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Regulation and stability in fish assemblages of neotropical floodplain lakes

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Abstract Neotropical floodplain lakes provide an excellent opportunity to examine the regulation and stability of fish assemblages. At low water, when lakes are separated, fish are concentrated in the lakes and are presumably subject to strong interspecific interactions that can shape assemblage structure. At high water, when the lakes and river channels become broadly interconnected, ample potential exists for alteration of assemblage structure because eggs, larvae, and older fish may undergo spatial reshuffling among waterbodies. Twenty lakes of the Orinoco River floodplain in Venezuela were surveyed in the early and late dry seasons of two consecutive years. Marked differences in assemblage structure among lakes were established in the early dry season. Changes in assemblage structure during the dry season were large and detectable even at the ordinal level; they reflected a strong reduction of visually oriented fish relative to fish with adaptations to low light. Changes were similar in the two years and were apparently due to species-specific differences in mortality, which was high over the dry season. The annual flood is a strong natural fluctuation that greatly modifies assemblage properties during the wet season. Nevertheless, the potential for alteration of assemblage structure by reshuffling was not realized: assemblage properties early and late in the dry season were similar in the two years, indicating a regular and predictable annual cycle of change in assemblage structure. This regularity can be explained by mechanisms of regulation which appear to be linked to piscivory and the optical environment. In contrast with the prevailing views on neotropical fish assemblages, there seems to be a strong deterministic component to assem-

blage structure and dynamics in Orinoco floodplain lakes.

Key words Equilibrium · Environmental fluctuation · Community structure · Seasonality · Orinoco

Introduction

During the past decade there has been much discussion of the relative effects of stochastic and deterministic mechanisms, and of the role of nonequilibrium processes that affect community structure (Price et al. 1984; Strong et al. 1984; Diamond and Case 1986; Gee and Giller 1987). An important motivation for this debate is that theoretical models of community structure, which very often are based on equilibrium assumptions, are unlikely to apply if a community is usually kept far from equilibrium by repeated disturbance (significant and abrupt change in an assemblage characteristic of interest; Connell and Sousa 1983), or by rapid changes in resource availability or the abiotic environment. An equilibrium may be static (point equilibrium) or dynamic (e.g., stable limit cycle; more generally, moving equilibrium; Wolda 1989). For natural communities, the distance from equilibrium should depend on the frequency and magnitude of disturbance and on the ability of component populations to "track" the equilibrium (Schoener 1987; Wolda 1989). If a natural or experimental disturbance is strong, recovery to the pre-existing condition (a point or a trajectory) indicates regulation, defined here as the process of adjustment toward equilibrium. Regulated communities thus exhibit "adjustment stability" (Margalef 1969); the related notions of "elasticity" (Orians 1975) and "resilience" (Pimm 1984) refer to the rate of return toward equilibrium. Communities that can recover rapidly from disturbance presumably remain closer to equilibrium than those with poor regulatory capability (Schoener 1987; Rodríguez 1992). Characteristics of the former community may be patterned and predictably related to local environmental conditions even when variation in

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abiotic factors is strong, whereas in the latter they are more likely to appear stochastic and unpredictable (Schoener 1987).

