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STRUCTURE OF FISH ASSEMBLAGES ALONG ENVIRONMENTAL GRADIENTS IN FLOODPLAIN LAKES OF THE ORINOCO RIVER

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Abstract. Fish assemblages of temperate lakes are structured primarily by an interaction between piscivory and a small number of environmental variables, but tropical floodplain assemblages have often been viewed as unpredictably structured. We tested the predictability of fish assemblage structure in floodplain lakes of the Orinoco River, Venezuela, in relation to 22 variables describing environmental variation at the microhabitat, habitat, and supra-lake levels. Fish species abundances were estimated through electrofishing surveys of 20 lakes in three regions for the early and late dry seasons of each of two consecutive years. Canonical correspondence analyses indicated that assemblage structure was predictably related to only four descriptors of lakes: transparency, conductance, depth, and area. Discriminant function analyses revealed that transparency ("clear": Secchi transparency >20 cm; or "turbid": Secchi transparency ≤20 cm) was tightly associated with the numerical density of six major taxa (82% classification accuracy) and the numerical density of piscivorous species (89% accuracy). Depth and area probably derived their significance from causal relationships to transparency and availability of cover, whereas the influence of conductance arose incidentally through an association with biogeographical zonation. Mantel tests indicated that similarity in structure of assemblages was not strongly related to the distance between lakes. Transparency was a remarkably reliable predictor of species composition. Fish with sensory adaptations to low light were dominant in turbid lakes, whereas visually oriented fishes predominated in clear lakes; seasonal change involved decline in the proportion of visually oriented fishes concomitant with a decline in transparency. The effect of transparency on assemblage structure was probably mediated by the relationship of transparency to visibility of prey. The structuring of Orinoco fish assemblages by piscivory, under the influence of transparency as controlled by depth and area, contrasts with previous views emphasizing random assemblage variation in neotropical floodplain lakes and extends the applicability of a conceptual model originally developed for temperate lakes.

Key words: *abiotic factors; community organization; multivariate analyses; Orinoco River floodplain; piscivory; predator-prey interactions; predictability; seasonality; tropical ecology; turbidity; water; Venezuela; vision.*

INTRODUCTION

The processes that control structure of freshwater fish assemblages have been clarified by the use of simple conceptual models (Schlosser 1987, Robinson and Tonn 1989, Tonn et al. 1990, Rahel and Hubert 1991, Jackson et al. 1992). Most of these models explicitly relate assemblage structure to the abiotic environment, species interactions, and biogeographical events (e.g., Schlosser 1987, Robinson and Tonn 1989, Tonn et al. 1990, Rahel and Hubert 1991, Kodric-Brown and Brown 1993). The generality of the relationships between assemblage structure and the environment has been tested across distinct assemblages over several geographical regions (Tonn et al. 1990). Comparative

surveys of lakes have provided excellent opportunities for examining the effects of biotic and abiotic factors on fish assemblage structure at large and intermediate geographical scales that encompass very substantial variation in the abiotic environment (Jackson and Harvey 1989, Tonn et al. 1990, Hinch 1991). Despite the essentially correlative nature of comparative surveys, appropriate designs incorporating repeated sampling support inferences about ecological process (Tonn and Magnuson 1982). Conclusions from such surveys have sometimes been supplemented with small-scale experiments involving manipulation of piscivore abundances (Tonn et al. 1992, Hinch et al. 1994).

Robinson and Tonn (1989) postulated that piscivory, in conjunction with a small number of environmental variables including lake maximum depth, surface area, and isolation, have widespread influence on the structure of fish assemblages in small temperate lakes. This simple conceptual model is consistent with the results of more recent studies (Tonn et al. 1990, Hinch 1991,

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Hinch et al. 1991). All tests of Robinson and Tonn's model, however, have been conducted in temperate regions. The marked taxonomic and environmental contrasts between temperate and tropical lakes make the latter a very suitable system for testing the robustness of Robinson and Tonn's model. Tropical floodplain lakes are comparable in size to the temperate lakes for which fish assemblages have been most intensively analyzed. Tropical floodplain lakes support highly diverse fish assemblages that differ taxonomically from their temperate counterparts at the ordinal level (Lowe-McConnell 1975, Welcomme 1979). Abiotic conditions in floodplain lakes (e.g., temperature, seasonal flooding) also differ considerably from those in temperate lakes (Lowe-McConnell 1975, Welcomme 1979). Over a broad geographic range in South America, from Venezuela to Argentina, a number of widespread fish genera recur as dominant taxa in floodplain lake assemblages, yet assemblage composition can vary strikingly even among neighboring lakes (Bonetto et al. 1970a, b, Mago-Leccia 1970, Goulding et al. 1988, Rodríguez and Lewis 1994). Major reviews of tropical river systems (Lowe-McConnell 1975, 1987, Welcomme 1979, 1985, Goulding et al. 1988) fail to show clear relationships between characteristics of floodplain lakes and the structure of their fish assemblages. Although Welcomme's (1979, 1985) summaries point out that size and bottom type of lakes may influence fish species composition and body size, several authors have suggested instead that fish assemblages in these lakes are largely random associations of species (Bonetto et al. 1970a, b, Lowe-McConnell 1987: 154, 274, 304, Goulding et al. 1988:106–107, 116).

We have tested the applicability of Robinson and Tonn's model to floodplain lakes of the Orinoco River, Venezuela. Our test involves the analysis of fish assemblages in 20 lakes of three different regions in relation to environmental variables and piscivory. The analysis is based on abundances of species as shown by standardized sampling of fishes in the early and late dry seasons of two consecutive years.

SITE DESCRIPTION AND METHODS

Study area

The annual cycle in Orinoco floodplain lakes can be divided into a high-water season, when the lakes are connected to each other, and a dry season, when lakes are isolated. Each season lasts ≈ 6 mo. Floodwater usually enters the lakes in June, after which the water level rises rapidly; in 2 mo the depths of lakes can increase from 1–2 m to >7 m. During the high-water season, connections between the river and the lakes facilitate movement of adult and juvenile fish as well as dispersal of eggs and larvae, which appear predominantly during this period (Lowe-McConnell 1975, 1987, Welcomme 1979, 1985). Population densities of all fish species are low in the lakes until December, when the flood recedes

and lakes once more become isolated and spatially discrete (Rodríguez and Lewis 1994). During isolation, the depth of lakes declines because of evaporation, and transparency decreases as inorganic particulate matter is resuspended by wind and phytoplankton populations increase (Hamilton and Lewis 1987). Under these conditions, the water is often turbid and brown; Secchi transparency may be <5 cm. Conductance increases during isolation as evaporation increases the concentration of major ions (Hamilton and Lewis 1987). Species richness of fishes is high during isolation, averaging 35 species per lake (Rodríguez and Lewis 1990).

Fish and environmental data were collected from 20 floodplain lakes (median surface area = 16 ha; range = 3–251 ha) in three regions of the lower Orinoco River basin in Venezuela (Table 1): near Caicara (4 lakes); near Ciudad Bolívar, ≈ 400 km downstream from Caicara (12 lakes); and along the Caura River, near its confluence with the Orinoco, between Caicara and Ciudad Bolívar (4 lakes). Every year the Caura lakes are flooded by transparent and ionically dilute blackwater from the Caura River, whereas the Caicara and Ciudad Bolívar lakes are flooded by more turbid water of higher ionic concentration (whitewater) from the Orinoco River. Human population densities are low in the study area; the river and adjacent waterbodies are in nearly pristine condition.

Fish sampling and taxonomy

The 20 lakes were sampled over a 20-d period in January (early dry season) and in April or May (late dry season) during 1987 and 1988. One lake (Lake Madera) was not sampled in the late dry season of 1988. Fish samples were collected with an aluminum electrofishing boat following the guidelines in Novotny and Priegel (1974) and Reynolds (1983). Current intensity (fast-rise, slow-decay, 4-ms pulses at 120 Hz) usually was maintained within the 3- to 6-amp range recommended by Reynolds (1983). Fish samples were collected during the day (0700–1815) along shoreline intervals selected at random. Between two and seven intervals, summing to 50–280% of a lake's perimeter, were sampled during each survey. Individual sampling runs lasted 20 min and covered ≈ 900 m of shoreline.

Proper analysis and interpretation of assemblage patterns require a sampling method that provides an unbiased representation of the actual assemblages. Electrofishing with pulsed current is one of the least selective of all active fishing methods (Lagler 1978). In the present study, it yielded abundant catches (a total of 18,869 fish), a very similar distribution of species among orders, but a higher mean number of species per lake than that obtained for five other South American lake systems sampled by use of rotenone or of a variety of net types (Rodríguez and Lewis 1990). Although electrofishing can be biased against small fish (Reynolds 1983, Zalewski and Cowx 1990), many small species were captured in great abundance and the

TABLE 1. Geographic location and sample sizes for fish collection sites in the Orinoco floodplain.

Lake	Region	Coordinates		Catch numbers		
		North	West	Total	Tetras	
a	Aguilera	Ciudad Bolívar	08°11'30"	63°26'45"	577	7
b	Bartolico	Caicara	07°38'30"	66°07'00"	471	51
c	Burro	Caicara	07°39'30"	66°12'30"	127	3
d	Caño Largo	Ciudad Bolívar	08°14'50"	63°15'55"	1514	978
e	Castillero	Caicara	07°38'20"	66°09'00"	761	82
f	Curita	Ciudad Bolívar	08°09'30"	63°35'55"	172	1
g	Jobera	Ciudad Bolívar	08°09'55"	63°32'05"	1248	626
h	Larga II	Caicara	07°38'55"	66°13'40"	1838	164
i	Madera	Caura	07°33'40"	65°00'50"	142	5
j	Maldonado	Ciudad Bolívar	08°06'00"	63°45'50"	1243	628
k	Merecure	Ciudad Bolívar	08°12'55"	63°17'25"	1941	596
l	Orsinera	Ciudad Bolívar	08°09'25"	63°34'25"	1680	830
m	Paramuto	Caura	07°33'05"	64°59'50"	199	31
n	Paso Acosta	Caura	07°21'55"	65°11'40"	1518	749
o	Playa Blanca	Ciudad Bolívar	08°09'10"	63°35'00"	1766	797
p	Potrero	Caura	07°36'40"	64°49'50"	775	248
q	Tejita	Ciudad Bolívar	08°09'15"	63°26'55"	518	346
r	Terecaya	Ciudad Bolívar	08°11'30"	63°27'20"	1271	2
s	Tineo	Ciudad Bolívar	08°11'25"	63°28'20"	764	216
t	Venado	Ciudad Bolívar	08°10'30"	63°37'35"	344	19

distribution of species sizes (standard lengths, SL) showed little indication of a distinct lower cutoff (Table 2). Species inadequately sampled by electrofishing during the day include those living in close association with floating vegetation (e.g., *Apistogramma* spp., *Polycentrus schomburgkii*, *Synbranchus marmoratus*; M. A. Rodríguez, *personal observation*), and small catfishes that hide in logs and other submerged substrata (Lowe-McConnell 1975, Rodríguez et al. 1990). These biases should not greatly affect the results, however, because few lakes had abundant floating vegetation (Table 3), and all samples were collected in daylight, so that sampling biases related to diurnal rhythms would be similar across lakes.

