
Diversity and Species Composition of Fish Communities of Orinoco Floodplain Lakes

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Fish communities of Neotropical floodplains are often characterized as highly variable in space and time, but basic patterns of species diversity, distribution, abundance, and temporal dynamics are still poorly described. To document these patterns and to quantify the relative magnitudes of spatial and temporal variation in species composition, floodplain fish communities in Venezuela were studied for two years. Fish were collected from 20 lakes in one blackwater and two whitewater regions along a 400-km stretch of the lower Orinoco River. Characoids and catfishes predominated in the collection of 170 species, followed by knifefishes and cichlids. Patterns of species richness hardly varied from year to year. Year-to-year variation in species composition of individual lakes was small compared with spatial variation among lakes. Most of the spatial variation in species composition was due to differences between the blackwater region and the two whitewater regions; the two whitewater regions hardly differed from each other, even though they were 400 km apart. The main finding is that species richness and species composition were strikingly constant from year to year at three levels: individual lakes, regions, and whole basin. The authors suggest that site-specific environmental attributes vary slowly with time and constrain the potentially high rates of change in floodplain fish communities.

In the past two decades a considerable amount of effort has been devoted to ecological studies of fish communities of South American fresh waters, most notably by Argentinian and Brazilian researchers working in the Paraná and Amazon Rivers. However, the present state of knowledge regarding even basic patterns of species diversity, distribution, abundance, and temporal dynamics is still fragmentary. Studies of fish communities in the Neotropics are often hampered by taxonomic uncertainties and by the logistic difficulties involved in collecting repeated samples at several localities, a prerequisite for adequate description of spatial and temporal variability. A solid understanding of the causes of variation of freshwater fish populations can be used to mitigate the undesirable effects of impending hydrological developments and forest exploitation throughout much of South America.

During the past few years, the authors have been studying fish communities in floodplain lakes of the lower Orinoco River, Venezuela. The goal has been to characterize the scope of spatio-temporal variation in these communities and to identify the main processes underlying such variation. This paper documents patterns of species diversity and distri-

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bution, and quantifies the relative magnitudes of spatial and temporal variation in the species composition of floodplain fish communities.

Methods

Study Area

Fish and environmental data were collected from 20 lakes in three regions within the lower Orinoco Basin (Figure 1). Four of the lakes are located along the Caura River near its confluence with the Orinoco, four lakes are located along the Orinoco near Caicara, and the remaining 12 lakes are located along the Orinoco near Ciudad Bolívar, ~400 km downstream from Caicara. Every year the Caura lakes are flooded by transparent blackwaters from the Caura River, whereas the Caicara and Ciudad Bolívar lakes are flooded by more turbid whitewaters from the Orinoco River. In general, water conductivity—which reflects ionic concentration—is highest in the Ciudad Bolívar lakes, intermediate in the Caicara lakes, and lowest in the Caura lakes. Other physicochemical and morphological variables of lakes differ little among regions.

This 20-lake sample represents ~2% of the fringing floodplain lakes in the study area (S.K. Hamilton, personal communication). During the high water season (July to November), the interconnections of the river and the lakes facilitate migration and reshuffling of adult and juvenile fish as well as widespread dispersal of eggs and larvae, which predominantly appear during this period. During the low water season (December to June), after river waters have receded, lakes become isolated and spatially discrete.

Sample Collection

The 20 lakes were sampled once in January (early dry season) and once in April or May (late dry season) during 1987 and 1988. Fish samples were collected with an electrofishing boat designed for operation in ionically dilute waters (Figure 2). This method yielded abundant catches and provided access to sites where conventional sampling methods such as netting would have been impracticable. Samples were taken near the shoreline along stretches selected at random. Fish were preserved in buffered 15% formalin and subsequently transferred to 70% ethanol. Specimens were identified and processed in the lab. Voucher specimens of nearly all species were deposited in the Museo de Biología, Universidad Central de Venezuela in Caracas. Additional specimens will be deposited in the Museum of the Academy of Natural Sciences of Philadelphia and the Museo UNELLEZ in Guanare, Venezuela.

Data Analysis

Species lists of the early and late dry season were pooled for each lake, yielding one list per lake for 1987 and one for 1988. The compositional similarity of the resulting 40 samples (20 lakes \times 2 years) was evaluated by computation of pairwise similarity indices for all pairs to generate a 40 \times 40 matrix. Two approaches were used to summarize the relationships expressed by similarity values. First, nonmetric multidimensional scaling was used to generate an ordination diagram in which the compositional affinities among all samples are graphically represented by the spacing of the samples on the diagram. Second, because some of the information contained in the similarity matrix is not contained in the ordination, several statistics for selected subsets of samples were calculated directly from the matrix. The objective of both approaches was to assess the relative magnitude of changes in species composition that

could be attributed to spatial variation (within and among regions) and to temporal (year to year) variation.