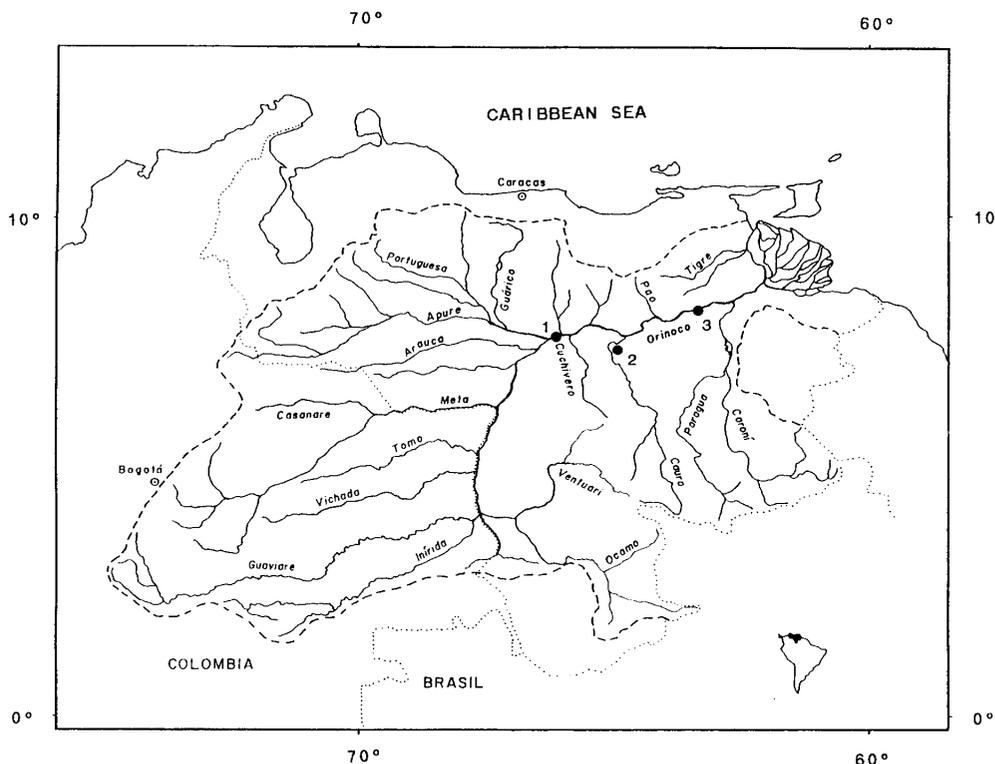
Fish ecologists have heatedly debated the relative influence of stochastic and deterministic factors on assemblage structure, with emphasis on coral reefs, temperate streams, and intertidal pools. The stability of coral reef fish assemblages is contingent upon the size and geographic location of the sampling area, the timing of sample collection, and recruitment variability, which is greatly influenced by local currents that transport eggs and larvae (Doherty and Williams 1988; Mapstone and Fowler 1988; Sale 1988, 1991; Harmelin-Vivien 1989). In temperate streams and in intertidal pools, assemblage properties seem to be less variable than in reefs. Although the suggestion by Grossman et al. (1982, 1985) that temperate stream fish assemblages are largely stochastic generated considerable interest and controversy (references in Heins and Matthews 1987; Grossman et al. 1990; Rahel 1990), recent studies seem to support the opposite view (Matthews 1986; Freeman et al. 1988; Matthews et al. 1988; Meffe and Berra 1988; Meffe and Sheldon 1988, 1990). Intertidal fish assemblages are persistent (but see Yoshiyama et al. 1986) and show adjustment stability over time scales ranging from a few weeks to several years (Thomson and Lehner 1976; Grossman 1982, 1986a; Beckley 1985; Collette 1986; Matson et al. 1986; Mistry et al. 1989).

Tropical floodplain lakes offer excellent opportunities for analysis of regulation and stability and for comparison of stochastic and deterministic effects on fish assem-

blages. In many tropical areas, rivers rise during the wet season and inundate the adjacent floodplain. Stochastic effects may operate at high water, when there is an opportunity for extensive spatial reshuffling of juvenile and adult fish and for widespread dispersal of eggs and larvae, which appear predominantly during this period (Lowe-McConnell 1975, 1987; Welcomme 1979, 1985). As waters recede and the lakes become isolated and shrink, fish are left in the lakes and pools. Selection pressures due to predation, deoxygenation, high temperature, desiccation, and food scarcity can be strong then (Zaret and Rand 1971; Lowe-McConnell 1975; Welcomme 1979, 1985). In extratropical systems, marked effects of seasonal flooding and waterbody contraction on fish assemblage structure have been demonstrated in the Everglades marshes (Kushlan 1976) and in lakeshore lagoons of Lake Erie (Mahon and Balon 1977).

Properties of species assemblages can be expected to recur from year to year if deterministic factors associated with individual lakes (e.g., location, morphology, and physicochemical characteristics of the water and sediments) outweigh the potential for stochastic reassortment during the flood period through reproduction, dispersal, and spatial reorganization of populations. This study exploited the natural variability and the large number of lakes found in the Orinoco floodplain in Venezuela as a means of quantifying the regulation and adjustment stability of fish assemblages. Specifically, we tested whether fish assemblage properties during the low-water season followed a similar temporal trajectory in two consecutive years despite the large fluctuation caused by the in-

Fig. 1 Map of the Orinoco River basin, showing the location of the study sites. (1 Caicara region, 2 Caura region, 3 Ciudad Bolívar region)



tervening annual flood. We also examined the proposal that deterministic factors associated with lake features underlie the year-to-year similarity of fish assemblages.