Because water transparency, conductance, and depth can affect electrofishing effectiveness (Reynolds 1983, Zalewski and Cowx 1990), it is possible that assemblage-level patterns related to these environmental variables result from sampling artifacts, but statistical evidence suggests otherwise. Fishing success (total numerical density) was not significantly related (by Spearman rank correlation) to Secchi depth, conductance, or lake depth (Rodríguez and Lewis, *unpublished data*). Furthermore, our results are inconsistent with the expected direction of possible sampling biases related to visibility (Zalewski and Cowx 1990).

Fish larger than 400 mm standard length (SL) were usually returned to the water after identification and measurement. Other fish were preserved within 6 h in buffered formaldehyde (6%) and transported to the laboratory, where they were identified, measured to the nearest millimeter, and weighed to the nearest 0.1 g. Species identifications were confirmed by systematists at the Instituto de Zoología Tropical, Universidad Central de Venezuela (UCV) in Caracas, and at the Academy of Natural Sciences of Philadelphia. Voucher spec-

imens of all species were deposited at the Museo de Biología UCV (MBUCV; Table 2), at the Museum of the Academy of Natural Sciences of Philadelphia (ANSP), and at the Museo de la Universidad Experimental de Los Llanos Ezequiel Zamora (MCNG), in Guanare, Venezuela.

Environmental measurements

Because factors that influence fish distribution and abundance may operate over a broad range of spatial scales, we included in the analyses sets of environmental variables differing in spatial coverage (Table 3). Each variable was assigned to one of three categories: intra-lake, whole-lake, and supra-lake. Intra-lake variables reflect small-scale spatial heterogeneity and measure structural attributes of microhabitats. Whole-lake variables reflect environmental features that are broadly distributed across a lake, and correspond to the notion of habitat. Supra-lake variables are physically external to the lake and have little or no direct effect on fish during the dry season, but may affect the distribution and abundance of fish at the onset of the dry season, when lakes first become isolated.

Intra-lake variables were measured along the shoreline sampling intervals (length \approx 900 m) defined by 20-min electrofishing runs. Nearshore depth was measured with a staff gauge six times per shoreline interval. Shoreline types were recorded and transformed to a fraction. Shoreline categories include: (1) submerged live terrestrial vegetation, (2) submerged wood, (3) floating grasses, (4) water hyacinth, (5) other floating plants, (6) rocks, (7) overhanging vegetation, and (8) open shoreline (usually open, gently sloping, shallow beaches).

Whole-lake variables include physico-chemical variables, which were measured at the deepest point in the

TABLE 2. Summary data and canonical correspondence analysis scores for fish species in Orinoco floodplain lakes.

Order Family (number of species) Species	MBUCV catalog number	Length range (SL, mm)	Total catch numbers	Axis 1 score	Axis 2 score	Distribution†	
						Occur- rence	Mean density
Atheriniformes							
Belontiidae (1)							
<i>Potamorhaphis guianensis</i>	V-17196	45-213	16	0.54	0.45	+	+
Hemirhamphidae (1)							
<i>Hyporhamphus</i> sp. a	...	125-125	1
Characiformes							
Anostomidae (8)							
<i>Anostomus ternetzi</i>	...	40-59	2
<i>Laemolyta orinocensis</i>	V-17198	57-202	218	0.16	0.86	+	+
<i>Laemolyta taeniata</i>	V-17697	69-155	10	1.13	-0.66	+	+
<i>Leporinus agassizi</i>	V-17678	99-211	5	-0.13	0.30	+	+
<i>Leporinus cf. friderici</i>	V-17681	81-199	2
<i>Leporinus fasciatus</i>	V-17187	38-248	147	0.05	0.62	+	+
<i>Leporinus</i> sp. a	...	61-61	1
<i>Schizodon</i> sp. a	V-17223	88-300	38	-0.11	0.21	+	-
Ctenoluciidae (3)							
<i>Boulengerella cf. lucia</i>	...	170-170	1
<i>Boulengerella lucia</i> ‡	V-17218	101-359	71	0.34	0.81	+	+
<i>Boulengerella maculata</i>	...	250-317	4
Curimatidae (17)							
" <i>Curimata</i> " sp. a	V-19104	23-51	17	1.19	-0.95	+	+
" <i>Curimata</i> " sp. b	...	84-89	3
<i>Curimata cerasina</i>	...	123-123	1
<i>Curimata cf. incompta</i>	V-17252	32-100	306	0.27	-0.11	+	+
<i>Curimata cf. ocellata</i>	V-17695	86-172	13	1.57	-0.30	+	+
<i>Curimata cf. vittata</i>	V-17706	52-181	13	1.57	-0.82	+	+
<i>Curimata incompta</i>	V-17208	51-142	120	-0.07	0.53	+	+
<i>Curimatella cf. immaculata</i>	V-17222	41-70	18	0.37	0.17	-	+
<i>Curimatella dorsalis</i>	V-17253	41-79	65	0.03	0.27	+	+
<i>Curimatella immaculata</i>	V-17224	40-90	100	0.28	0.44	+	+
<i>Curimatopsis macrolepis</i>	...	40-41	2
<i>Cyphocharax cf. spilurus</i>	V-17226	23-62	274	1.03	-0.87	+	+
<i>Potamorhina altamazonica</i>	V-17689	68-169	15	-0.46	-0.07	-	-
<i>Psectrogaster ciliata</i>	V-17209	57-157	243	-0.10	0.80	+	+
<i>Steindachnerina argentea</i>	V-17205	34-80	80	0.31	-0.28	-	+
<i>Steindachnerina bimaculata</i>	V-17710	58-86	4
<i>Steindachnerina guentheri</i>	V-17250	27-67	188	-0.01	-0.14	-	-
Cynodontidae (3)							
<i>Hydrolycus scomberoides</i> ‡	V-17176	151-504	113	-0.35	0.25	-	-
<i>Rhaphiodon gibbus</i> ‡	V-17181	90-243	97	-0.38	-0.37	-	-
<i>Rhaphiodon vulpinus</i> ‡	V-17168	132-451	107	-0.30	0.17	-	-
Characidae (49)							
<i>Acestrorhynchus cf. britskii</i>	...	81-81	1
<i>Acestrorhynchus cir. microlepis</i>	...	115-115	1
<i>Acestrorhynchus grandoculis</i>	...	62-78	3
<i>Acestrorhynchus heterolepis</i>	...	197-224	2
<i>Acestrorhynchus microlepis</i> ‡	V-17240	72-197	300	0.87	0.30	+	+
<i>Acestrorhynchus nasutus</i> ‡	V-17254	41-80	189	1.51	-1.00	+	+
<i>Agoniatas cf. anchovia</i> ‡	V-17238	96-147	13	2.00	0.77	+	+
<i>Aphyocharax alburnus</i>	V-17246	25-42	37	0.19	0.11	-	-
<i>Brycon cf. whitei</i>	V-17684	147-181	11	0.03	1.03	+	+
<i>Bryconops cf. alburnoides</i>	V-17239	63-114	23	1.32	1.17	+	+
<i>Bryconops cf. caudomaculatus</i>	...	56-61	2
<i>Characidium cf. fascianum</i>	...	28-28	1
<i>Charax cf. gibbosus</i>	...	32-72	15	-0.36	-0.60	-	-
<i>Charax gibbosus</i>	V-17711	42-91	4
<i>Colossoma macropomum</i>	...	146-147	2
<i>Ctenobrycon hauxwellianus</i>	V-17206	29-52	548	-0.12	-0.38	-	-
<i>Eucynopotamus biserialis</i>	V-17682	28-46	65	-1.39	-1.30	-	-
<i>Hemigrammus rhodostomus</i>	V-17256	23-35	34	1.75	-0.60	+	+
<i>Hypheobrycon gracilior</i>	...	32-32	1
<i>Iguanodectes spilurus</i>	V-18398	53-65	19	1.08	-1.24	+	-
<i>Markiana geayi</i>	...	65-65	1

TABLE 2. Continued.

