commercial fishery. Barbarino-Duque *et al*. (1998) estimated 9,360,000 individuals occupying 9.0 ha along a 2.5 km stretch of the río Apure. Upstream migrations commence at the onset of the falling-water period, with school density decreasing as individuals settle out, are caught by fishermen, or are consumed by predators along the gradient. Recently, a combination of deforestation, overfishing, pollution, and river impoundment has had a dramatic effect on the size of ribazónes. Barbarino-Duque *et al*. (1998) characterized the status of ribazónes in western Venezuela as being either completely eliminated or greatly diminished in almost 80% of the primary Andean piedmont rivers (only 4 of the 24 rivers surveyed had substantial migrations).

The río Portuguesa is a white-water river in western Venezuela, extending over 300 km from its confluence with the río Apure in the lowland llanos to the foothills of the Andean piedmont (Fig. 1), and is one of the four rivers surveyed by Barbarino-Duque *et al*. (1998) that maintained a significant ribazón. Although the Portuguesa is one of the few rivers in western Venezuela that until recently remained in a relatively natural state, little work has been conducted on fish ecology in this river. In the last few years substantial deforestation in the piedmont headwaters has had a major impact, with the river almost drying completely during the most recent dry season. This study analyzes museum archives collected prior to the recent disturbances at 28 locations along the longitudinal gradient of the río Portuguesa to assess similarity of species composition from the edge of the Andean piedmont to the floodplains of the llanos, and tests for possible biotic regions of the río Portuguesa Basin. This study contributes toward a faunal baseline for future studies of fish ecology in this region.

Materials and Methods

Fish assemblage and field data were obtained from archives of the Museo de Ciencias Naturales de UNELLEZ (MCNG), Guanare, Estado Portuguesa, Venezuela. Sampling locations ranged from the low llanos near Camaguan in Estado Guarico (ca. 50 m elevation) to the foothills of the Andean piedmont (ca. 200 m elevation) northeast of Guanare, Estado Portuguesa (Fig. 1). Samples were included only if they fulfilled two primary requirements: 1) similar sampling methodology, and 2) high resolution location data (i.e. descriptional and/or GPS data). To reduce bias associated with sampling methodology,

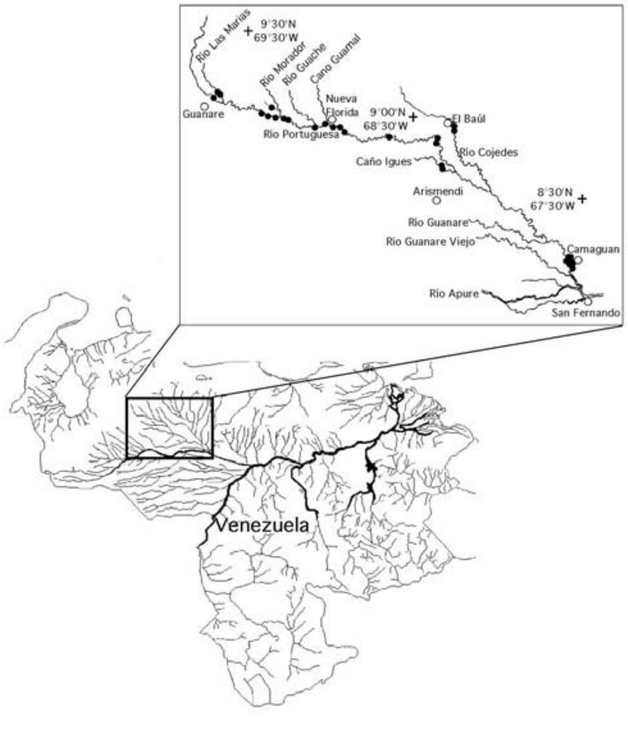

Fig.1. Map of Venezuela with inset showing locations of survey sites (n=28, filled circles) along the río Portuguesa elevational gradient.

presence/absence (*i.e.* species composition) data from samples collected using seines with mesh sizes between 3.2 and 6.4 mm were analyzed. Consequently, 28 of 37 available survey datasets were included in this analysis. Samples were collected by various researchers between 1981 and 1996 (Appendix A). Undescribed species were labeled by generic name only (*e.g. Hyphessobrycon* sp.). For cases in which species identity was questionable or unknown, all specimens and species within that genus were grouped for purposes of our analyses (*e.g. Eigenmannia* spp.).