Two similarity indices (Jaccard's and Ochiai's) that do not use joint absences of species were used, because such absences convey little information about ecological resemblance. Ochiai's index incorporates a centering translation that reduces the effect of species richness on the evaluation of compositional similarity, and also performs well in non-metric multidimensional scaling ordinations. (See Jackson et al. 1989 for detailed descriptions of the indices and evaluation of index performances.) Because both indices yielded virtually identical qualitative results, only those based on Ochiai's index are presented here.

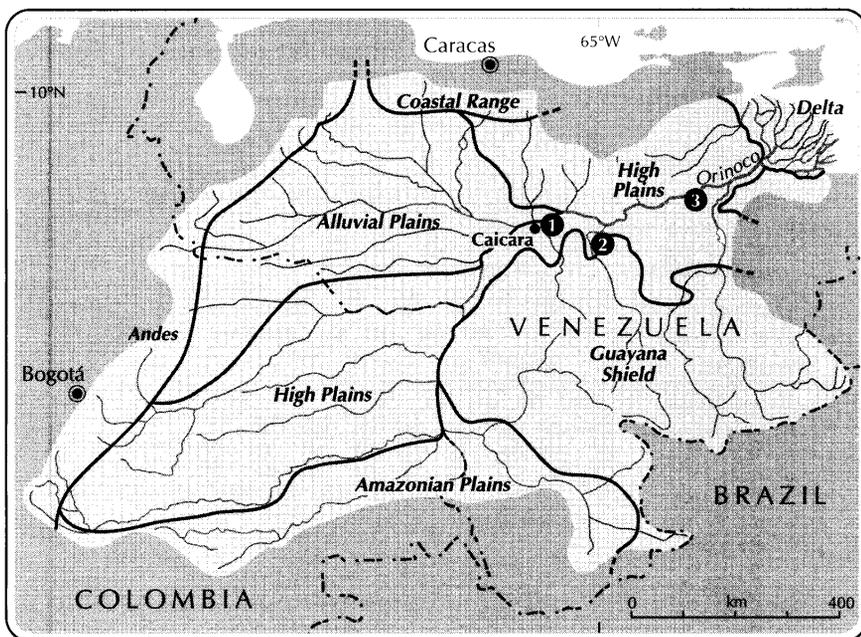


Figure 1. The Orinoco Basin, showing major geographic areas and the location of the study sites: 1, Caicara; 2, Caura; and 3, Ciudad Bolívar.

Results

Patterns of Species Richness

In all, 18822 fish were collected. Table 1 is a species checklist. Several species of small tetras, mainly of the genera *Astyanax* and *Moenkhausia*, abounded but were excluded here because of the vast difficulties involved in properly sorting and identifying these specimens. This should not influence the results, because seldom were more than three or four of these species excluded from a sample. A total of 170 species was distributed among 109 genera, 30 families, and 8 orders.

Table 2 summarizes the distribution of species among orders, and provides a comparison with other intensive collecting efforts in South America. The Characiformes (including tetras, silver dollars, headstanders, and hatchfishes) and Siluriformes (catfishes) predominate, followed by the Perciformes (mainly cichlids) and Gymnotiformes (knifefishes), in agreement with the findings of other authors. These four orders include ~90% of the species in all the collections. Other orders represented were Clupeiformes (herrings and anchovies, 6%), Atheriniformes (needlefish and halfbeaks, 1%), Tetraodontiformes (puffers, <1%), and Pleuronectiformes (soles, <1%).

Table 3 shows the distribution of species among regions. The results are highly consistent from one year to the next, and show that Caicara