Order Family (number of species) Species	MBUCV catalog number	Length range (SL, mm)	Total catch numbers	Axis 1 score	Axis 2 score	Distribution†	
						Occur- rence	Mean density
<i>Metynnis hypsauchen</i>	V-17211	50-121	19	1.32	-1.24	+	+
<i>Metynnis lippincottianus</i>	V-17685	79-163	12	1.33	-1.12	+	+
<i>Metynnis luna</i>	V-17183	34-121	227	0.75	-0.33	+	+
<i>Moenkhausia ceros</i>	...	37-37	1
<i>Moenkhausia cf. lepidura</i>	...	23-48	22	0.55	1.45	+	+
<i>Moenkhausia chrysargyrea</i>	V-17708	44-47	2
<i>Moenkhausia doceana</i>	V-19103	25-34	32	-0.06	-0.72	-	-
<i>Moenkhausia intermedia</i>	V-17227	27-58	541	-0.30	-0.22	-	-
<i>Myleus cf. rubripinnis</i>	V-17692	57-156	4
<i>Mylossoma aureum</i>	V-17688	66-125	20	-0.31	0.70	+	+
<i>Mylossoma duriventre</i>	V-17191	19-217	226	-0.41	0.47	-	-
<i>Paragoniates alburnus</i>	...	64-117	2
<i>Piaractus brachypomus</i>	V-17184	91-251	23	-0.46	0.27	+	-
<i>Poptella longipinnis</i>	V-17214	32-62	274	-0.28	-0.03	+	+
<i>Pristobrycon calmoni</i>	...	53-156	3
<i>Pristobrycon striulatus</i>	...	40-130	4
<i>Pygocentrus caribe</i> †	V-17202	83-237	14	-0.73	-0.32	-	-
<i>Roebooides cf. affinis</i>	V-17215	37-86	96	-0.51	-0.41	-	-
<i>Roebooides dayi</i>	...	44-48	3
<i>Roebooides myersi</i>	V-17195	62-93	11	-1.00	-0.57	-	-
<i>Serrasalmus elongatus</i> †	V-17200	76-175	6	0.68	0.95	+	+
<i>Serrasalmus irritans</i>	V-17197	33-148	24	-0.17	0.18	-	-
<i>Serrasalmus rhombeus</i> †	V-17707	70-223	5	-1.07	-0.27	-	-
Tetragonopterinae spp.	...	<40	6379
<i>Tetragonopterus argenteus</i>	...	57-74	2
<i>Triportheus angulatus</i>	V-17201	36-180	538	-0.28	0.27	-	-
<i>Triportheus culter</i>	V-17199	73-203	34	-0.55	0.64	-	-
<i>Triportheus elongatus</i>	V-17190	15-151	180	-0.16	0.64	+	+
<i>Triportheus rotundatus</i>	V-17691	62-157	15	-1.12	-0.36	-	-
Chilodontidae (1)							
<i>Caenotropus labyrinthicus</i>	V-17189	51-106	109	-0.09	0.55	+	+
Erythrinidae (1)							
<i>Hoplias malabaricus</i> †	V-17194	90-346	25	-0.18	-0.12	-	-
Gasteropelecidae (1)							
<i>Thoracocharax stellatus</i>	V-17182	29-52	139	-0.85	-0.22	-	-
Hemiodontidae (6)							
<i>Anodus orinocensis</i>	V-17193	108-182	61	0.24	1.02	+	+
<i>Argonectes longiceps</i>	...	95-102	5	0.38	-0.29	-	-
<i>Hemiodopsis argentea</i>	...	94-182	2
<i>Hemiodopsis gracilis</i>	V-17693	38-70	97	1.73	-0.67	+	+
<i>Hemiodopsis immaculata</i>	V-17220	83-139	66	0.87	0.42	+	+
<i>Hemiodus unimaculatus</i>	V-17217	63-131	134	0.80	0.23	+	+
Lebiasinidae (1)							
<i>Pyrrhulina cf. eleanorae</i>	...	27-27	1
Prochilodontidae (3)							
<i>Prochilodus mariae</i>	V-17230	97-346	60	-0.24	0.31	-	-
<i>Semaprochilodus kneri</i>	V-17207	85-236	185	0.59	0.18	+	+
<i>Semaprochilodus laticeps</i>	V-17204	85-293	45	0.23	0.34	+	+
Clupeiformes							
Clupeidae (3)							
<i>Pellona castelnaeana</i>	...	234-234	1
<i>Pellona flavipinnis</i>	V-17241	31-250	37	-0.34	0.28	-	-
<i>Rhinosardinia amazonica</i>	V-17237	12-61	600	-0.27	0.29	-	-
Engraulidae (7)							
<i>Anchovia surinamensis</i>	V-17249	17-94	80	-0.05	-0.29	+	+
<i>Anchoviella guianensis</i>	V-17248	36-73	8	0.40	1.42	+	+
<i>Anchoviella sp. b</i>	...	19-78	335	0.20	0.13	-	+
<i>Anchoviella perezii</i>	V-19105	14-50	1989	0.45	-0.11	+	+
<i>Lycengraulis cf. batesii</i>	V-18397	61-156	2
<i>Lycengraulis cf. grossidensis</i> †	V-17251	22-156	23	0.89	0.01	+	+
<i>Pterengraulis atherinoides</i>	V-17699	40-157	24	-0.68	0.79	-	-

TABLE 2. Continued.

Order Family (number of species) Species	MBUCV catalog number	Length range (SL, mm)	Total catch numbers	Axis 1 score	Axis 2 score	Distribution†	
						Occur- rence	Mean density
Gymnotiformes							
Apteronotidae (4)							
<i>Adontosternarchus devenanzii</i>	V-17173	80-124	17	-1.41	-1.41	-	-
<i>Apteronotidae</i> sp. b	...	229-229	1
<i>Apteronotus albifrons</i>	V-17680	207-281	3
<i>Sternarchorhamphus muelleri</i>	V-17690	325-412	5	-0.31	-0.55	-	-
Hypopomidae (1)							
<i>Hypopomus</i> sp. a	...	157-157	1
Rhamphichthyidae (2)							
<i>Rhamphichthys</i> cf. <i>reinhardtii</i>	V-17172	75-702	27	-0.48	-0.74	-	-
<i>Rhamphichthys marmoratus</i>	V-17179	217-676	36	-0.95	-0.92	-	-
Sternopygidae (6)							
<i>Distocycclus conirostris</i>	V-17679	146-192	8	-0.24	-0.77	-	-
<i>Eigenmannia humboldtii</i>	V-17234	69-298	29	-0.46	0.55	-	-
<i>Eigenmannia macrops</i>	V-17701	71-163	96	-0.76	-0.73	-	-
<i>Eigenmannia virescens</i>	V-17709	78-142	18	-1.12	-1.41	-	-
<i>Rhabdolichops troscheli</i>	...	175-175	1
<i>Sternopygus macrurus</i>	V-17180	115-408	9	-1.19	-1.35	-	-
Perciformes							
Cichlidae (12)							
<i>Aequidens pulcher</i>	V-17231	65-65	1
<i>Astronotus ocellatus</i>	...	209-229	3
<i>Biotoecus opercularis</i>	V-17713	13-42	117	1.73	-0.71	+	+
<i>Caquetaia kraussii</i>	V-17686	26-182	3
<i>Chaetobranchius flavescens</i>	...	105-166	3
<i>Cichla orinocensis</i> ‡	V-17177	71-416	110	0.39	0.03	+	+
<i>Cichla temensis</i> ‡	V-17694	148-490	11	1.51	-1.04	+	+
<i>Geophagus surinamensis</i>	V-17216	24-195	289	0.13	0.14	+	+
<i>Mesonauta insignis</i>	...	16-48	4
<i>Satanoperca daemon</i>	V-17212	78-165	14	1.47	-0.73	+	+
<i>Satanoperca jurupari</i>	V-17213	36-181	49	0.53	-0.31	+	+
Sciaenidae (2)							
<i>Pachypops</i> sp. a	V-17696	30-174	7	0.05	-0.27	-	-
<i>Plagioscion squamosissimus</i> ‡	V-17175	16-366	71	-0.32	-0.42	-	-
Pleuronectiformes							
Achiridae (1)							
<i>Hypoclinemus mentalis</i>	V-17712	36-140	9	-1.14	-1.50	-	-
Siluriformes							
Aspredinidae (1)							
<i>Bunocephalus</i> sp. a	...	34-55	6	-0.64	0.19	-	+
Auchenipteridae (3)							
<i>Auchenipterus nuchalis</i>	V-17704	84-142	25	-0.51	-0.15	-	-
<i>Entomocorus gameroi</i>	V-17186	46-58	7	-1.35	-0.93	-	-
<i>Parauchenipterus galeatus</i>	V-17698	102-141	2
Callichthyidae (1)							
<i>Hoplosternum littorale</i>	V-19106	129-202	16	-1.59	-1.15	-	-
Doradidae (4)							
<i>Amblydoras hancocki</i>	V-17702	39-90	17	1.40	-1.27	+	+
<i>Hassar notospilus</i>	V-17229	50-124	75	0.49	-0.28	-	-
<i>Opsodoras</i> sp. a	...	101-101	1
<i>Pseudodoras niger</i>	V-17219	112-426	47	-0.38	0.05	-	-
Hypophthalmidae (1)							
<i>Hypophthalmus edentatus</i>	V-17185	151-389	51	-0.91	0.15	-	-
Loricariidae (9)							
<i>Cochliodon plecostomoides</i>	V-17178	66-244	3
<i>Glyptopterichthys punctatus</i>	V-17203	148-340	25	-0.64	-0.19	-	-
<i>Glyptopterichthys gibbiceps</i>	V-17687	154-370	21	-0.38	-0.82	-	-
<i>Hypoptopoma joberti</i>	V-17236	39-76	61	-0.34	0.75	-	-
<i>Hypostomus</i> cf. <i>watwata</i>	V-17169	114-114	1

TABLE 2. Continued.

Order Family (number of species) Species	MBUCV catalog number	Length range (SL, mm)	Total catch numbers	Axis 1 score	Axis 2 score	Distribution†	
						Occur- rence	Mean density
<i>Hypostomus plecostomus</i>	V-17170	16-277	53	-0.52	-0.34	-	-
<i>Loricaria cf. cataphracta</i>	V-17171	81-311	17	-0.65	-0.31	-	-
<i>Loricariichthys brunneus</i>	V-17242	31-281	325	-0.67	-0.40	-	-
<i>Sturisma cf. tenuirostre</i>	V-17174	95-315	8	-0.43	-0.47	-	-
Pimelodidae (17)							
<i>Duopalatinus malarmo</i>	...	81-81	1
<i>Hemisorubim platyrhynchost</i> ‡	V-17683	95-325	12	-1.36	-0.69	-	-
<i>Leiarius marmoratus</i>	...	196-196	1
<i>Pimelodella cf. metae</i>	...	41-41	1
<i>Pimelodella cristata</i>	V-17221	50-200	49	0.19	0.02	+	+
<i>Pimelodella sp. a</i>	V-17244	47-92	22	-0.99	-0.32	-	-
<i>Pimelodina flavipinnis</i>	V-19101	86-250	9	-0.68	-0.39	-	-
<i>Pimelodus aff. blochii</i>	...	127-127	1
<i>Pimelodus blochii</i>	V-17232	48-175	538	-0.62	-0.33	-	-
<i>Pimelodus cf. blochii</i>	V-17245	73-203	18	-0.65	-0.32	-	-
<i>Pimelodus cir. blochii</i>	V-17233	115-115	1
<i>Pinirampus cf. pinirampu</i>	...	266-390	3
<i>Pseudoplatystoma fasciatum</i> ‡	V-18396	194-540	12	-0.48	0.54	-	-
<i>Pseudoplatystoma tigrinum</i> ‡	V-17210	208-550	23	-0.52	0.40	-	-
<i>Rhandaia cf. sebae</i>	...	141-160	2
<i>Sorubim latirostris</i> ‡	V-17225	117-344	59	-0.55	0.09	-	-
<i>Sorubim lima</i> ‡	V-17192	95-326	99	-0.57	0.25	-	-
Tetraodontiformes							
Tetraodontidae (1)							
<i>Colomesus asellus</i>	V-17700	47-47	1

† Occurrence denotes whether the species was more commonly found in turbid lakes (Secchi transparency ≤ 20 cm; minus sign) or in clear lakes (Secchi transparency > 20 cm; plus sign); "Mean density" denotes whether the species' density ($\ln(\text{CPUE} + 1)$) averaged across lakes) was higher in turbid lakes (minus sign) or in clear lakes (plus sign).