To evaluate compositional similarity among sites, data were analyzed by correspondence analysis (CA) using CANOCO (Version 4, Microcomputer Power). The Guttman effect (arch effect), a mathematical artifact resulting from a systematic relationship between the first axis and subsequent axes, was present in the resulting ordination (likely the combined result of using presence/absence data and strong compositional differences among regions; Hill & Gauch, 1980; Gauch, 1982; Palmer, 1993; ter Braak & Smilauer, 1998; Quinn & Keough, 2002). Detrended correspondence analysis (DCA) was therefore performed to remove the arch. In the DCA, we detrended by segments and the resulting axes are scaled in units of standard deviation (SD), with a half turnover of species in samples occurring in 1 SD, and full species turnover in 4 SD (ter Braak & Smilauer, 1998).

Multivariate analysis of variance (MANOVA) and discriminant function analysis (DFA) were conducted to test for significance of groupings elucidated by DCA. Both analyses were conducted using "region" as a categorical variable and samples scores on the four axes obtained from DCA as dependent variables. Although the third and fourth DCA axes typically explain a very small proportion of the total explained variance (see Results), using variance explained on all DCA axes provides more robust MANOVA and DFA evaluations than using values from the first and second axes alone. DFA predicts region of origin for each sample, with the null hypothesis equal to the percentage of correct predictions expected by chance (in this case approximately 35%). Results from DFA are presented as percent correct classification. Both analyses were performed using the statistical package JMP (Version 4.04, SAS Institute Inc.).

Results

The 28 samples archived at MCNG included in this analysis contained at least 133 species representing 6 orders and 27 families, dominated by characiforms (61 species) and siluriforms (52 species) which together comprised 84% of all species collected (Appendix B). Most species occurred at relatively few survey sites, with 78% collected at fewer than 25% of the sites sampled. The most frequently collected species were the characids *Cheirodon pulcher* (Gill) and *Roeboides dayi* (Steindachner) (collected at 17 and 16 sites respectively), followed by siluriforms of the genus *Pimelodella* and gymnotiforms of the genus *Eigenmannia* (both collected at 15 sites; Appendix B).

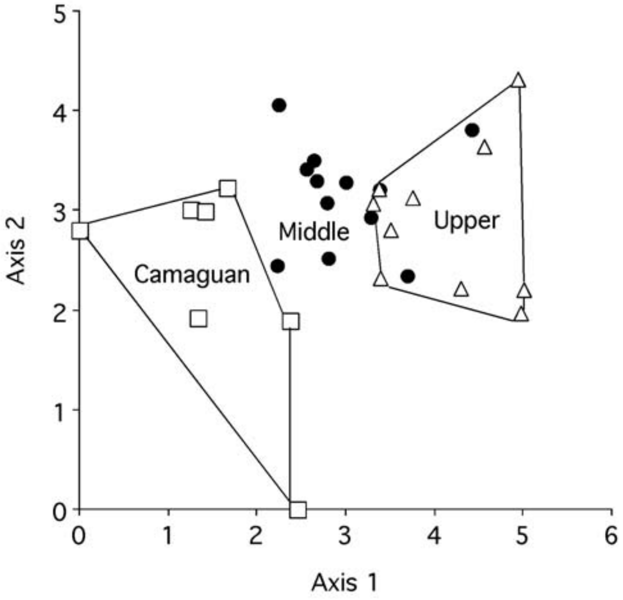

Fig. 2. DCA ordination of species assemblages at survey sites in three different elevational zones along the longitudinal gradient of the Portuguesa River, Venezuela: Camaguan, 50-100 m (open squares); Middle, 100-150 m (filled circles); and Upper, 150-200 m (open triangles). The three regions were significantly different in assemblage composition (MANOVA, p < 0.0001).