Table 1. Fish Species, Orinoco Floodplain Lakes

Family Genus and species	MBUCV* Cat. No.	Family Genus and species	MBUCV* Cat. No.	Family Genus and species	MBUCV* Cat. No.
ACHIRIDAE (1)		<i>R. dayi</i>		GASTEROPELECIDAE (1)	
<i>Hypoclinemus mentalis</i>	V-17712	<i>R. myersi</i>	V-17195	<i>Thoracocharax stellatus</i>	V-17182
ANOSTOMIDAE (8)		<i>Serrasalmus elongatus</i>	V-17200	HEMIODONTIDAE (6)	
<i>Anostomus ternetzi</i>		<i>S. irritans</i>	V-17197	<i>Anodus orinocensis</i>	V-17193
<i>Laemolyta orinocensis</i>	V-17198	<i>S. rhombeus</i>	V-17707	<i>Argonectes longiceps</i>	
<i>L. taeniata</i>	V-17697	<i>Tetragonopterus argenteus</i>		<i>Hemiodopsis argentea</i>	
<i>Leporinus</i> sp. a		<i>Triporthus angulatus</i>	V-17201	<i>H. gracilis</i>	V-17693
<i>Le. agassizi</i>	V-17678	<i>T. culter</i>	V-17199	<i>H. immaculata</i>	V-17220
<i>Le. cf. friderici</i>	V-17681	<i>T. elongatus</i>	V-17190	<i>Hemiodus unimaculatus</i>	V-17217
<i>Le. fasciatus</i>	V-17187	<i>T. rotundatus</i>	V-17691	HEMIRHAMPHIDAE (1)	
<i>Schizodon</i> cf. <i>fasciatum</i>	V-17223	CHILODONTIDAE (1)		<i>Hyporhamphus</i> sp. a	
APTERONOTIDAE (4)		<i>Caenotropus labyrinthicus</i>	V-17189	HYPOPHthalmIDAE (1)	
<i>Adontosternarchus</i>		CICHLIDAE (11)		<i>Hypophthalmus edentatus</i>	V-17185
<i>devenanzii</i>	V-17173	<i>Aequidens pulcher</i>	V-17231	HYPOPOMIDAE (1)	
<i>Apteronotidae</i> sp. b		<i>Astronotus ocellatus</i>		<i>Hypopomus</i> sp. a	
<i>Apteronotus albifrons</i>	V-17680	<i>Biotoecus opercularis</i>	V-17713	LEBIASINIDAE (1)	
<i>Sternarchorhamphus</i>		<i>Caquetaia kraussii</i>	V-17686	<i>Pyrrhulina</i> cf. <i>eleonorae</i>	
<i>muelleri</i>	V-17690	<i>Chaetobranchius flavescens</i>		LORICARIIDAE (9)	
ASPREIDINIDAE (1)		<i>Cichla ocellaris</i>	V-17177	<i>Cochliodon plecostomoides</i>	V-17178
<i>Bunocephalus</i> sp. a		<i>C. temensis</i>	V-17694	<i>Hypoptopoma joberti</i>	V-17236
AUCHENIPTERIDAE (3)		<i>Geophagus surinamensis</i>	V-17216	<i>Hypostomus</i> cf. <i>watwata</i>	V-17169
<i>Auchenipterus nuchalis</i>	V-17704	<i>Mesonauta festinus</i>		<i>H. plecostomus</i>	V-17170
<i>Entomocorus gameroi</i>	V-17186	<i>Satanoperca daemon</i>	V-17212	<i>Loricaria</i> cf. <i>cataphracta</i>	V-17171
<i>Parauchenipterus galeatus</i>	V-17698	<i>S. jurupari</i>	V-17213	<i>Loricariichthys brunneus</i>	V-17242
BELONIDAE (1)		CLUPEIDAE (3)		<i>Pterygoplichthys</i> cf.	
<i>Potamorhaphis guianensis</i>	V-17196	<i>Pellona castelnaeana</i>		<i>punctatus</i>	V-17203
CALLICHTHYDAE (1)		<i>P. flavipinnis</i>	V-17241	<i>P. gibbiceps</i>	V-17687
<i>Hoplosternum littorale</i>	V-19106	<i>Rhinosardinia amazonica</i>	V-17237	<i>Sturisoma</i> cf. <i>tenuirostre</i>	V-17174
CHARACIDAE (49)		CTENOLUCIIDAE (3)		PIMELODIDAE (18)	
<i>Acestrorhynchus</i> cf. <i>britskii</i>		<i>Boulengerella</i> cf. <i>lucia</i>		<i>Callophysus</i> cf. <i>macropterus</i>	
<i>A. cir. microlepis</i>		<i>B. lucia</i>	V-17218	<i>Duopalatinus malarma</i>	
<i>A. grandoculis</i>		<i>B. maculata</i>		<i>Hemisorubim platyrhynchus</i>	V-17683
<i>A. heterolepis</i>		CURIMATIDAE (17)		<i>Leiarius marmoratus</i>	
<i>A. microlepis</i>	V-17240	<i>“Curimata”</i> sp. a	V-19104	<i>Pimelodella</i> sp. a	V-17244