‡ Piscivores included in the discriminant function analysis.

TABLE 3. Distribution parameters (medians, lower quartiles (LQ), upper quartiles (UQ), minima, and maxima) for environmental variables in Orinoco floodplain lakes. Within- and supra-lake variables without explicit mention of units are expressed as proportions.

	Median	LQ	UQ	Min.	Max.
Within-lake variables					
Nearshore depth (m)	0.80	0.65	1.15	0.45	1.55
Submerged vegetation	0.14	0.01	0.53	0.00	0.97
Overhanging vegetation	0.12	0.02	0.38	0.00	1.00
Floating grasses	0.01	0.00	0.21	0.00	0.99
Open shoreline	0.15	0.03	0.55	0.00	1.00
Submerged deadwood	0.02	0.00	0.08	0.00	0.22
Water hyacinth	0.00	0.00	0.02	0.00	0.99
Other floating plants	0.00	0.00	0.00	0.00	0.88
Emergent rocks	0.00	0.00	0.00	0.00	0.08
Whole-lake variables					
Secchi transparency (cm)	22.5	10.0	40.0	5.0	130.0
Conductance ($\mu\text{S}/\text{cm}$)	30.5	13.0	46.5	5.0	420.0
Oxygen concentration (mg/L)	7.0	5.9	7.9	3.0	12.3
pH	6	6	6	6	6
Surface area (ha)	16.5	9.5	113.9	2.9	250.8
Fetch (km)	0.89	0.58	1.77	0.16	3.84
Breadth (km)	0.31	0.17	0.82	0.10	1.69
Perimeter (km)	2.52	1.39	6.18	1.2	13.3
Shoreline development	1.64	1.41	1.91	1.13	2.49
Maximum depth (m)	1.50	1.05	2.35	0.45	4.60
Supra-lake variables					
Distance from river channel (km)	0.8	0.4	1.4	0.2	2.9
Distance from floodplain edge (km)	0.6	0.3	1.0	0.1	2.8
Non-forested perimeter	0.05	0.00	0.40	0.00	0.80

lake, as follows: depth, transparency (by depth at which Secchi disk is visible), conductance (YSI model 33 meter), pH (paper strips), and dissolved oxygen (YSI model 57 meter, 0.15 m below the water surface). Also, area, fetch, width, and perimeter were measured on photographically enlarged 1:100 000 maps from the Venezuelan Dirección de Cartografía Nacional (for low-water conditions). Shoreline development, a standardized measure of the relation between lake perimeter (P) and surface area (A), was calculated as $P/(4\pi A)^{0.5}$.

Supra-lake variables were measured on maps, and were verified in the field as necessary. Two distances describing the position of each lake on the floodplain were measured: lake centroid to main river, and lake centroid to the edge of the flooded area. The fractions of shoreline length with and without forest cover (≥ 100 m away from the shoreline) were also measured.

Quantitative analyses

Species represented by < 5 individuals (53 of 169 species) were not included in analyses of species abundance. The low abundance of these species would have given them negligible weighting in the analyses even if they had been included. Species of small (< 40 mm SL; mean SL = 24 mm) characids of the subfamily Tetragonopterinae (tetras; probably fewer than eight species, mostly in the genera *Astyanax*, *Moenkhausia*, and *Hypessobrycon*) that could not be identified were also excluded from analyses of relative abundance, but seven tetra species (five of > 40 mm SL; two of < 40 mm SL) that could be reliably identified were retained. As a group, the unidentified small tetras accounted for 29% by numbers but only 0.39% by mass of all fish captured in this study; their median percent numerical abundance (across lakes) was 5.6% (interquartile interval 0–36.2%). Aggregation of these species as if they were a single species would have distorted the analyses. The response of these fishes to environmental variation was examined separately.

Raw catch data were converted to catch per unit effort (CPUE = number of fishes caught divided by shocker time). The CPUE data for individual species were transformed as $\ln(X + 1)$ because an analysis of the power relationship between the means and variances of species across sites indicated that this transformation was appropriate for stabilizing variances (Rodríguez and Lewis 1994). When necessary, environmental variables were transformed as $\ln(X)$ or, for proportions, as arcsine ($p^{0.5}$) to make the data conform better to statistical assumptions.

Statistical associations between assemblage structure and environmental variables were quantified by use of canonical correspondence analysis (CCA), a nonlinear eigenvector ordination technique especially designed for direct analysis of the relationships between multivariate ecological data sets (ter Braak 1986; program CANOCO version 2.1, ter Braak 1988). Separate anal-

yses were conducted for each combination of season (early and late dry season) and year (1987 and 1988), and for all samples combined. Surface area was not included among the environmental variables in the late dry season because accurate estimates of it were not available for these dates. Significance tests for models relating assemblage structure to environmental variables were based on Monte Carlo permutation tests (10^3 permutations) for the sum of all eigenvalues. Variables entering final models were selected by a stepwise procedure analogous to backward elimination in multiple regression analysis (Draper and Smith 1981). The significance of relationships between ordination axes and individual environmental variables was evaluated by t tests for the inter-set correlations and the canonical coefficients (ter Braak 1988, 1990). The weighted average site scores (ter Braak 1988) were used in the ordination plot of lake samples.

A two-part discriminant function analysis (Wilkinson 1988: SYSTAT program version 5.03) was used to determine the degree to which categories of lakes defined by environmental data corresponded to two aspects of assemblage structure: the numerical densities of major taxa, and the numerical densities of piscivorous species. In the first part of the analysis, CPUE for each lake was summed across species for each of six major taxonomic groups: siluriforms (catfishes), characiforms (e.g., silver dollars, hatchetfishes, curimatas), cichlids (e.g., peacock bass, earth eaters), clupeomorphs (anchovies and herrings), gymnotiforms (knifefishes), and other taxa (Table 2). Log-transformed CPUE totals for the six groups were then used as predictor variables for a discriminant function. In the second part of the analysis, log-transformed CPUE values for each of the 20 most abundant piscivorous species were used as predictors.

Scatterplots were used to depict changes in relative abundance, transformed as arcsine ($p^{0.5}$) to reduce the dependence of the variance on the mean, along an environmental gradient (Wilkinson 1988: SYSTAT program version 5.03). Jittering, i.e., adding a small amount of random noise to the data before graphing (Cleveland 1985), was used to improve visibility when many data points overlapped. Robust locally weighted regression (Cleveland 1985: LOWESS) was used to summarize patterns of dependence between the y variable and the x variable in the scatterplots.

We used Mantel tests (Mantel 1967) to evaluate whether similarities in assemblage structure among lakes were a simple function of geographical distance. Mantel's test shows whether two square matrices show a statistically significant association. In the present study, one of the matrices represented a set of geographical distances among lakes and the other matrix contained a measure of assemblage dissimilarity. Maps were used to obtain geographical distances, measured as the shortest pairwise distances "as the fish swims" between each lake and all other lakes. Two transfor-

mations of species numerical densities, standardization by site norm (Noy-Meir et al. 1975) and $\ln(X + 1)$, were used in the Mantel analyses. Assemblage dissimilarity was quantified as pairwise Euclidean distances between lakes positioned in a multidimensional space in which each axis represented the transformed abundance of a species. For each set of dissimilarities, Mantel tests were performed for each combination of year and season, and within each combination tests were done at three levels differing in spatial extent: all lakes (three geographic regions), only lakes from Ciudad Bolívar and Caicara (two regions), and only lakes from Ciudad Bolívar (the region with the largest number of lakes). Significance levels were determined by reference to a null distribution derived from a random subset of permutations of one of the original matrices (Dietz 1983). To ensure the stability of the estimated probabilities (Jackson and Somers 1989), a minimum of 2500 permutations were used to generate the random null distribution; when probability estimates approached the 5% significance level, 20 000 permutations were performed. For most simulations, significance values expressed as fractions were stable to the second decimal digit after 1500–2000 permutations.

RESULTS

Relationship between assemblage structure and environmental variables

There were no significant associations between assemblage structure and supra-lake or within-lake variables in the canonical correspondence analyses. Among the whole-lake variables, only Secchi depth, conductance, depth, and area were significantly related to assemblage structure in the early dry season (Table 4). Secchi depth, conductance, and depth also were significantly related to assemblage structure in the late dry season (lake area was unavailable for late dry season analyses). These results were similar in the two years of the study (Table 4). The strongest correlations among environmental variables were between area and other measures of lake size (fetch, breadth, and perimeter: Appendix). The correlations among the best predictors in the canonical correspondence analyses (transparency, conductance, depth, and area) were generally low, as were those of transparency, conductance, and depth with other environmental variables (Appendix).

A CCA for all samples combined showed the overall relationships between species distributions, environmental variables, and the seasonal shifts in assemblage structure (Table 4, Fig. 1). Secchi transparency increased and conductance decreased along the first ordination axis, whereas the second axis reflected a gradient in lake depth (Table 4, Fig. 1). For most species, Axis-1 scores predicted well whether the species had higher occurrence and mean density in lakes with transparency above average (clear lakes, Secchi depth >20

cm) or below average (turbid lakes, Secchi depth \leq 20 cm) (Fig. 1, Table 2). The majority of species fell within an elongated cluster (running from bottom left to top right in Fig. 1) that was closely aligned with the transparency gradient. Within this cluster, species distributions were not strongly related to conductance (Fig. 1). The conductance gradient primarily separated the main species cluster from a second, smaller cluster (lower right in Fig. 1) composed mainly of species that were common in the Caura region but rare or absent in the two other regions. For several major taxa, the midpoint of the transparency gradient (Secchi depth = 20 cm) was associated with conspicuous contrasts in species distributions (Fig. 1). All nine knifefishes species had their center of distribution, corresponding to modal or peak abundance, in turbid lakes (Fig. 1, left of origin). Catfishes also were most abundant in turbid lakes: only three of 25 catfish species were positioned above the gradient midpoint (Fig. 1, right of origin; Table 2). In contrast, cichlids (six species) were most abundant in clear lakes; all cichlid species were positioned above the gradient midpoint (Fig. 1, Table 2). The distributions of species modes for characiforms (36 of 64 species above the transparency midpoint), clupeomorphs (four of eight species), and other taxa (one of four species) were less clearly patterned relative to transparency or to the other environmental variables in the plot (Fig. 1, Table 2).