The first two DCA axes are presented for interpretation (axis 1-4 eigenvalues: 0.565, 0.363, 0.268, and 0.196 respectively). Ordination of samples by DCA revealed a continuous gradient of assemblage composition along the río Portuguesa longitudinal gradient, with lowland sites (Camaguan) scoring lowest and upland sites (100-200 m) tending to score highest on axis 1 (Fig. 2). Middle elevation sites (100-150 m) tended to have intermediate scores on axis 1 and 2, although there was overlap with upper elevation sites (150-200 m). Overall, the three regions had significantly different DCA loadings (MANOVA, $F_{8,44}= 7.22$, $p<0.0001$), and DFA correctly classified 83% of samples according to region (null of 35% correct classification). Divisions between these three regions can be roughly defined as the confluence of the río Guache with the río Portuguesa, and somewhere between the confluence of the río Cojedes with the río Portuguesa and Camaguan (an insufficient spatial distribution of sites was available in the lower reaches of the basin to more closely define the faunal break between the Camaguan and Middle regions, see Fig. 1).

Species composition of the Camaguan region was characterized by the large catfish species *Phractocephalus hemioliopterus* (Bloch and Schneider), *Pseudoplatystoma fasciatum* (Linnaeus) and *P. tigrinum* (Valenciennes) plus large characids such as the "cachama" [*Colossoma macropomum* (Cuvier)] and "morocoto" [*Piaractus brachypomus* (Cuvier)] (Table 1). The Camaguan region also has several smaller species that were not collected in middle and upper sites of the basin, including the poeciliid *Fluviphylax obscurum* (Costa) and cichlid species *Mesonauta egregius* Kullander & Silfvergrip and *Chaetobranchus flavescens* Heckel. The apteronotid knifefish *Sternarchorhamphus muelleri* (Steindachner), a species typically associated with the substrate of main-channels, was only collected from the Camaguan region.

Species characteristic of upper and middle reaches of the Portuguesa Basin included loricariid catfishes [*e.g. Lamontichthys llanero* Taphorn & Lilyestrom, *Panaque nigrolineatus* (Peters), *Loricaria cataphracta* Linnaeus, and an undescribed species *Pseudohemiodon* sp.], small pimelodid and trichomycterid catfishes (*Imparfinis* spp., *Cetopsorhamdia* sp., *Homodiaetus haemomyzon* Myers, and *Haemomaster venezuelae* Myers), and small characiforms (*Creagrutus* spp., *Bryconamericus* spp., and *Parodon apolinari* Myers) (Table 1). Species captured only from the upper region were *Parodon apolinari* and *Cetopsorhamdia* sp.

Table 1. Scores and frequencies of occurrence for species scoring highest and lowest values on the first two DCA ordination axes (see also Appendix B).

Species	Axis 1	Axis 2	No. sites
Mesonauta egregius	-2.00	2.71	1
Phractocephalus hemioliopterus	-0.83	1.39	2
Astronotus sp.	-0.78	3.10	2
Colossoma macropomum	-0.51	2.92	2
Chaetobranchus flavescens	-0.40	2.01	3
Pseudoplatystoma fasciatum	-0.40	2.01	3
Mylossoma duriventre	-0.10	3.15	3
Piaractus brachypomus	0.18	4.33	3
Hydrolycus armatus	0.44	3.51	1
Hypophthalmus marginatus	0.44	3.51	1
Pseudoplatystoma tigrinum	0.44	3.51	1
Acanthopoma bondi	1.48	6.78	1
Agamyxis albomaculatus	1.48	6.78	1
Bujurquina pulcher	1.48	6.78	1
Galeocharax sp.	1.48	6.78	1
Ageneiosus vittatus	2.07	-1.28	1
Fluviphylax pygmaeus	2.07	-1.28	1
Bryconamericus cismontanus	4.52	4.49	4
Astyanax superbus	4.63	4.37	3
Homodiaetus haemomyzon	4.87	1.29	3
Parodon apolinari	4.90	1.93	6
Creagrutus spp.	5.00	3.32	11
Bryconamericus sp.	5.09	2.69	8
Lamontichthys llanero	5.23	1.72	5
Engraulisoma taeniatum	5.30	2.49	4
Sternarchorhynchus curvirostris	5.36	1.54	3
Imparfinis spp.	5.37	4.25	7
Astyanax metae	5.45	5.65	2
Sturisoma tenuirostre	5.51	5.47	1
Hemibrycon metae	5.55	4.02	3
Loricaria cataphracta	5.55	1.80	3
Panaque nigrolineatus	5.65	1.45	4
Hyphessobrycon sp.	5.78	4.93	1
Pseudocetopsis sp.	5.78	4.93	1
Pseudohemiodon sp.	6.14	1.35	3
Cetopsorhamdia spp.	6.56	1.47	4
Haemomaster venezuelae	6.57	1.78	1
Hypoclinemus mentalis	6.57	1.78	1
Paraloricaria sp.	6.57	1.78	1