<i>A. nasutus</i>	V-17254	<i>“Curimata”</i> sp. b		<i>P. cf. metae</i>	
<i>Agoniatas</i> cf. <i>anchovia</i>	V-17238	<i>C. cerasina</i>		<i>P. cristata</i>	V-17221
<i>Aphyocharax alburnus</i>	V-17246	<i>C. cf. incompta</i>	V-17252	<i>Pimelodina</i> sp. a	V-19101
<i>Brycon</i> cf. <i>whitei</i>	V-17684	<i>C. cf. ocellata</i>	V-17695	<i>Pimelodus blochii</i>	V-17232
<i>Bryconops</i> cf. <i>alburnoides</i>	V-17239	<i>C. cf. vittata</i>	V-17706	<i>P. aff. blochii</i>	
<i>B. cf. caudomaculatus</i>		<i>C. incompta</i>	V-17208	<i>P. cf. blochii</i>	V-17245
<i>Characidium</i> cf. <i>fasciatum</i>		<i>Curimatella bolivarensis</i>	V-17253	<i>P. cir. blochii</i>	V-17233
<i>Charax</i> cf. <i>gibbosus</i>	V-17711	<i>Cu. cf. immaculata</i>	V-17222	<i>Pinirampus</i> cf. <i>pinirampu</i>	
<i>C. gibbosus</i>		<i>Cu. immaculata</i>	V-17224	<i>Pseudoplatystoma</i>	
<i>Colossoma macropomum</i>		<i>Curimatopsis macrolepis</i>		<i>fasciatum</i>	V-18396
<i>Ctenobrycon hauzwillianus</i>	V-17206	<i>Cyphocharax</i> cf. <i>spilurus</i>	V-17226	<i>Ps. tigrinum</i>	V-17210
<i>Eucynopotamus biserialis</i>	V-17682	<i>Potamorhina altamazonica</i>	V-17689	<i>Rhamdia</i> cf. <i>sebae</i>	
<i>Hemigrammus</i>		<i>Psectrogaster ciliata</i>	V-17209	<i>Sorubim latirostris</i>	V-17225
<i>rhodostomus</i>	V-17256	<i>Steindachnerina argentea</i>	V-17205	<i>S. lima</i>	V-17192
<i>Hypessobrycon gracilior</i>		<i>S. cf. bimaculata</i>	V-17710	PROCHILODONTIDAE (3)	
<i>Iguanodectes spilurus</i>	V-18398	<i>S. metae</i>	V-17250	<i>Prochilodus mariae</i>	V-17230
<i>Markiana geayi</i>		CYNODONTIDAE (3)		<i>Semaprochilodus kneri</i>	V-17207
<i>Metymnis hypsauchen</i>	V-17211	<i>Hydrolycus scomberoides</i>	V-17176	<i>S. laticeps</i>	V-17204
<i>M. lippincottianus</i>	V-17685	<i>Rhaphiodon gibbus</i>	V-17181	RHAMPHICHTHYDAE (2)	
<i>M. luna</i>	V-17183	<i>R. vulpinus</i>	V-17168	<i>Rhamphichthys</i> cf.	
<i>Moenkhausia ceros</i>		DORADIDAE (4)		<i>reinhardtii</i>	V-17172
<i>Mo. cf. lepidura</i>		<i>Amblydoras hancocki</i>	V-17702	<i>R. marmoratus</i>	V-17179
<i>Mo. chrysargyrea</i>	V-17708	<i>Hassar</i> sp. a		SCIAENIDAE (2)	
<i>Mo. doceana</i>	V-19103	<i>H. notospilus</i>	V-17229	<i>Micropogon furnieri</i>	V-17696
<i>Mo. intermedia</i>	V-17227	<i>Pseudodoras niger</i>	V-17219	<i>Plagioscion squamosissimus</i>	V-17175
<i>Myles</i> cf. <i>rubripinnis</i>	V-17692	ENGRAULIDAE (7)		STERNOPYGIDAE (6)	
<i>Mylossoma aureum</i>	V-17688	<i>Anchovia surinamensis</i>	V-17249	<i>Distocyclus conirostris</i>	V-17679
<i>My. duriventre</i>	V-17191	<i>Anchoviella</i> sp. b		<i>Eigenmannia humboldtii</i>	V-17234
<i>Paragoniatas alburnus</i>		<i>Anchoviella</i> sp. c	V-19105	<i>E. macrops</i>	V-17701
<i>Piaractus brachypomus</i>	V-17184	<i>A. guianensis</i>	V-17248	<i>E. virescens</i>	V-17709
<i>Poptella orbicularis</i>	V-17214	<i>Lycengraulis</i> cf. <i>batesii</i>	V-18397	<i>Rhabdolichops troscheli</i>	
<i>Pristobrycon calmoni</i>		<i>L. cf. grossidens</i>	V-17251	<i>Sternopygus macrurus</i>	V-17180
<i>P. striulatus</i>		<i>Pterengraulis atherinoides</i>	V-17699	TETRAODONTIDAE (1)	
<i>Pygocentrus notatus</i>	V-17202	ERYTHRINIDAE (1)		<i>Colomesus asellus</i>	V-17700
<i>Roeboidea</i> cf. <i>affinis</i>	V-17215	<i>Hoplias malabaricus</i>	V-17194		