Methods and study area

Fish were collected from 20 lakes (median surface area = 16 ha; range = 3–251 ha) in three regions within the lower Orinoco Basin (Rodríguez and Lewis 1990). Four of the lakes were located along the Orinoco River near Caicara (Fig. 1: region 1), four were located along the Caura River near its confluence with the Orinoco River (Fig. 1: region 2), and the remaining 12 were located along the Orinoco River near Ciudad Bolívar, approximately 400 km downstream from Caicara (Fig. 1: region 3). The onset of the high-water season occurs in June, after which the water level rises rapidly. In 2 months lake depths can increase from 1–2 m to over 7 m, and the river, forest, plains, and lakes become broadly interconnected until December, when the flood recedes and the lakes once more become isolated and spatially discrete (Hamilton and Lewis 1987). During isolation lake depth is reduced, largely by evaporation, and turbidity increases as inorganic particulates are resuspended by wind (Hamilton and Lewis 1987; Rodríguez 1990).

The 20 lakes were surveyed once in January (early dry season) and once in April or May (late dry season) in both 1987 and 1988. Each survey of all 20 lakes was completed within a 20 day period. Late in the dry season of 1988, one lake in the Caura region could not be sampled. Lakes Terecaya and Tineo in the Ciudad Bolívar region were sampled on two consecutive days every 3 weeks beginning on 8 January 1987 and ending on 30 May 1988 (except in mid-February 1987). These two lakes were chosen for intensive sampling because a pilot study in 1986 had shown that the fish faunas of the two lakes differed greatly from each other late in the dry season. The lakes are separated by a distance of only 600 m, but contrast strongly in size and morphology: Lake Terecaya is a small channel lake devoid of macrophytes, whereas Lake Tineo is a large dish lake with abundant macrophyte cover, and is shallower than Lake Terecaya.

The hydrological cycle at Ciudad Bolívar is unimodal and approximately sinusoidal. The bankfull level, the stage height at which the river overflows into the adjacent floodplain, separates

the inundation phase (stage heights above bankfull) from the isolation phase (stage heights below bankfull). Several hydrological indices (Welcomme 1979) were computed for the Ciudad Bolívar region from the river stage height data supplied by the Venezuelan Ministerio del Ambiente: (1) FIL (floodplain inundation level), the total area of the water-level curve above the bankfull level, calculated as the sum of (stage height - bankfull level) over all days in which stage height exceeded bankfull; (2) FIL2, the same as FIL but beginning when bankfull was first exceeded and extending only to the day when peak water level was reached, and (3) DIP (duration of the isolation phase), the number of days in the preceding hydrological year during which river height was below bankfull. FIL and FIL2 provide an estimate of the magnitude of the inundation at different stages of the flood cycle, and therefore of the potential of the inundated area to provide fish with food, cover, spawning substrata, and diminished predator densities (Welcomme 1979). DIP is a measure of the exposure of lake-dwelling fish to low-water conditions. The duration of the low-water period in a given year may affect fish populations in subsequent years if the duration of the low-water season affects growth, recruitment, or mortality rates (Welcomme 1979). The flood preceding the 1987 surveys peaked early (FIL2), and the total duration and magnitude of the flood (FIL) was large relative to historical records (Table 1). In 1988 the magnitude of the flood was near the long-term average and the peak flood was delayed; the isolation phase preceding the flood (DIP) was unusually short.

Fish samples were collected with an aluminum electrofishing boat following the guidelines in Novotny and Priegel (1974) and Reynolds (1983). Electrofishing with pulsed current was used in this study because it is one of the least selective of all active fishing methods (Lagler 1978); it yielded abundant catches (a total of 18,869 fish) and was effective where conventional sampling methods such as netting would have been impractical. Pulsed current attracted fish to dropper anodes near the surface, which allowed them to be easily retrieved with a dipnet (6 mm mesh) even in very turbid water (Secchi transparency <5 cm). An operator equipped with polarized sunglasses and a visor captured fish upon sighting. The operator always attempted to avoid concentrating more strongly on particular species or on larger fish. Current intensity (fast-rise, slow-decay pulses at 120 Hz) was usually maintained between 4 and 6 amperes, within the range (3 to 6 amperes) recommended by Reynolds (1983). No significant relationship (Spearman rank correlation, ρ ; $n = 79$) was found between fishing success (total numerical density, defined below) and Secchi depth ($\rho = 0.001$), lake conductivity ($\rho = -0.127$), or lake depth ($\rho = -0.155$). Fish samples were collected during the day along shoreline stretches selected at random. Between 2 and 7 stretches summing to 50–280% of lake perimeter were sampled from each lake. Individual sampling runs lasted 20 min and covered approximately 900 m of shoreline length.