Samples from the middle region were transitional with most all species also collected from the upper and Camaguan regions. Species composition of the Middle region more closely resembled the Upper region than the Camaguan region (Fig. 2). Several species were only captured in the Middle region, but based on other survey information (Taphorn & Lilyestrom, 1984; Taphorn, 1992) only two of these seem to be unique to this region (*Epapterus blohmi* Vari, Jewett, Taphorn & Gilbert and *Galeocharax* sp.). The other species that were unique in Middle region surveys are known to occur in low-llanos habitats in Apure [*e.g. Agamyxis albomaculatus* (Peters), *Anostomus ternetzi* Fernández-Yépez, *Corydoras septentrionalis* Gosline, *Platynematichthys notatus* (Schomburgk), and *Potamorhina altamazonica* (Cope)]. Two species not collected from the Middle region, *Astronotus* sp. and *Pseudoplatystoma fasciatum*, have been collected at other sites within this elevation range within the basin (Winemiller, 1996).

Discussion

Based mostly on work from North America and Europe, longitudinal gradients of species composition in rivers and streams have long been recognized by aquatic ecologists [*e.g.* Burton & Odum (1945); Sheldon (1968); Horwitz (1978); Matthews (1986); Rahel & Hubert (1991)]. In general, compositional changes have been characterized as distinct faunal breaks or zones reflective of species additions as environmental complexity increases downstream [reviewed in Rahel & Hubert (1991)]. Patterns generated from temperate systems do not necessarily hold for tropical systems having greater taxonomic and ecological diversity. Yet several studies conducted on Neotropical rivers and streams over the last two decades have found significant patterns of fish assemblage differentiation along longitudinal gradients [*e.g.*, Ibarra & Stewart (1989); Winemiller & Leslie (1992); Rodiles-Hernández *et al*. (1999); Silvano *et al*. (2000); Abes & Agostinho (2001); Bistoni & Hued (2002)].

Our analyses examined fish assemblage composition in three elevational zones along the lower and middle reaches of the río Portuguesa (high Andean and piedmont zones were not included), which we termed the Camaguan (Lower), Middle (high llanos), and Upper regions (high llanos to piedmont transition). Assemblages of the Upper and Middle reaches are distinguished by certain species of small characiforms and siluriforms, especially loricariids. The Camaguan region differs in having more species of large catfishes, characiforms, and cichlids. Species composition in the Middle region was more similar to the Upper region than the Camaguan region. We observed highest species richness in the Middle region, in contrast to previous longitudinal gradient studies that generally have described patterns of increasing species richness in lower river stretches.

This observed pattern of species richness is probably an artifact due to sampling biases (*i.e.* collecting methods and effort, seasons, and habitats). For example, marginal floodplain pools (such as those common in the Camaguan region during the dry season) may shift to piscivore-dominated communities as the dry season progresses and small species are consumed with species diversity declining as a result. Also, some of the collections from the Camaguan region emphasized larger species (field notes of O. Castillo, UNELLEZ), and probably do not provide reliable samples of the complete fish assemblage in the lower reach of the río Portuguesa. Taphorn & Lilyestrom (1984) surveyed fishes in artificial floodplain pools in the low llanos of Apure, a region with aquatic habitats similar to those in the Camaguan region. They collected over 100 fish species, including most of the species recorded from Camaguan plus several reported only from our Middle region. The Camaguan region probably has highest species richness, and new species appear to be added at a higher rate than species are lost as one moves downstream from the piedmont to the low llanos of Apure. The distinct faunal break between the Camaguan and the Middle region suggested by the DCA ordination probably resulted from both sampling bias and a lack of sites between the Camaguan and Middle region. Data from surveys performed at additional sites in this area would probably yield a more gradual pattern of transition.