The relative abundance of major taxa (CPUE summed across species for each major taxon, divided by total CPUE) was predictably related to the transparency gradient; the relative abundances of characiforms, cichlids, and clupeomorphs were highest in clear lakes, whereas catfishes, knifefishes, and other taxa (mostly the sciaenid *Plagioscion squamosissimus*, a piscivorous croaker) were most abundant in turbid lakes (Fig. 2, Table 5). Despite marked differences in relative abundance of major taxa between clear lakes and turbid lakes, the total numerical densities were comparable in the two lake types (Table 5). As did other characiforms, the small tetras had higher numerical densities in clear lakes than in turbid lakes (Table 5).

Members of the piscivore guild could be separated into two associations on the basis of their position along Axis 1. The first association included eight species with positive scores on Axis 1; these were most abundant in clear lakes with low conductance. The numerically dominant species in this group were the peacock bass, *Cichla orinocensis*, and the pike-like characiforms *Acestrorhynchus microlepis*, *A. nasutus*, and *Boulengerella lucia* (Fig. 3, Table 2). The second group included 12 species with negative scores on Axis 1; these were most abundant in turbid lakes with high conductance. The numerically dominant species in this group were the cynodontid characiforms *Hydrolycus scomberoides*, *Rhaphiodon vulpinus*, and *R. gibbus*, the croaker *P. squamosissimus*, and the catfishes *Sorubim lima* and *S. latirostris* (Fig. 3, Table 2). The distribu-

TABLE 4. Results of canonical correspondence analyses for fish assemblages of lakes in the Orinoco floodplain. Significance values for all samples combined (part C) are approximate because of the lack of independence among the four surveys.

A) Early dry season

1987				1988			
Variable	Axis 1	Axis 2	Axis 3	Variable	Axis 1	Axis 2	Axis 3
Canonical coefficients for environmental variables				Canonical coefficients for environmental variables			
Depth	-0.149	0.600*	0.463*	Depth	-0.206	0.495*	0.626*
Transparency	0.303*	0.625*	0.041	Transparency	0.167	0.550*	0.189
Conductivity	-0.951*	0.233	-0.352	Conductivity	-1.042*	0.159	-0.344*
Area	-0.737*	-0.249	0.741*	Area	-0.766*	-0.362*	0.691*
Correlations of environmental variables with ordination axes				Correlations of environmental variables with ordination axes			
Depth	-0.312	0.711*	0.212	Depth	-0.231	0.676*	0.400
Transparency	0.486*	0.519*	0.280	Transparency	0.272	0.635*	0.231
Conductivity	-0.651*	0.308	-0.513*	Conductivity	-0.649*	0.399	-0.531*
Area	-0.141	-0.327	0.734*	Area	-0.188	-0.587*	0.665*
Summary statistics for ordination axes				Summary statistics for ordination axes			
Eigenvalue	0.432	0.297	0.216	Eigenvalue	0.474	0.313	0.238
Species-environment correlation	0.917	0.904	0.833	Species-environment correlation	0.914	0.959	0.936
Monte Carlo probability for significance of the sum of all eigenvalues (1000 permutations): 0.027				Monte Carlo probability for significance of the sum of all eigenvalues (1000 permutations): 0.001			

B) Late dry season

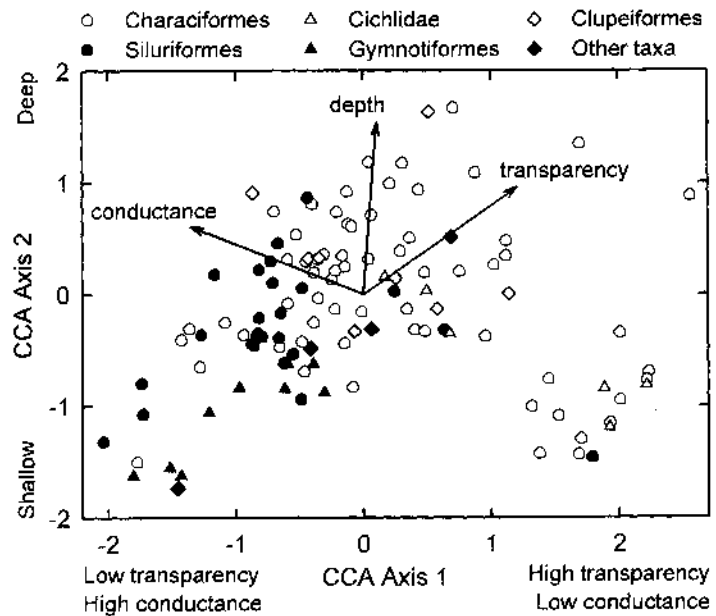
1987				1988			
Variable	Axis 1	Axis 2	Axis 3	Variable	Axis 1	Axis 2	Axis 3
Canonical coefficients for environmental variables				Canonical coefficients for environmental variables			
Depth	-0.051	0.994*	-0.155	Depth	-0.340*	1.161*	0.481*
Transparency	0.694*	0.041	0.759*	Transparency	0.881*	-1.170*	0.709*
Conductivity	-0.593*	0.134	0.824*	Conductivity	-0.356*	-0.899*	0.910*
Correlations of environmental variables with ordination axes				Correlations of environmental variables with ordination axes			
Depth	0.062	0.881*	-0.102	Depth	0.246	0.590*	0.669*
Transparency	0.772*	0.115	0.508*	Transparency	0.858*	-0.078	0.398
Conductivity	-0.699*	0.059	0.603*	Conductivity	-0.798*	-0.373	0.346
Summary statistics for ordination axes				Summary statistics for ordination axes			
Eigenvalue	0.600	0.341	0.260	Eigenvalue	0.628	0.301	0.274
Species-environment correlation	0.947	0.888	0.898	Species-environment correlation	0.956	0.930	0.919
Monte Carlo probability for significance of the sum of all eigenvalues (1000 permutations): 0.006				Monte Carlo probability for significance of the sum of all eigenvalues (1000 permutations): 0.001			

C) All samples combined

Variable	Axis 1	Axis 2	Axis 3
Canonical coefficients for environmental variables			
Depth	-0.133	0.690*	-0.856*
Transparency	0.609*	0.437*	0.906*
Conductivity	-0.633*	0.452*	0.761*
Correlations of environmental variables with ordination axes			
Depth	0.056	0.745*	-0.372*
Transparency	0.665*	0.462*	0.254*
Conductivity	-0.728*	0.288*	0.323*
Summary statistics for ordination axes			
Eigenvalue	0.390	0.246	0.131
Species-environment correlation	0.859	0.846	0.795
Monte Carlo probability for significance of the sum of all eigenvalues (1000 permutations): 0.001			

* Significant at $P < 0.05$.

FIG. 1. Canonical correspondence analysis (CCA) ordination plot showing species distributions in relation to environmental variables for 1987 and 1988 combined (116 species). Each symbol represents an individual species. The orthogonal projection of a species point onto an environmental arrow represents the approximate center of the species distribution along that particular environmental gradient. Labelled arrows indicate the direction along which each environmental variable changes most. Average values for environmental variables are found at the origin of the arrows, and the numerical value of an environmental variable increases from the origin toward the tip of the arrow corresponding to that variable. The origin corresponds to values of 20 cm for Secchi transparency, 28 $\mu\text{S}/\text{cm}$ for conductance, and 147 cm for lake depth.



tions of mean density and relative abundance of piscivorous species in relation to the transparency gradient were in agreement with their assignment to the clear or turbid associations on the basis of CCA scores (Fig. 3, Table 2).

The lake plot (ordination based on all samples combined) illustrated pronounced seasonal shifts in assemblage structure and environmental variables (Fig. 4). For most lakes, the lines connecting samples from the early and late dry season were approximately parallel and were most strongly aligned with the arrow representing water transparency, indicating a common direction of seasonal change in assemblage structure and an association between such change and transparency, both in 1987 and 1988 (Fig. 4). Seasonal change in assemblage structure during the dry season involved primarily increases in the relative abundance of catfishes, knifefishes, and other major taxa, and reduction in the relative abundance of characiforms and clupeomorphs (Fig. 2 [cf. Figs. 1 and 4]; Rodríguez and Lewis 1994). Because during the dry season immigration and emigration cannot occur and reproduction is negligible, the numerical abundances of species can only decrease. Thus seasonal change in relative abundances is due to differential mortality (Rodríguez and Lewis 1994). Year-to-year variation in the lake ordination scores was small; the Pearson correlation between lake scores in 1987 and 1988 ($n = 39$ lakes) was $r = 0.95$ for Axis 1 and $r = 0.79$ for Axis 2.

The lake ordination revealed mostly continuous variation in assemblage structure within the Caicara and Ciudad Bolívar regions but marked discontinuity between the Caura region, which had the highest scores on Axis 1, and the two other regions (Fig. 4). The position of samples relative to environmental arrows

indicates that differences in assemblage structure between the Caura region and the two other regions were associated primarily with conductance and to a lesser extent with transparency (Fig. 4).

The frequency distribution of $\ln(\text{transparency})$ is approximately uniform and the relative abundances of major taxa and of most individual species vary continuously along the transparency gradient (Figs. 2, 3). Nevertheless, the discontinuity in the distribution of species modes near the mean Secchi depth of 20 cm (Fig. 1) suggests that this is a convenient break-point for lake classification. The discriminant function analysis showed that lakes could be accurately classified into two discrete categories (clear, Secchi depth >20 cm; or turbid, Secchi depth ≤ 20 cm) on the basis of either the numerical density of six major taxa, or the numerical density of piscivorous species, as the two analyses yielded virtually identical results (Fig. 5). Conversely, knowing whether a lake is clear or turbid was useful in predicting which major taxa and which piscivorous species predominated in the lake. Among the major taxa, the correlation between the biotic predictors and the discriminant scores (not shown) was negative for the characiforms, the cichlids, and the clupeomorphs, and positive for the catfishes, the knifefishes, and the other taxa. In the analysis based on piscivore densities, the correlation with the discriminant scores (not shown) was negative for all species that were most abundant in clear lakes (eight species, Table 2) and positive for all species that were most abundant in turbid lakes (12 species, Table 2). In both analyses the dispersion of scores was similar across categories (Fig. 5), indicating that the critical assumption of equal variance-covariance matrices was not grossly violated (Williams 1983). Alternative discrim-