Fish were identified, measured to the nearest millimeter (standard length, SL), and weighed to the nearest 0.1 g in the laboratory. Species identifications were confirmed by systematists at the Instituto de Zoología Tropical, Universidad Central de Venezuela (UCV) in Caracas, and the Academy of Natural Sciences of Philadelphia. Voucher specimens of all collected species were deposited at the Museo de Biología UCV, at the Museum of the Academy of Natural Sciences of Philadelphia, and at the Museo de la Universidad Experimental de Los Llanos Ezequiel Zamora, in Guanare. A species list was given by Rodríguez and Lewis (1990). Species were partitioned into 8 trophic guilds, based on examination of stomach contents (617 individuals in 58 species) and on the data of Goulding (1980, 1988), Lowe-McConnell (1987), Machado-Allison (1987), and Winemiller (1987).

Species for which fewer than 5 individuals were captured were not included in analyses of species abundance. These species did not affect the results because their low abundance gave them negligible influence on the analyses. Of a total of 169 species, 53 were represented by fewer than 5 individuals. Most species of small (less than 4 cm SL; mean SL = 24 mm) characids of the subfamily Tetragonopterinae (tetras) were also dropped from analyses of species relative abundance, but tetra species larger than 4 cm SL were retained. The smaller tetras were excluded from these analyses be-

Table 1 Hydrological indices for the Ciudad Bolívar region. FIL2 and FIL are estimates of the magnitude of the inundation at different stages of the flood cycle. DIP is a measure of the exposure of lake-dwelling fish to low-water conditions. (FIL2 Area under the water-level curve between spillover and peak flood, in meter.day units; FIL area under the water-level curve between spillover and the end of the flood, in meter.day units. For FIL2 and FIL, values in parentheses indicate the duration, in days, of a given phase. DIP Duration, in days, of the isolation phase in the preceding year). The distributions of the indices are approximately normal

	Inundation		Isolation		
	Peak (FIL2)	Total (FIL)	(FIL)		(DIP)
1987	277.9	(69)	816.0	(196)	188
1988	359.7	(104)	680.6	(184)	153
1940–1988 ^a					
Mean	330.9	(86.4)	643.8	(173.8)	190.5
Minimum	134.0	(53.0)	371.3	(133.0)	153.0
Maximum	466.3	(113.0)	903.8	(197.0)	217.0
SD	92.8	(14.9)	153.0	(17.3)	19.2

^a Includes values calculated at 5-year intervals between 1940 and 1975, and yearly between 1977 and 1988

cause they are extremely difficult to identify or even to sort at the species level, and because their high numerical density might have caused analyses of species relative abundance to reflect primarily variations in tetra densities. Tetras smaller than 4 cm SL accounted for 29% by numbers and 0.39% by weight of all fish captured in this study; their median relative abundance (calculated across lakes based on numerical density; $n = 79$) was 5.6% with an interquartile interval of 0–36.2%. Although they were numerous in the floodplain lakes, their distribution was highly clumped both among and within lakes, and even within single electrofishing runs. Within a run, one sweep of the net in a location where tetras were concentrated could sometimes yield more individuals than the catch of all other species for the whole lake. The contribution of smaller tetras to the total fish biomass was negligible, yet their high numbers and small size make them potentially important as forage fish for larger piscivores, as consumers of zooplankton and food items associated with macrophytes (Araujo-Lima et al. 1986), and as competitors for food with the young of larger characiform species (Goulding 1980). Therefore, the unidentified small tetras were lumped into a single group and their numerical density was examined in separate analyses.