Differences in species assemblage composition along the longitudinal gradient of the río Portuguesa probably reflect differences in environmental characteristics. Survey sites located at highest elevations in our Upper region experience flash floods during the wet season, have relatively coarse substrates, and tend to have narrow floodplains. Survey sites at lower reaches had finer substrates, broad floodplains that are seasonally inundated, and more lentic habitats. Several species of algivorous armored catfishes are characteristic of the Upper region, potentially due to preferences for grazing smooth rock surfaces, such as cobble (Flecker, 1997). Ibarra & Stewart (1989) found greatest species assemblage turnover along the longitudinal gradient in association with major changes in substrate composition (*i.e.* absence of rock/cobble in lower stretches).

Our results are similar to findings from Baskin *et al.*'s (1980) study of trichomycterid and cetopsid catfishes in the Portuguesa Basin. They divided the río Portuguesa into three regions based on elevation: piedmont (above 200 m), high llanos (between 100 and 200 m), and low llanos (below 100 m). A single species (*Ochmacanthus alternus* Myers) was present below 100 m elevation, with 9 species found above 100 m. While these authors suggested that these species could be competitively excluded from the more diverse lowland areas, they also noted that the variation closely corresponded with a change from faster to slower-moving waters. Silvano *et al.* (2000) attributed faunal turnover in the Upper río Juruá of Brazil primarily to differences in water flow, as well as habitat specializations for some species (*e.g.* curimatids adapted for feeding on fine, organic-rich sediments).

Greater species richness of larger species in lower reaches may be associated with a more predictable (*i.e.* less stochastic) disturbance regime for the major aquatic habitats. Higher gradient upland reaches are more temporally variable and stochastic, and thus are expected to be inhabited by small species efficient at re-colonizing habitats following flash floods or other disturbances such as desiccation [*sensu* Schlosser (1987)]. In contrast, fish assemblages in tropical floodplain systems undergo seasonal changes determined by physical characteristics of the aquatic habitat and biotic interactions, both of which vary according to hydrological stage (Boujard, 1992; Rodríguez & Lewis, 1994; Winemiller, 1996; Tejerina-Garro *et al.*, 1998; Arrington, 2002; Hoeinghaus *et al.*, 2003).

Large-scale seasonal migrations of some species during rising- and falling-water periods could have a homogenizing effect on species composition during these periods. Our analysis included samples from different hydrologic periods, which could have reduced spatial variation in assemblage composition. Nevertheless, significantly different regional species compositions were observed. Results from this broad-scale approach are applicable to the development of future studies of fish ecology in the río Portuguesa, and the baseline this work provides for research and conservation is especially important in light of recent environmental threats (*e.g.* piedmont deforestation) within the basin.

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Appendix A. MCNG designation, date collected, and location for each collection included in the analyses. Dashed lines separate samples from the Camaguan, Middle and Upper regions.

MCNG Label	Date	Location
DCT85-55	22-Mar-81	Camaguan pool ca. 17 km N of San Fernando de Apure
OCI82-4	21-Jan-82	Río Camaguan, Fundo los Jagues
OC84-902	09-Aug-84	Río Camaguan near CANTV transmission tower
OCVI82-19	22-Jun-82	Río Camaguan near CANTV transmission tower
OCI82-3	14-Jan-82	Río Camaguan, KM 271
OCI82-2	11-Jan-82	Río Camaguan, km 271
OC82-1	11-Jan-82	Río Camaguan, Fundo los Chorros
KOW96-7	13-Aug-96	Igues Creek at Hwy 8
KOW96-9	14-Aug-96	Río Portuguesa 0.5 km upstream of Caño Guayabo
KOW96-8	14-Aug-96	Caño Guayabo near Hwy 8 bridge with Río Portuguesa
KOW96-10	15-Aug-96	Río Cojedes at El Baul
DCT84-84	06-Oct-84	Caño Igues, N of Arismendi
DCT84-87	06-Oct-84	Río Tinaco at El Baul and confluence With Río Cojedes
KOW96-5	10-Aug-96	Small creek, Río Portuguesa W bank, near Nueva Florida
DCT84-11	22-Jan-84	Río Portuguesa at La Aduana, ca. 40 km E of Papelón
KOW96-3	09-Aug-96	Caño Cocito near Nueva Florida
KOW96-6	11-Aug-96	Caño Guamal near Nueva Florida
DCT84-10	22-Jan-84	Caño Salado ca. 5 km S of Nueva Florida
KOW96-4	10-Aug-96	Río Portuguesa above confluence with Río Guache
DCT86-1	15-Jan-86	Río Las Marías at Rt. 5 bridge, NE of Guanare
KOW96-2	08-Aug-96	Río Portuguesa at Rt. 5 bridge, E of Guanare
LN84-66	13-Oct-84	Small creek ca. 6 km downstream from La Quebrada
DCT93-2	01-Jan-93	Río Portuguesa in Mata Larga
LN84-64	12-Oct-84	Río Portuguesa ca. 3 km upstream from La Quebrada
LN84-65	13-Oct-84	Río Portuguesa ca. 3 km downstream from La Quebrada
LN84-68	14-Oct-84	Slough upstream from La Quebrada
DCT84-23	10-Mar-84	Caño Mamon ca. 9 km SE of Rt. 5 towards La Quebrada
DCT84-66	08-May-84	Río Las Marías just below Rt. 5 bridge