*Voucher specimens of nearly all species were deposited in the Museo de Biología, Universidad Central de Venezuela (MBUCV) in Caracas. Additional specimens will be deposited in the Museum of the Academy of Natural Sciences of Philadelphia and the Museo UNELLEZ in Guanare, Venezuela.

has the highest species richness, followed by Ciudad Bolívar. Species richness in the Caura region is substantially lower than in the two other regions. Two of the lakes in the Caicara region are on the left margin of the Orinoco and are influenced by the silt-laden Apure River which enters the Orinoco on the left margin, ~25 km upriver from Caicara. The two other Caicara lakes are on the right margin of the Orinoco and are influenced by low-conductivity waters from the middle Orinoco, but not by Apure waters. Left and right margin lakes in Caicara thus differ in conductivity, and this heterogeneity of water types might underlie the high species richness of the region. Figure 3 shows that Caicara and Ciudad Bolívar share a high proportion of species, but that a much lower proportion is shared by either region with the Caura region: 43% of the



S.K. Hamilton

Figure 2. Electrofishing boat designed for waters of low conductivity. Pulsed electric current induces fish to swim toward the circular anodes, where they are stunned. Specimens are easily retrieved with a dip net, even in turbid, silt-laden waters.

species found in the Caura region are not found in the two other regions. A “core” group of widespread and ubiquitous species occurs in all three regions. Species in this group are taxonomically and ecologically diverse (Figure 4) and pose the difficult challenge of determining which attributes allow them to be so successful.

Table 4 presents the number of species captured per lake in both years. These numbers are somewhat higher than those obtained in similar lake systems by use of rotenone (Mago-Leccia 1970: ~25 spp.), seine hand nets (Cordiviola de Yuan 1980: $n=14$, mean=13.8, SD=6.3, range=4 to 25), trawl nets (Oldani & Tablado 1985: 25 spp.), and seines (Pignalberi de Hassan & Cordiviola de Yuan 1985: $n=28$, mean=14.8, SD=12.5, range=3 to 50; Lasso In press: $n=13$, mean=22.0, SD=14.7, range=5 to 50), in part because samples from the early and late dry season were pooled. In spite of the high year-to-year variability in species richness for some lakes, the overall mean, standard deviation, and range for the 20 lakes are remarkably similar for both years.

Spatial and Temporal Variation of Species Composition

The nonmetric multidimensional scaling ordination based on sample similarities is shown in Figure 5. Caura samples for both years are neatly separated along dimension 1 from those of Ciudad Bolívar and Caicara, whereas the two latter regions overlap considerably along both dimensions. On average, year-to-year variation for individual lakes is smaller than the spatial variation found each year among lakes. This holds for

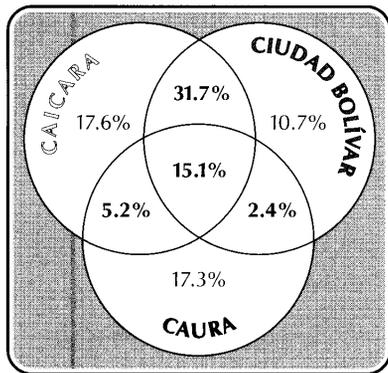


Figure 3. Venn diagram of the distribution of species among the three study regions. The percentages are averages of 1987 and 1988.

each region considered singly and for the 20-lake ensemble.

Some distortion of intersample similarities must be introduced when compressing the information contained in the 40×40 matrix onto a two-dimensional representation. To determine whether this effect biased interpretation of the ordination, the authors calculated directly from the matrix summary statistics of similarity values among regions, within regions, and between years (Table 5). When all lakes are considered jointly (upper sector of Table 5), year-to-year variation is considerably smaller than spatial variation within years. When regions are considered individually (middle sector of Table 5), again year-to-year variation is smaller than spatial variation within years. The lower sector of Table 5 shows that Ciudad Bolívar and Caicara resemble each other more than either resembles Caura. Furthermore, the mean similarities between Ciudad Bolívar and Caicara (46.1 and 42.3) are comparable with those within Ciudad Bolívar (47.7 and 49.2) and Caicara (48.7 and 40.6), indicating that these two regions differ little from each other. Thus, there is complete agreement between the results of the nonmetric multidimensional scaling ordination and those shown in Table 5. These results can be summarized as follows:

- Year-to-year variation in the species composition of individual lakes is small relative to the spatial variation among lakes within any year—a result that holds when regions are considered individually and also when the 20 lakes are considered jointly.