Raw data were converted to catch-per-unit-effort (CPUE: catch divided by shocker time). Total numerical density, numerical density of small tetras, total harvested biomass (biomass per effort), "species density", defined here as the number of species represented in a sample with a standardized number of individuals, and the numerical density of individuals (excluding small tetras) within each of six size classes (50-mm intervals ranging from <50 to ≥ 250 mm) were calculated for each lake and date. Species density was calculated by the method of rarefaction (Heck et al. 1975). To stabilize the variances and normalize the data, the $\ln(X + 1)$ transformation was used on total numerical density and size-class numerical density, and the square root transformation was used on total harvested biomass. The species density data did not require transformation. The $\ln(X + 1)$ transformation was applied to numerical density of individual species because the means and variances of species across sites were related by a power function (linear regression of log-transformed variance on log-transformed mean: slope = 1.79, $r^2 = 0.97$, $P < 0.001$). The appropriate transformation for stabilizing the variance in this case is X^q , with $q = 1 - \text{slope}/2$ (Elliott 1977). The resulting q value of 0.1 was rounded to zero, leading to the logarithmic transformation.

Because each lake was sampled on four occasions corresponding to two years (1987 and 1988) and two stages of the dry season (early and late), multivariate analyses of variance (MANOVA, 2×2 factorial design) were used in testing for year-to-year and within-season effects (the multivariate approach to repeated measures: Tabachnick and Fidell 1989). The statistical hypothesis tested by MANOVA was that year, season, or the year by season interaction had no effects on total numerical density, numerical density of small tetras, total harvested biomass, species density, or numerical density of individuals within each of six size classes. This design can detect year or season effects much more effectively than a conventional MANOVA with independent samples for each of the four factor combinations because sampling each lake under each factor combination greatly reduces the effects of variation among lakes.

A similar analysis (2×2 factorial MANOVA with repeated measures: doubly multivariate approach; Tabachnick and Fidell 1989) was used to test whether assemblage structure differed between years or between seasons, and whether there was a year by season interaction. In a doubly multivariate analysis of variance the number of dependent variables is given by the number of species times the number of cells; to prevent multicollinearity this number must not exceed the number of cases per cell (Tabachnick and Fidell 1989), which was 19 in this study. To reduce the number of dependent variables, a principal components analysis (PCA) was performed on the variance-covariance matrix of the full sample, and the first three component scores were retained as input for the MANOVA. The rationale for retaining a reduced set of components is that PCA extracts most of the patterned variation in a sample in the first few components, with noise being selectively deferred to the lower components (Gauch 1982). A test of extraction

adequacy, the scree test (Cattell 1966), indicated that only the first three components should be retained for further analysis. These components accounted for 40% of the total variance in the data set. With three components, the number of dependent variables in the MANOVA was reduced from 464 (116×4) to 12 (3×4).

In addition to the MANOVA test, the effects of year and season on assemblage structure were analyzed by means of ordination plots generated by detrended correspondence analysis (DCA; Hill and Gauch 1980) as implemented in the program CANOCO (ter Braak 1988). Ordination was performed on the full data set for the four 20-lake surveys (79 samples by 116 species) to produce plots that represent the similarities in assemblage structure among the 79 samples. The sequential tri-weekly samples from Lakes Terecaya and Tineo were also analyzed by ordination.

Multivariate analyses of community change were used because of their advantages over analyses based on simpler measures (similarity indices, rank order coefficients, coefficients of variation) which have several undesirable properties, such as sensitivity to total abundance and species richness, poorly known parent distribution, and subjective definition of "similarity", that can hinder comparisons between samples and between studies (Steinhorst 1979; Wolda 1981). These measures do not allow for simultaneous visualization of the direction and magnitude of community change in multiple samples as does ordination. The use of ordination trajectories for assessment of temporal change in community structure is illustrated by Evans (1988), Boulton et al. (1992), and Gelwick and Matthews (1992).

Results

Seasonal change in fish assemblages of Lakes Terecaya and Tineo

The magnitude of the fluctuation caused by flooding and the trajectory of change in fish assemblages during the isolation phase were documented with the tri-weekly samples from Lakes Terecaya and Tineo. In Lake Terecaya, total numerical density and harvested biomass decreased during the isolation phase, and were reduced to zero as the flood peaked (Fig. 2). During inundation, the number of species was much less than during isolation (Table 2). Much of the variability in total numerical density during the flood was caused by fluctuations in the abundance of a single species, *Rhinosardinia amazonica*, a small (< 50 mm SL) herring which abounded at high water but was rare during the isolation phase. The density of small tetras was very low during the isolation phase in both years and peaked strongly toward the end of the flood (Fig. 2).