Appendix B. Combined species list from all sites (n=28) and frequency of occurrence. Some species are grouped by genus due to limited taxonomic resolution for some specimens.

Order (n=6) Family (n=27)	Species (n≥133)	No. sites
Characiformes		
Anostomidae	*Abramites hypselonotus*	1
Anostomidae	*Anostomus ternetzi*	2
Anostomidae	*Leporinus friderici*	6
Anostomidae	*Leporinus striatus*	2
Anostomidae	*Schizodon* n sp.	6
Characidae	*Acestrocephalus* n sp.	1
Characidae	*Aphyocharax alburnus*	14
Characidae	*Astyanax bimaculatus*	7
Characidae	*Astyanax integer*	7
Characidae	*Astyanax metae*	2
Characidae	*Astyanax superbus*	3
Characidae	*Brycon whitei*	3
Characidae	*Bryconamericus beta*	10
Characidae	*Bryconamericus cismontanus*	4
Characidae	*Bryconamericus* sp.	8
Characidae	*Charax notulatus*	6
Characidae	*Cheirodon pulcher*	17
Characidae	*Cheirodontops geayi*	8
Characidae	*Colossoma macropomum*	2
Characidae	*Creagrutus* spp.	11
Characidae	*Ctenobrycon spilurus*	10
Characidae	*Cynopotamus bipunctatus*	4
Characidae	*Engraulisoma taeniatum*	4
Characidae	*Galeocharax* sp.	1
Characidae	*Gephyrocharax valenciae*	14
Characidae	*Hemibrycon metae*	3
Characidae	*Hemigrammus marginatus*	2
Characidae	*Hemigrammus micropterus*	1
Characidae	*Hemigrammus newboldi*	1
Characidae	*Hemigrammus* sp.	5
Characidae	*Hyphessobrycon* sp.	1
Characidae	*Markiana geayi*	4
Characidae	*Moenkhausia copei*	1
Characidae	*Moenkhausia dichroura*	5
Characidae	*Mylossoma duriventre*	3
Characidae	*Paragoniates alburnus*	3
Characidae	*Piaractus brachypomus*	3
Characidae	*Poptella compressa*	2
Characidae	*Pygocentrus cariba*	4
Characidae	*Roeboides affinis*	4
Characidae	*Roeboides dietonito*	16
Characidae	*Serrasalmus irritans*	8
Characidae	*Serrasalmus medinai*	1
Characidae	*Serrasalmus rhombeus*	6
Characidae	*Tetragonopterus argenteus*	3
Characidae	*Triportheus* spp.	6
Characidae	*Xenagoniates bondi*	8
Crenuchidae	*Characidium* spp.	11
Curimatidae	*Curimata cerasina*	7
Curimatidae	*Cyphocharax spilurus*	2
Curimatidae	*Potamorhina altamazonica*	1
Curimatidae	*Psectrogaster ciliata*	1
Curimatidae	*Steindachnerina argentea*	9
Cynodontidae	*Hydrolycus armatus*	1
Erythrinidae	*Hoplerythrinus unitaeniatus*	2
Erythrinidae	*Hoplias malabaricus*	8
Gasteropelecidae	*Thoracocharax stellatus*	13
Lebiasinidae	*Pyrrhulina lugubris*	1
Parodontidae	*Parodon apolinari*	6
Parodontidae	*Parodon* sp.	2
Prochilodontidae	*Prochilodus mariae*	9
Gymnotiformes		
Apteronotidae	*Adontosternarchus devenanzi*	2
Apteronotidae	*Apteronotus albifrons*	4
Apteronotidae	*Apteronotus bonapartii*	1
Apteronotidae	*Sternarchorhamphus muelleri*	1
Apteronotidae	*Sternarchorhynchus curvirostris*	3
Gymnotidae	*Gymnotus carapo*	2
Rhamphichthyidae	*Rhamphichthys marmoratus*	4
Sternopygidae	*Eigenmannia* spp.	15
Sternopygidae	*Sternopygus macrurus*	2
Siluriformes		
Aspredinidae	*Bunocephalus amaurus*	3
Auchenipteridae	*Ageneiosus magoi*	1
Auchenipteridae	*Auchenipterus ambyiacus*	1
Auchenipteridae	*Entomocorus gameroi*	2
Auchenipteridae	*Epapterus blohmi*	1
Auchenipteridae	*Parauchenipterus galeatus*	7
Callichthyidae	*Corydoras habrosus*	2
Callichthyidae	*Corydoras septentrionalis*	1