Table 2. Distribution of Species among Orders in Studies of South American Water-bodies

Habitat	Characiformes (%)	Siluriformes (%)	Perciformes (%)	Gymnotiformes (%)	Source
Summary data for the Amazon River	43	39	—	3	Lowe-McConnell (1987)
Amazon River near Manaus	41	29	13	7	Bayley (1982)
Middle Paraná floodplain lakes	49	27	11	6	Cordiviola de Yuan (1980)
Lower Orinoco floodplain lakes	35	33	18	6	Lasso (In press)
Napo and Aguarico Rivers, Ecuador	51	39	—	—	Ibarra & Stuart (1989)
Lower Orinoco floodplain lakes	55	22	8	8	this study

Table 3. Distribution of Species among Regions, 1987 and 1988

	1987		1988	
	No. of Species	Adjusted*	No. of Species	Adjusted*
Total species, all regions	150	133	146	132
Total Ciudad Bolívar (12 lakes)	111	79	108	79
Total Caicara (4 lakes)	91	91	93	93
Total Caura (4 lakes)	52	52	54	54
Ciudad Bolívar only	32	15	34	14
Caicara only	17	25	14	21
Caura only	19	22	22	24
Ciudad Bolívar and Caicara only	49	41	50	43
Ciudad Bolívar and Caura only	8	5	5	1
Caicara and Caura only	3	6	2	8
Ciudad Bolívar, Caicara, and Caura	22	19	29	21

*Species richness increases with number of lakes sampled, and more lakes were sampled in Ciudad Bolívar than in Caicara or Caura. Therefore, to validate comparisons among regions the following adjustment was made: the 12 Ciudad Bolívar lakes were randomly divided into three subsets of four lakes each; for each subset the number of species in each category was recalculated; and the three sets of values were averaged. These adjusted totals represent expected values, had only four lakes been sampled in Ciudad Bolívar.