Seasonal variation in total numerical density was less patterned in Lake Tineo than in Lake Terecaya (Fig. 3), because of high variability in the densities of *R. amazonica* and of another small clupeomorph, *Anchoviella perezi*, both of which were very abundant during inundation. The numerical density of smaller tetras was also highly variable in time; it underwent reduction during the flood but otherwise showed patterns similar to those of the small clupeomorphs (Fig. 3). Most critical for Lake Tineo were the densities of individual species on the two sampling dates nearest to peak flood, 29 August 1987 and 20 September 1987. Apart from the smaller tetras, on these dates no fish were captured in Lake Terecaya (Fig. 2), and in Lake Tineo only three species other than *R. amazonica* and *A. perezi* were represented in the

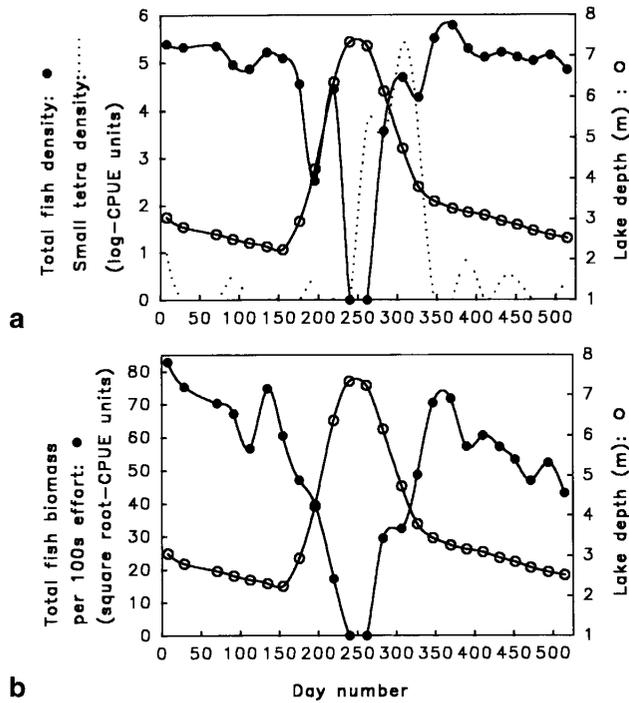


Fig. 2a, b Seasonal variation of fish density and harvested biomass in relation to water depth in Lake Terecaya. **a** Density (CPUE: numbers per 100 s shocker time). **b** Harvested biomass (CPUE: g per 1000 s shocker time). The small tetras were excluded from calculations of total density and harvested biomass. Day 1 = 1 January 1987, day 514 = 30 May 1988

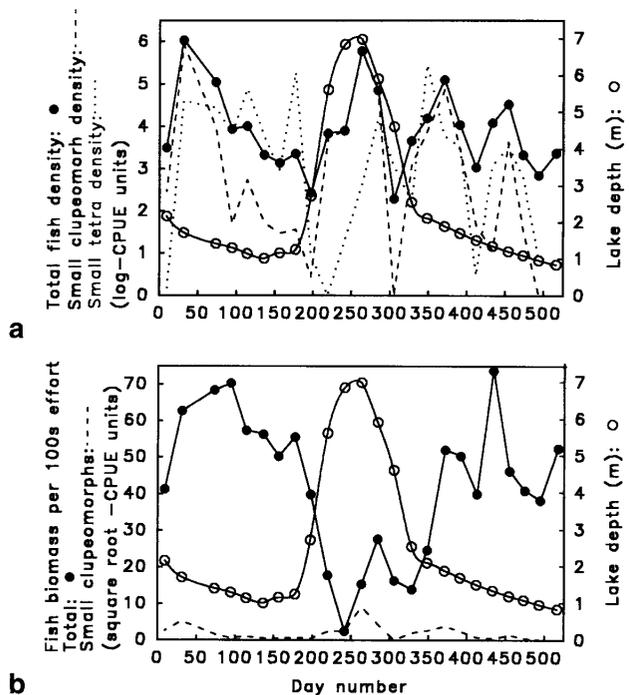


Fig. 3a, b Seasonal variation of fish density and harvested biomass in relation to water depth in Lake Tineo. **a** Density (CPUE: numbers per 100 s shocker time). **b** Harvested biomass (CPUE: g per 1000 s shocker time). The small tetras were excluded from calculations of total density and harvested biomass. Day 1 = 1 January 1987 day 514 = 30 May 1988