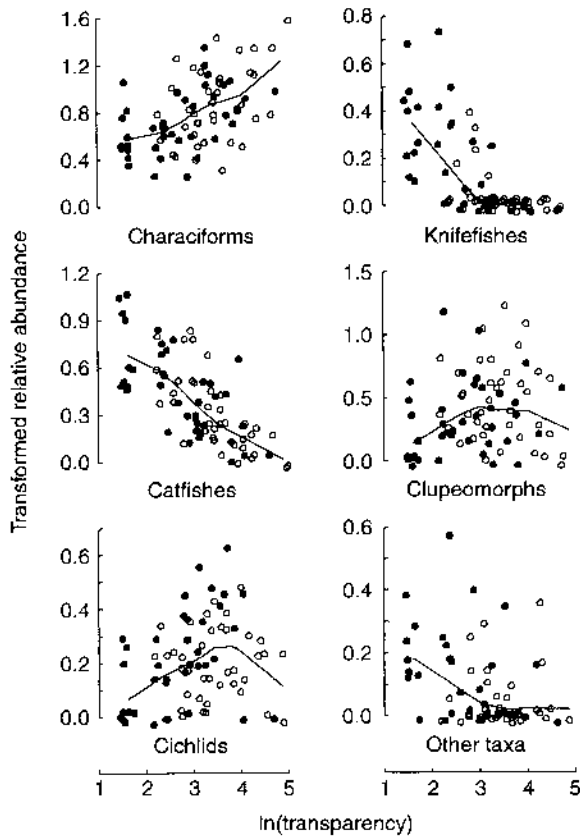


FIG. 2. Arcsine-transformed relative abundance (abundance measured as proportion of total CPUE [catch per unit effort]) of major taxa in relation to water transparency (\ln -transformed Secchi depth, cm). The characiforms (silver dollars, hatchetfishes), cichlids (peacock bass, earth eaters), and clupeomorphs (herrings, anchovies) are visually oriented whereas the catfishes (Siluriformes) and knifefishes (Gymnotiformes) have sensory adaptations to low visibility. A value of 3 along the abscissa corresponds approximately to 20 cm Secchi depth. Each data point is for one lake (\circ : early dry season; \bullet : late dry season). Solid lines in data fields are LOWESS regression curves.

inant analyses based on either three or four categories, corresponding to equally spaced intervals along the \ln (transparency) gradient, had lower classification accuracy than the simpler analysis with two categories.

Variation of assemblage structure with geographical distance between lakes

The Mantel tests based on log-transformed abundances did not reveal significant associations between geographical distance and assemblage structure for any combination of year and season (Table 6). For the site-standardized data, the tests involving all three regions yielded significant results for the early dry season in 1987 ($P = 0.046$) and 1988 ($P = 0.048$) (Table 6). This apparent effect of geographical distance on assemblage structure was caused by differences between the Caura region and the two other regions rather than by differences between the Ciudad Bolívar and Caicara

regions or differences within regions. The contrast in species composition between the Caura region and the other two regions was large relative to variation within regions, as were the geographical distances between the Caura region and the two other regions. Because Mantel's test is essentially a regression procedure (Smouse et al. 1986), large geographical distances (e.g., between regions) can influence the outcome of the test more than small distances (e.g., within regions). The average geographical distances between regions, calculated as distances between region centroids, were 194 km for Caura–Caicara, 234 km for Caura–Ciudad Bolívar, and 367 km for Caicara–Ciudad Bolívar. When the Caura region was excluded from the analysis (parts b and b' of Table 6), no effect of geographical distance on assemblage structure was detected, despite the fact that this analysis retained the two most widely separated regions. When both the Caura region and the Caicara region were excluded (parts c and c' of Table 6), no effects of geographical distance were detected within the Ciudad Bolívar region. As regions were dropped from the analysis, there was a trend toward larger significance values (Table 6). In general, geographical distance between lakes was per se a poor predictor of similarity in assemblage structure. The Mantel tests also showed that there is no strong spatial autocorrelation in assemblage structure among lakes, i.e., sites are spatially independent, and thus fulfill an important requirement of the statistical tests of relationships between assemblage structure and environmental variables (Hinch et al. 1994).

DISCUSSION

The results revealed an unexpectedly tight relationship between fish assemblage structure and four abiotic environmental features of Orinoco floodplain lakes: transparency, conductance, depth, and area (Table 4). Most lakes showed similar trajectories of seasonal assemblage change during isolation. This change involved reduction in the abundance of visually oriented fish relative to others concomitant with decline in transparency (Figs. 1 and 4). The classification of lakes into clear and turbid types based on major taxa was nearly identical to that based on piscivores (Fig. 5), suggesting a close association between these two aspects of assemblage structure and water transparency.

Microhabitat characteristics did not appear to influence assemblage structure during isolation, even though numerous taxa were associated with specific microhabitats (Lowe-McConnell 1975, Reid 1986, Rodríguez et al. 1990). The absence of spatial effects, as shown by the Mantel tests, and the low predictive power of the supra-lake environmental variables suggest that floodplain features surrounding the lakes, which could have affected fish movement and reshuffling over flooded terrain at high water and thus their assortment into lakes at drawdown, contributed little to assemblage structure during isolation. These results

TABLE 5. Fish abundances in clear lakes (Secchi depth > 20 cm) and turbid lakes (Secchi depth ≤ 20 cm) of the Orinoco floodplain. Densities are given as ln (CPUE+1), where CPUE = catch per unit effort; n = number of lakes. Standard errors are given in parentheses.

Taxon	1987		1988	
	Clear (n = 23)	Turbid (n = 17)	Clear (n = 17)	Turbid (n = 22)
Relative abundance (% of total CPUE)				
Characiformes	60.0 (5.4)	36.6 (4.7)	66.1 (5.6)	40.4 (5.0)
Siluriformes	9.3 (2.4)	29.5 (5.2)	3.9 (0.9)	29.5 (4.6)
Gymnotiformes	0.6 (0.4)	8.4 (3.0)	0.0 (0.0)	6.6 (2.1)
Cichlidae	7.7 (2.0)	3.3 (1.1)	8.2 (1.4)	4.5 (1.1)
Clupeiformes	21.6 (4.3)	18.3 (6.5)	20.8 (6.5)	16.9 (3.7)
Others	0.8 (0.5)	3.9 (1.7)	1.0 (0.7)	2.1 (0.8)
Total numerical density	4.1 (0.2)	4.1 (0.2)	4.4 (0.2)	4.3 (0.3)
Density of small tetras	2.23 (0.48)	1.11 (0.32)	3.09 (0.52)	2.08 (0.46)
Secchi transparency (cm)	50.0 (5.8)	13.5 (1.3)	44.1 (6.4)	11.4 (1.2)

point to local processes operating at the habitat scale as major determinants of assemblage structure during the dry season.

Assemblage structure in Caicara and Ciudad Bolívar lakes varied more or less continuously along an environmental gradient defined primarily by water transparency, but a marked discontinuity associated with conductance separated Caura lakes from those in the two other regions (Fig. 4). This discontinuity was due not only to differences in relative abundances of shared species, but also to regional differences in species pools. Only 23% of all species in the Caura and Caicara regions were found in both regions, and 21% of all species in the Caura and Ciudad Bolívar regions were found in both regions (Rodríguez and Lewis 1990). In contrast, 57% of all species in the Caicara and Ciudad Bolívar regions were common to both regions (Rodríguez and Lewis 1990). The discontinuity in fish assemblage structure between the Caura region and the two others is amenable to a biogeographical interpretation based on vicariance: former connections between the Caura and Upper Orinoco drainages may have affected large portions of the Caura ichthyofauna (Chernoff et al. 1991) independently of the Caicara and Ciudad Bolívar regions. Because conductance had limited value in explaining seasonal, within-region, or between-region (Caicara vs. Ciudad Bolívar) variation in fish assemblage structure (Fig. 4), its significance in this study probably resulted incidentally from the association of water type with biogeographical zonation.

A working model of fish assemblage variation in Orinoco floodplain lakes

Water transparency, by setting limits to underwater visibility, largely determines which major taxa and pis-

civore types predominate in a given lake during the dry season. Among the major taxa, catfishes and knifefishes, which are primarily nocturnal and have sensory adaptations to low light (Bennett 1971, Hara 1971, Lowe-McConnell 1975, Fink and Fink 1979), are dominant in turbid lakes, whereas characiforms, cichlids, and clupeomorphs, which usually are diurnal and rely on vision (Lowe-McConnell 1975, Fink and Fink 1979, Goulding 1980), predominate in clear lakes. The tactile and chemical sensors in catfishes and the electric sensors in knifefishes allow these fish to forage efficiently in turbid waters, which provide refuge from visual predators (Miller 1979, Blaber and Blaber 1980, Gregory 1993). In contrast, the visually oriented characiforms, cichlids, and clupeomorphs should be more vulnerable to predation when reaction distances are low (Vinyard and O'Brien 1976, Confer et al. 1978, Bruton 1985, Fraser et al. 1987); as light intensity decreases the visual advantage switches from the prey to the predator (Cerri 1983, Howick and O'Brien 1983, Pitcher and Turner 1986). For catfishes and knifefishes, the protective role of turbidity may be particularly critical during the dry season in dish lakes with a low depth/area ratio, where structural cover declines progressively as the shoreline recedes and fish become concentrated in a relatively featureless basin. This interpretation is consistent with the patterns of the CCA ordinations (Table 4, early dry season), for which Axis 2 reflects primarily a contrast between the assemblages of turbid dish lakes and those of clear lakes of greater relative depth. The selection procedure used in the ordinations includes individual environmental variables on the basis of their significance once the effect of other environmental variables has been partialled out (ter

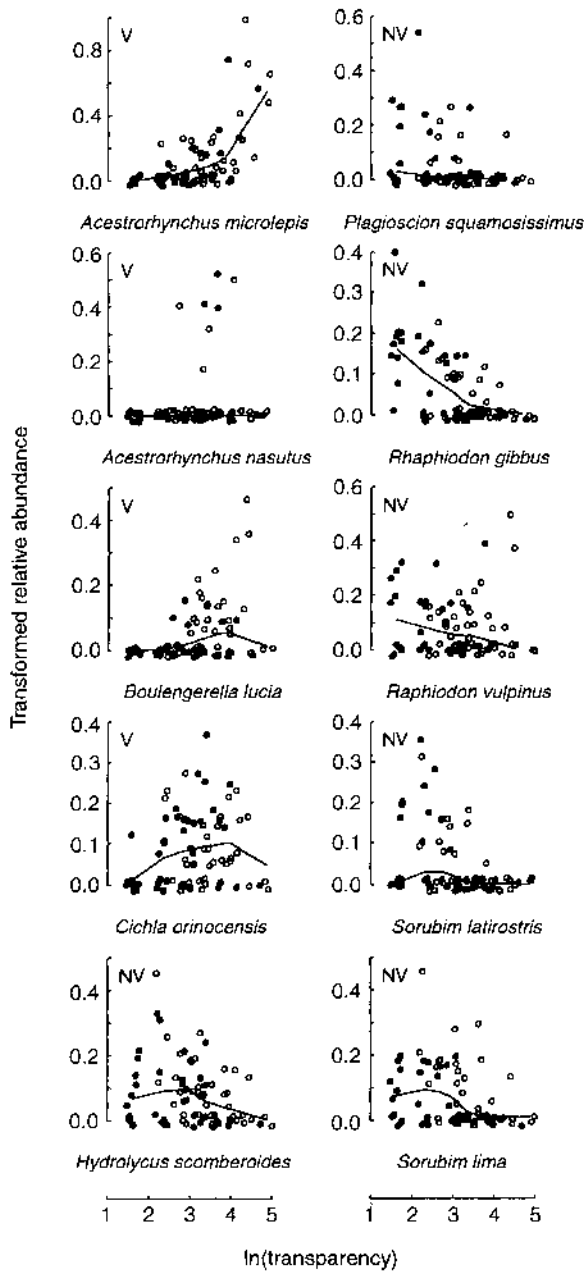


FIG. 3. Arcsine-transformed relative abundance (abundance measured as proportion of total CPUE) of the 10 dominant piscivorous species in relation to water transparency (ln-transformed Secchi depth, measured in cm). V: visual predators; NV: predators with adaptations to low visibility. Data presentation otherwise as in Fig. 2.