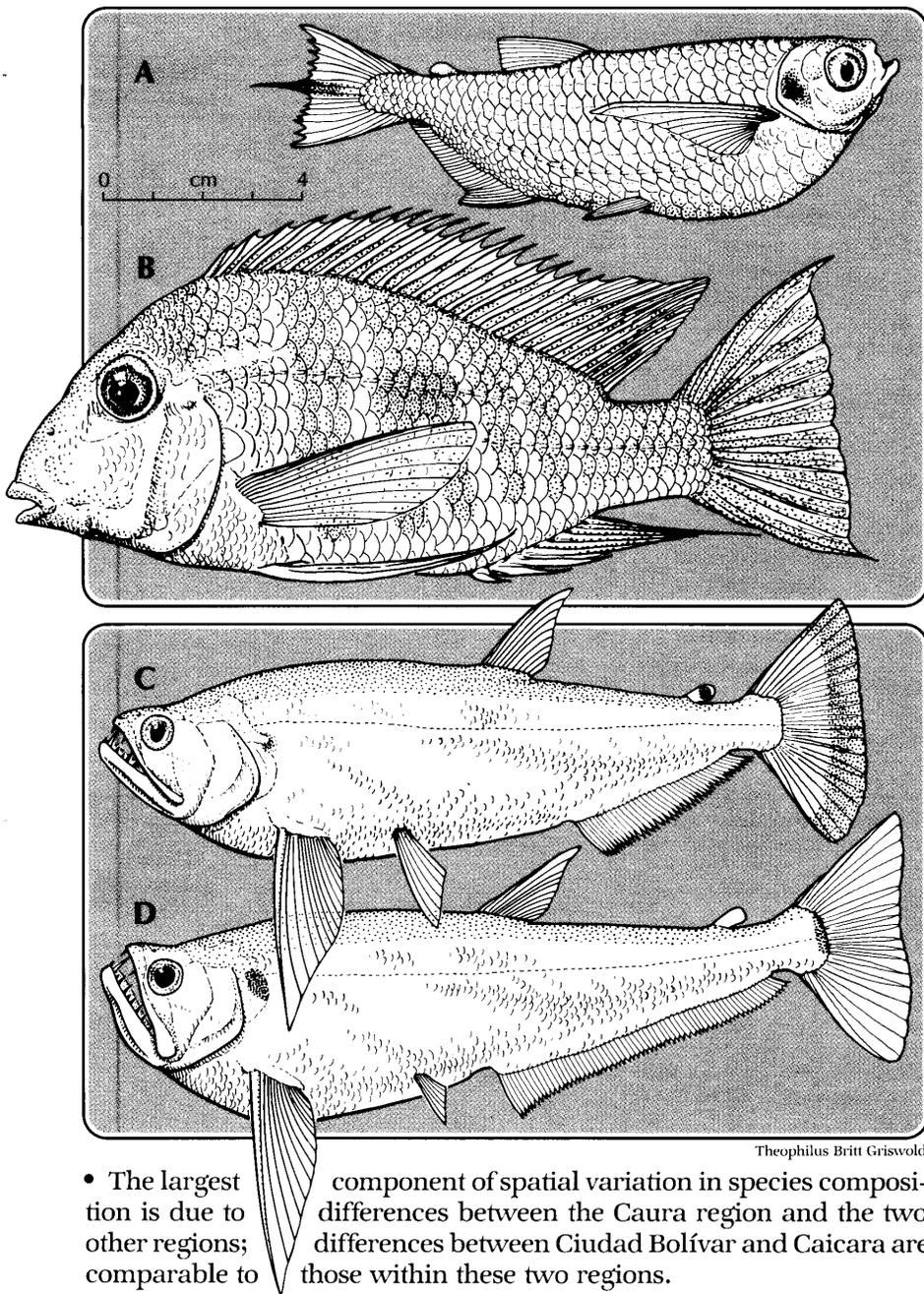


Figure 4. Examples of ubiquitous “core” species: **A**, *Triportheus angulatus*, an omnivorous characid well-adapted to pick food items from the water surface ($\times 0.67$); **B**, *Geophagus surinamensis*, a bottom-feeding cichlid that sifts through mud in search of invertebrates ($\times 0.67$); **C**, *Hydrolycus scomberoides*, a piscivorous characid commonly found in open waters (about one third actual size); **D**, *Rhaphiodon gibbus*, a piscivorous characid of widespread distribution (about one third actual size). Notice the striking resemblance in overall morphology between *H. scomberoides* and *R. gibbus*.

- The largest component of spatial variation in species composition is due to differences between the Caura region and the two other regions; differences between Ciudad Bolívar and Caicara are comparable to those within these two regions.

Discussion

Most studies available to date seem to support the view that variation in fish communities of floodplain lakes is largely unpatterned and unpredictable. Two major reviews of tropical river systems (Lowe-McConnell 1987, Welcomme 1979) fail to find clear relationships between lake characteristics and fish community structure, although Welcomme (1979) points out that species diversity and average size of species can increase with water-body size. Bonetto et al. (1970a, b) have found great year-to-year variability in lakes of the Paraná system, and have detected no relationship between community structure and lake characteristics. Data for lower Orinoco lakes (Lasso In press) show great variability in space and time of fish community composition. In a study covering 680

Table 4. Species Richness for Individual Lakes, 1987 and 1988

Lake	Region	No. of Species, 1987	No. of Species, 1988	\bar{x}	Difference between Years
1	Ciudad Bolívar	35	36	35.5	1
2	Caicara	46	30	38.0	16
3	Caicara	24	20	22.0	4
4	Ciudad Bolívar	39	38	38.5	1
5	Caicara	63	38	50.5	25
6	Ciudad Bolívar	37	15	26.0	22
7	Ciudad Bolívar	41	41	41.0	0
8	Caicara	43	65	54.0	22
9	Caura	14	11	12.5	3
10	Ciudad Bolívar	36	50	43.0	14
11	Ciudad Bolívar	48	59	53.5	11
12	Ciudad Bolívar	32	37	34.5	5
13	Caura	8	32	20.0	24
14	Caura	19	27	23.0	8
15	Ciudad Bolívar	43	37	40.0	6
16	Caura	30	25	27.5	5
17	Ciudad Bolívar	26	23	24.5	1
18	Ciudad Bolívar	38	41	39.5	3
19	Ciudad Bolívar	44	36	40.0	8
20	Ciudad Bolívar	34	39	36.5	5
Mean		35.0	35.0		9.2
SD		12.6	13.3		8.4
Range		8–63	11–65		0–25

Table 5. Summary Statistics for Selected Subsets of the Similarity Matrix*

Subset	\bar{x}	SD	n	Maximum	Minimum	Similarity Values < 55 (%) [†]
SIMILARITIES WITHIN AND BETWEEN YEARS, ALL LAKES						
Between years	60.0	12.5	20	76.7	31.3	20
1987	36.7	16.5	190	68.6	0.0	89
1988	39.2	14.2	190	79.5	8.2	87
SIMILARITIES WITHIN AND BETWEEN YEARS, CIUDAD BOLIVAR						
Between years	62.8	7.5	12	73.6	46.7	8
1987	47.7	10.1	66	68.6	22.9	76
1988	49.2	11.5	66	79.5	26.5	70
SIMILARITIES WITHIN AND BETWEEN YEARS, CAICARA						
Between years	61.0	11.3	4	72.7	45.6	25
1987	48.7	9.2	6	65.0	38.6	83
1988	40.6	4.6	6	47.4	36.2	100
SIMILARITIES WITHIN AND BETWEEN YEARS, CAURA						
Between years	50.5	22.5	4	76.7	31.3	50
1987	23.8	14.7	6	47.2	6.5	100
1988	43.0	9.8	6	53.9	30.2	100
SIMILARITIES BETWEEN CIUDAD BOLIVAR AND CAICARA						
1987	46.1	7.6	48	67.7	29.8	90
1988	42.3	11.3	48	63.0	18.9	90
SIMILARITIES BETWEEN CIUDAD BOLIVAR AND CAURA						
1987	17.9	9.7	48	36.9	0.0	100
1988	26.8	8.6	48	47.9	8.2	100
SIMILARITIES BETWEEN CAICARA AND CAURA						
1987	19.8	6.9	16	34.5	10.8	100
1988	21.2	6.6	16	34.4	10.5	100

*Similarities between two samples can range from 0 (no species in common) to 100 (all species shared).