Callichthyidae	*Hoplosternum littorale*	2
Cetopsidae	*Pseudocetopsis* sp.	1
Doradidae	*Agamyxis albomaculatus*	1
Doradidae	*Oxydoras sifontesi*	1
Doradidae	*Platydoras costatus*	1
Loricariidae	*Chaetostoma milesi*	1
Loricariidae	*Cochliodon plecostomoides*	1
Loricariidae	*Farlowella mariaelenae*	1
Loricariidae	*Farlowella vittata*	9
Loricariidae	*Hypoptopoma steindachneri*	2
Loricariidae	*Hypostomus* spp.	9
Loricariidae	*Lamontichthys llanero*	5
Loricariidae	*Lasiancistrus mystacinus*	2
Loricariidae	*Liposarcus multiradiatus*	1
Loricariidae	*Loricaria cataphracta*	3
Loricariidae	*Loricariichthys brunneus*	7
Loricariidae	*Nannoptopoma spectabilis*	2
Loricariidae	*Panaque nigrolineatus*	4
Loricariidae	*Paraloricaria* sp.	1
Loricariidae	*Pseudohemiodon* sp.	3
Loricariidae	*Rineloricaria caracasensis*	9
Loricariidae	*Sturisoma tenuirostre*	1
Pimelodidae	*Cetopsorhamdia* spp.	4
Pimelodidae	*Hemisorubim platyrynchos*	3
Pimelodidae	*Heptapterus rosae*	1
Pimelodidae	*Hypophthalmus marginatus*	1
Pimelodidae	*Imparfinis* spp.	7
Pimelodidae	*Leiarius marmoratus*	1
Pimelodidae	*Phractocephalus hemioliopterus*	2
Pimelodidae	*Pimelodella* spp.	15
Pimelodidae	*Pimelodus blochii*	9
Pimelodidae	*Pimelodus ornatus*	3
Pimelodidae	*Platynematichthys notatus*	1
Pimelodidae	*Pseudopimelodus apurensis*	1
Pimelodidae	*Pseudoplatystoma fasciatum*	3
Pimelodidae	*Pseudoplatystoma tigrinum*	1
Pimelodidae	*Rhamdia quelen*	5
Pseudopimelodidae	*Microglanis iheringi*	1
Trichomycteridae	*Acanthopoma bondi*	1
Trichomycteridae	*Haemomaster venezuelae*	1
Trichomycteridae	*Homodiaetus haemomyzon*	3
Trichomycteridae	*Ochmacanthus alternus*	5
Trichomycteridae	*Vandellia cirrhosa*	4
Cyprinodontiformes		
Poeciliidae	*Fluviphylax obscurum*	1
Poeciliidae	*Poecilia reticulata*	10
Rivulidae	*Rachovia maculipinnis*	4
Perciformes		
Cichlidae	*Astronotus* sp.	2
Cichlidae	*Bujurquina pulcher*	8
Cichlidae	*Caquetaia kraussii*	10
Cichlidae	*Chaetobranchus flavescens*	3
Cichlidae	*Cichlasoma orinocense*	3
Cichlidae	*Crenicichla geayi*	6
Cichlidae	*Crenicichla* sp.	2
Cichlidae	*Mesonauta egregius*	1
Pleuronectiformes		
Achiridae	*Hypoclinemus mentalis*	1