Braak 1988). Therefore, although transparency is correlated with lake morphometry (Hamilton and Lewis 1990), depth and area probably derive their significance in the CCA analyses from their effect on availability of cover rather than from indirect effects mediated by transparency.

Species distributions that cannot be explained on the basis of predominant sensory mode often could be in-

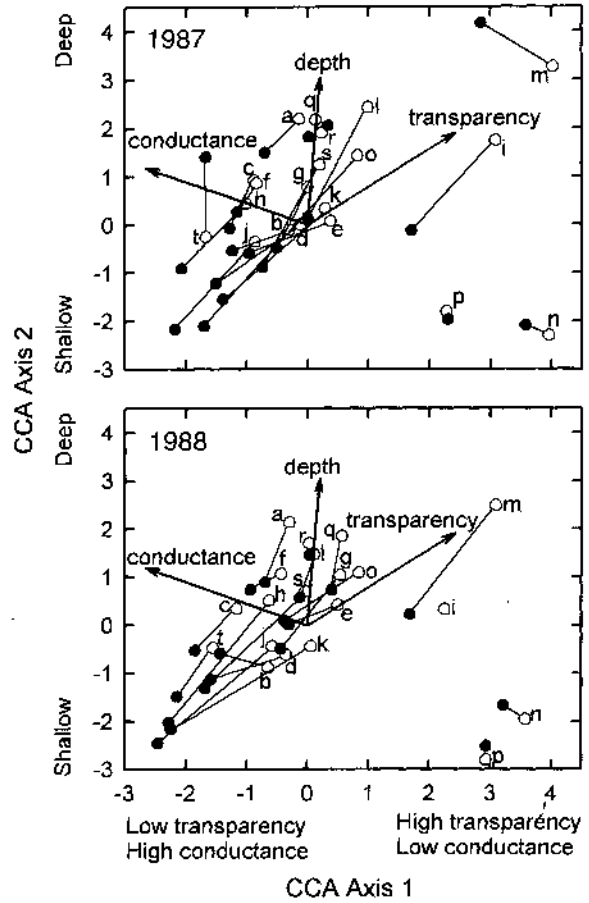


FIG. 4. Canonical correspondence analysis (CCA) ordination plot for lakes in the Orinoco floodplain (ordination based on all samples combined, $n = 79$ lakes), illustrating the seasonal shift in assemblage structure as transparency and depth decline and conductance increases. Samples for 1987 and 1988 are plotted separately for clarity. Lowercase letters identifying individual lakes correspond to those in Table 1. The direction and magnitude of seasonal change are indicated by the lines connecting early dry season (\circ) and late dry season (\bullet) samples. See Fig. 1 for explanation of environmental arrows.

terpreted in terms of other adaptations. Among the non-piscivorous taxa, many of the visually oriented species that are abundant in turbid lakes (Table 2) were found primarily near the surface where illumination is strongest (e.g., the tetras *Moenkhausia intermedia* and *Ctenopoma hauxwellianus*). Several of these species are morphologically specialized for feeding very near the water surface (Goulding 1980: the characiforms *Tripottheus angulatus*, *Tripottheus rotundatus*, *Tripottheus culter*, and *Thoracocharax stellatus*, and the clupeids *Rhinosardinia amazonica* and *Pellona flavipinnis*). Others, such as the characid scale-eaters *Roeboides myersi* and *Roeboides cf. affinis*, probably have nonvisual sensory adaptations to low light; *Roeboides* species feed at dusk or night and in water with extremely low visibility (Sazima 1983). This may be ac-

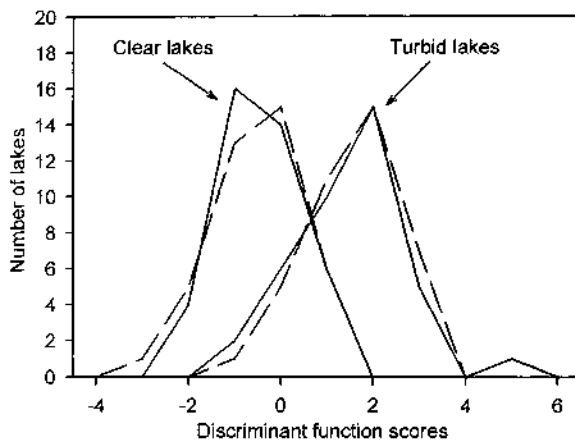


FIG. 5. Distribution of discriminant function scores for clear lakes (Secchi transparency >20 cm; $n = 40$ lakes) and turbid lakes (Secchi transparency ≤ 20 cm; $n = 39$ lakes). Solid lines: scores based on $\ln(\text{CPUE} + 1)$ of six major taxa; classification accuracy is 82% ($P < 0.001$; $df = 6, 72$). Dashed lines: scores based on $\ln(\text{CPUE} + 1)$ of the 20 most abundant piscivorous species; classification accuracy is 89% ($P < 0.001$; $df = 20, 58$).

completed through the use of sensory pores on the head (pit lines), which would allow nonvisual detection of prey (Sazima 1983). In fact, scale-eaters with special sensory capabilities may be more successful in very turbid waters, where they can approach visually oriented prey very closely before being detected (Sazima 1977, 1983).

Species-specific differences in mortality by piscivory underlie changes in relative abundance of species during the dry season (Rodríguez and Lewis 1994). Total mortality over the dry season, averaged across the Orinoco lakes, was $>75\%$ (Rodríguez and Lewis 1994). This rate is not uncommonly high for tropical floodplains, where yearly mortalities $>90\%$ have been found for 1-yr-old fish in several species (Welcomme

1985). In the Amazon floodplain, a very high proportion of the production by prey species is consumed by piscivorous fish (Bayley 1982). In the Orinoco lakes, fish with symptoms of disease or emaciation were very rare and terrestrial predators appeared to be of little significance; mass mortalities were never observed (Rodríguez and Lewis 1994). Although direct physiological stress can sometimes influence fish assemblages (winter anoxia and low pH in temperate lakes [Tonn and Magnuson 1982, Rahel 1984, 1986]; deoxygenation, desiccation, and hydrogen sulfide poisoning in tropical floodplain lakes [Welcomme 1985]), such factors seem unrelated to assemblage variation in the Orinoco lakes. No signs of lake desiccation or high concentrations of hydrogen sulfide were found during the dry season (M. A. Rodríguez, *personal observation*). Percent oxygen saturation near the lake bottom fell below 25% in only four of the 79 lake samples (Rodríguez and Lewis 1994), and oxygen concentration had no significant effect in the canonical correspondence analyses (Table 4). Furthermore, there appears to be no evidence that characiforms and cichlids systematically differ from catfishes and knifefishes as regards tolerance to hypoxia or high temperature (Rodríguez and Lewis 1994). Assemblage changes could not be explained in relation to pH, which showed no detectable variation in this study (Table 3).

The foraging performance of predators depends on their physiology, morphology, and behavior under prevailing environmental conditions (Ryder 1977, Hobson 1979, Miller 1979, Hobson et al. 1981). Piscivores of the *Cichla-Acestrorhynchus-Boulengerella* association, which characterizes clear lakes, are visual mid-water predators that lunge forward to capture prey (Zaret 1979, 1980, Menezes et al. 1981, Nico and Taphorn 1985). In well-lighted temperate lakes, dominant visual piscivores such as pike and muskellunge (*Esox* spp.) and bass (*Micropterus* spp.), which rely for their suc-

TABLE 6. Significance levels of Mantel tests evaluating the relationship between assemblage structure and geographical distance. The number of lakes is given in parentheses.

Regions included	1987		1988	
	Early dry season	Late dry season	Early dry season	Late dry season
Tests based on log-transformed data				
a) Ciudad Bolívar, Caicara, and Caura (20)	0.11	0.37	0.12	0.10
b) Ciudad Bolívar and Caicara (16)	0.17	0.46	0.19	0.20
c) Ciudad Bolívar (12)	0.05	0.81	0.34	0.75
Tests based on site-standardized data				
a') Ciudad Bolívar, Caicara, and Caura (20)	0.05	0.06	0.05	0.38
b') Ciudad Bolívar and Caicara (16)	0.11	0.20	0.11	0.65
c') Ciudad Bolívar (12)	0.67	0.28	0.86	0.66

cess on high acceleration and the ability to strike from cover (Guthrie 1986), are remarkably similar in overall morphology to the clearwater piscivores of the Orinoco lakes. *Boulengerella* species are solitary predators that strike from hiding places in submerged vegetation, whereas *Cichla* and *Acestrorhynchus* may hunt in groups. Some field evidence shows that the effect of *Cichla ocellaris* on prey populations depends on water transparency (Zaret 1979).

Piscivores in the cynodontid-catfish-*Plagioscion* association, which were found primarily in turbid lakes, differ in foraging mode. The three cynodontids, *Hydrolycus scomberoides*, *Rhaphiodon vulpinus*, and *R. gibbus*, are surface-oriented predators that have remarkably similar morphology. The narrow head allows stereoscopic vision anteriorly, ventrally, and dorso-anteriorly (Howes 1976). In very turbid waters, these fish likely detect prey from below (Ali 1959, Hobson 1979). The enlarged pectoral fins of these fish probably are used for rapid upward acceleration, followed by prey capture either by impalement on large inferior canines in the upturned mouth, or by suction caused by expansion of the buccal cavity (Howes 1976, Goulding 1980). In turbid lakes, the high upwelling illumination decreases the contrast between predator and background, making predators such as these less visible (Muntz 1982).