[†]This statistic indicates where the bulk of the values of the distribution lie, and therefore facilitates the comparison of sample distributions that are not normal.

km along the Paraná River, Cordiviola de Yuan (1980) found great spatial variability in relative abundance of species among 17 lakes. Species composition was also highly variable among lakes, but similarity in species composition increased with spatial proximity. In contrast, the picture that emerges from this study is one of relative constancy from year to year in species richness and species composition at three levels: individual lakes, regions, and whole basin (Tables 3–5; Figure 5). Relative constancy with time was found at spatial scales spanning three orders of magnitude, from ~100 m to 400 000 m. Variation in species composition among regions was high, and was unrelated to the distances separating the regions. In both years most of this variation was due to compositional differences between the Caura region and the two other regions.

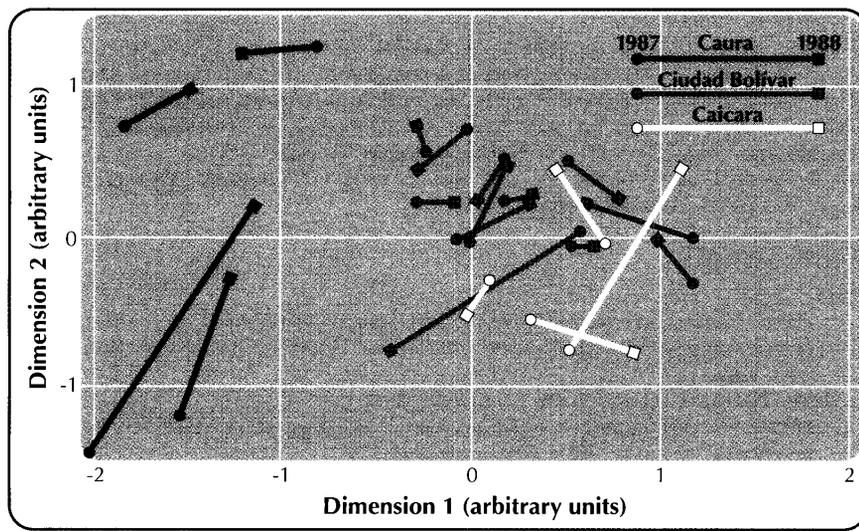


Figure 5. Multidimensional scaling ordination of the 20 lakes in 1987 and 1988. The distance between any two points on the ordination represents the dissimilarity in species composition of the corresponding samples. Straight lines connect individual lakes; for any lake, the length of the line reflects the magnitude of change in species composition from 1987 to 1988.

The relative constancy encountered in this study is striking in view of the potentially large and unpredictable disturbances to which the lakes are exposed each year during the high water period. At this time, extensive spatial reshuffling of adult and juvenile fish can occur after their entry into the flooded forest or their migration via the main river channel. Also, fluctuations in recruitment generated by variability in water levels, patterns of current flow, timing of rains, or number and spawning location of reproductive females—to name but a few factors—can strongly influence the spatial distribution of the numerically abundant young of the year, especially among highly fecund and mobile species. The authors suggest that site-specific environmental attributes (e.g., lake morphology, vegetation type, water chemistry), which remain constant or hardly vary from year to year, constrain the high potential for variation that exists during the high water period. Examples of mechanisms through which site-specific features could reduce year-to-year variation are behavioral site selection and differential extinction, both of which are affected by availability of cover, of spawning substrata, and of food. Fringing and floating vegetation in lakes often provide some or all of these, and the types of vegetation at any lake tend to recur annually.

Environmental attributes differ in the way they vary over spatial scales: some turn over very rapidly (e.g., lake morphology, vegetation type within lakes); others vary more slowly (e.g., water conductivity, mean annual rainfall). Differences in species composition between sites might therefore be strongly scale-dependent. For example, in this study, differences within regions might be explained in terms of environmental factors varying over small scales, such as lake morphology and vegeta-

tion. In contrast, differences among regions might result mainly from environmental variation over larger spatial scales, such as variations in water conductivity resulting from flooding by different rivers. Differences among regions due to small-scale factors would be averaged out and disappear if many lakes from each region were included in the comparisons. Future analyses of these data will test two intertwined hypotheses implicit in the above views: first, species composition can be statistically predicted from knowledge about a host of environmental attributes at a given site; second, the spatial scales of environmental variation can be identified a priori, and correspond to variation in species composition at the same spatial scales.

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