The piscivorous catfishes, such as *Pseudoplatystoma*, are predominantly benthic and probably rely mostly on tactile and chemical stimuli to detect prey (Reid 1983). The croaker *Plagioscion squamosissimus* is a silvery fish with a large mouth and a flattened ventrum. Croakers and drums (Sciaenidae) often live in turbid waters and have elaborate sound producing and receiving systems and a well-developed lateral line (Moyle and Cech 1988). Nico and Taphorn (1984) have shown that *P. squamosissimus* feeds near or on the bottom during the night, and Worthmann and de Oliveira (1983) have shown that this species feeds well in turbid lakes of the Amazon.

The model of fish assemblage structure that emerges from the associations of species groups with environmental variables involves causal relationships connecting piscivory to transparency and transparency to lake morphometry. Piscivores modify assemblage structure during the dry season by culling the most vulnerable prey species. Vulnerability in turn is strongly related to transparency. Transparency at low water is predictably related to the depth and size of lakes: resuspension of sediment leading to turbidity occurs at specific thresholds of depth and fetch (Hamilton and Lewis 1990). In addition to its role as a determinant of transparency, lake morphometry affects vulnerability through the relationship between lake relative depth and availability of structural cover. Furthermore, prey species may be able to use morphometric features of lakes as indicators of predation intensity, and predators may select lakes that are most compatible with their

mode of predation. This model emphasizes the interaction between lake transparency and the properties of individual species, in particular their sensory and foraging capabilities. Assemblage structure is strongly deterministic because lake morphometry channelizes the outcome of interactions between predators and prey in the same way from year to year. Thus, lakes with similar environmental features have similar fish assemblages, and such similarities are largely independent of geographical distance between lakes.

Generality of the model

The piscivory-transparency-morphometry (PTM) model may be applicable to other tropical floodplains. Turbid whitewaters are usually richer in nutrients and less acidic than more transparent clearwaters and blackwaters. Accordingly, Marlier (1967) and Goulding (1980) have stressed the effects of water chemistry and productivity when interpreting the marked faunal differences between these water types (Goulding and Ferreira 1984, Lowe-McConnell 1987). The PTM model may provide a more accurate description of influences on fish assemblages, however.

The PTM model is rich in testable predictions and suggests lines for further research at several levels. The environmental variables that proved to be significant in this study can be measured easily for other floodplains. Behavior and feeding performance of fishes can be assessed in experiments that involve manipulation of visibility. Physiological and behavioral studies can determine whether specific adaptations match the assumptions of the model. For example, the retinas of characiforms generally absorb at longer wavelength than those of cichlids and presumably confer increased sensitivity to characiforms in turbid waters (Muntz 1982), which may explain why characiforms are less restricted to transparent lakes than cichlids (Fig. 1).

The PTM model provides context for questions about fish adaptation and evolution. If trophic interactions are a major selective force whose outcome depends on the visual environment (Hobson et al. 1981), how does this phenomenon affect coloration patterns, microhabitat preferences, and selection of spawning sites? Does the timing of ontogenetic shifts differ among lakes with contrasting transparency? How do small zooplanktivores avoid predators while foraging in open waters and how do their adaptations depend on the optical environment?

To date, most extensive multi-lake surveys relating fish assemblage structure to lake features have been conducted in temperate zones. These studies have pointed to a biotic factor, piscivory, various abiotic factors such as area, depth, productivity, pH, alkalinity, winter hypoxia, and conductance, and biogeographic factors, including lake isolation or connectivity, as major determinants of fish assemblage structure (Johnson et al. 1977, Tonn and Magnuson 1982, Rahel 1984, 1986, Marshall and Ryan 1987, Jackson and Harvey

1989, Robinson and Tonn 1989, Tonn et al. 1990, Hinch et al. 1991, Jackson et al. 1992, Hinch et al. 1994). Although numerous studies have documented a marked influence of the underwater optical environment on individual foraging performance (e.g., Ali 1959, Ryder 1977, Fraser et al. 1987, McMahon and Holanov 1995), competition between species pairs (Bergman 1991), and spatial distributions of species (estuaries: Blaber and Blaber 1980, coral reefs: Roberts 1991), reports of a significant correlation between lake transparency and the structure of whole fish assemblages are rare (e.g., Johnson et al. 1977, Marshall and Ryan 1987). Marshall and Ryan (1987) attribute this correlation to a link between transparency and lake productivity without referring to a possible direct effect of transparency. In one of the few studies emphasizing the synecological effects of subsurface illumination in lakes, Ryder and Kerr (1989) discuss how light levels influence the geographic distributions of fish species, such as the congeners walleye (*Stizostedion vitreum*) and sauger (*S. canadense*), and suggest that competitive relationships between some species pairs may be determined by the light regime. The present study suggests that greater emphasis on the transparency-piscivory linkage may prove fruitful in explaining the distribution and abundance of fishes.

CONCLUSIONS

In agreement with the findings of Robinson and Tonn (1989), the fish assemblages of Orinoco floodplain lakes appear to be structured by a small number of environmental variables and one biotic variable, predation. Although water transparency has not been strongly linked to assemblage structure in earlier studies, transparency alone is a remarkably reliable predictor of which species, major taxa, and piscivore associations predominate in Orinoco lakes, and may explain correlations between environmental variables and fish assemblage structure in other studies. Fish with sensory adaptations to low light are dominant in turbid lakes, whereas fish relying on vision predominate in clear lakes, suggesting that the effect of transparency on assemblage structure is mediated by the constraints that the underwater optical environment places on foraging efficacy. The outcome of predator-prey interactions in floodplain lakes, and possibly other kinds of lakes as well, is dictated by transparency, which is predictable from morphometry. Thus fish assemblage structure is deterministic through relatively simple mechanisms on the Orinoco floodplain; a search for similar mechanisms elsewhere may prove fruitful.

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APPENDIX

Matrix of linear correlation coefficients for transformed environmental variables.

	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>	<i>f</i>	<i>g</i>	<i>h</i>	<i>i</i>	<i>j</i>
<i>b</i>	-0.33									
<i>c</i>	0.16	-0.09								
<i>d</i>	0.16	-0.51	0.70							
<i>e</i>	-0.08	-0.29	0.61	0.91						
<i>f</i>	0.30	-0.51	0.59	0.92	0.72					
<i>g</i>	-0.01	-0.36	0.62	0.96	0.95	0.84				
<i>h</i>	-0.52	0.35	0.08	0.24	0.50	0.06	0.50			
<i>i</i>	0.41	-0.05	-0.03	-0.02	0.07	0.06	0.05	0.21		
<i>j</i>	0.53	0.08	-0.08	-0.33	-0.35	-0.14	-0.33	-0.16	0.70	
<i>k</i>	-0.05	-0.49	0.21	0.56	0.52	0.56	0.53	0.05	-0.04	-0.20
<i>l</i>	-0.13	-0.01	0.25	0.47	0.55	0.37	0.52	0.42	0.05	-0.31
<i>m</i>	-0.27	0.63	-0.24	-0.44	-0.33	-0.36	-0.31	0.25	0.03	0.21
<i>n</i>	0.39	-0.36	0.12	0.42	0.37	0.26	0.37	0.09	0.20	0.17
<i>o</i>	0.34	-0.37	0.08	0.08	0.00	0.04	-0.02	-0.24	0.16	0.11
<i>p</i>	0.07	0.10	-0.14	0.06	-0.03	0.13	-0.02	-0.31	0.06	0.17
<i>q</i>	-0.44	0.42	0.07	-0.30	-0.17	-0.27	-0.19	0.29	-0.32	-0.34
<i>r</i>	0.10	0.21	0.21	0.01	0.11	0.00	0.09	0.28	0.32	0.19
<i>s</i>	-0.23	0.02	-0.34	0.08	0.06	0.22	0.17	0.24	0.13	0.10
<i>t</i>	-0.00	0.14	-0.05	-0.08	-0.10	-0.08	-0.10	-0.11	-0.14	-0.06
<i>u</i>	0.04	0.12	0.34	-0.06	-0.09	-0.01	-0.07	-0.01	0.09	-0.01

APPENDIX. Continued.

	<i>k</i>	<i>l</i>	<i>m</i>	<i>n</i>	<i>o</i>	<i>p</i>	<i>q</i>	<i>r</i>	<i>s</i>	<i>u</i>
<i>b</i>										
<i>c</i>										
<i>d</i>										
<i>e</i>										
<i>f</i>										
<i>g</i>										
<i>h</i>										
<i>i</i>										
<i>j</i>										
<i>k</i>										
<i>l</i>	0.32									
<i>m</i>	-0.58	-0.06								
<i>n</i>	0.15	0.19	-0.37							
<i>o</i>	0.25	-0.03	-0.50	0.23						
<i>p</i>	-0.34	-0.42	0.25	-0.14	-0.33					
<i>q</i>	-0.08	0.34	0.18	-0.57	-0.30	-0.35				
<i>r</i>	0.26	0.27	-0.06	0.10	0.31	-0.30	-0.12			
<i>s</i>	-0.01	0.01	0.48	-0.24	-0.36	0.14	-0.18	-0.09		
<i>t</i>	-0.12	-0.54	0.17	-0.06	-0.12	0.49	-0.23	-0.05	-0.02	
<i>u</i>	-0.15	-0.37	0.02	-0.06	0.19	-0.11	0.03	0.13	-0.14	0.05

Notes: *a* = Water transparency; *b* = Conductance; *c* = Oxygen concentration; *d* = Surface area; *e* = Fetch; *f* = Breadth; *g* = Lake perimeter; *h* = Shoreline development; *i* = Maximum depth; *j* = Nearshore depth; *k* = Distance from river; *l* = Distance from floodplain edge; *m* = Non-forested perimeter; *n* = Submerged vegetation; *o* = Overhanging vegetation; *p* = Floating grasses; *q* = Open shoreline; *r* = Submerged deadwood; *s* = Water hyacinth; *t* = Other floating plants; *u* = Emergent rocks.

Shoreline types (variables *n* through *u*) were not measured in early 1987. When necessary, correlations for these variables were calculated by pairwise deletion. pH was not included in the table because it showed no detectable variation.