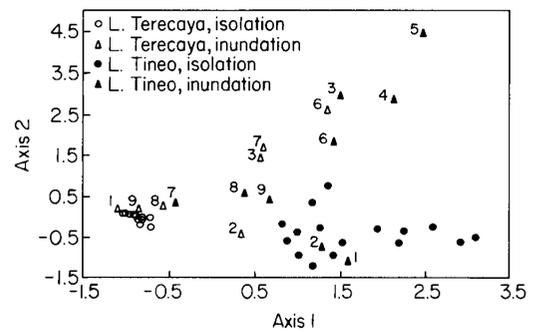


Fig. 4 DCA ordination showing seasonal change of assemblage structure (species relative abundance) in Lakes Terecaya and Tineo over a 17-month period. *Numbered symbols* represent samples from the inundation phase in chronological order: *number 1* is the first sample collected after flood water entered the lakes, in June 1987. The time interval between consecutive samples is 3 weeks. For Lake Terecaya, the two points corresponding to peak flood (*numbers 4 and 5*) are not represented in the plot because no fish were collected on these dates

catch, each by only one individual. Total harvested fish biomass, which in Lake Tineo was only marginally affected by the numerical fluctuations of the small clupeomorphs, was greatly reduced during inundation (Fig. 3b).

Reduction in total numerical density and harvested biomass in the lakes at high water could be caused by movement of fish out of the lakes or by dilution (reduction in density due solely to increase in lake size). Dilution ratios (ca. 5) for Lakes Terecaya and Tineo were much smaller than the observed proportional reductions in total numerical density (excluding *R. amazonica* and *A. perezii*), indicating that most fish species left the lakes during inundation. The destination of fish leaving the lakes is largely unknown. Even though the larger adults of many species undertake reproductive migrations in the main river channel (Lowe-McConnell 1975, 1987; Welcomme 1985), most individuals probably remain in the floodplain, exploiting the abundant food, cover, and spawning substrata in newly flooded habitats. Between 9 August and 20 September 1987, near peak flood, numerous young-of-the-year of 17 species were captured by electrofishing in the flooded forest between Lakes Terecaya and Tineo, a zone accessible to fish only during inundation.

DCA was used to generate an ordination plot of the tri-weekly samples from Lakes Terecaya and Tineo in 1987 and 1988, and of two additional samples collected from each lake in the late dry season of 1986 (Fig. 4). The isolation phase samples for all years are clustered together by lake, on the left of the plot for Lake Terecaya and on the right for Lake Tineo. Variability in assemblage structure within the isolation phase was less in Lake Terecaya than in Lake Tineo, as shown by the difference in scatter of the two clusters. As flood water entered the lake, assemblage structure was displaced, and the two lakes tended to converge. During inundation both lakes are displaced toward the top right of the plot, and subsequently each lake returns to its isolation-phase

Table 2 Major taxa relative abundance (%), total numerical density (CPUE), and species richness for Lakes Terecaya and Tineo, and Spearman rank correlation of relative abundance and

species richness with scores of the first two axes of DCA ordination of Lake Terecaya and Lake Tineo tri-weekly samples (see Fig. 4). Means and SE are presented

	Lake Terecaya			Lake Tineo			Rank correlation with first 2 DCA axes	
	Isolation 1987 (n = 7)	Flood (n = 9)	Isolation 1988 (n = 8)	Isolation 1987 (n = 7)	Flood (n = 9)	Isolation 1988 (n = 8)	A1	A2
Characiformes	94.1 (0.6)	43.1 (13.7)	92.2 (1.6)	42.1 (6.8)	28.7 (11.6)	37.0 (6.6)	-0.67	-0.30
Siluriformes	2.4 (0.2)	6.3 (4.2)	3.4 (0.9)	14.2 (3.5)	5.5 (3.6)	13.9 (3.4)	0.26	-0.75
Gymnotiformes	0.0 (0.0)	0.1 (0.1)	0.0 (0.5)	1.2 (0.8)	1.2 (1.2)	12.0 (6.1)	0.52	-0.41
Cichlidae	3.1 (0.6)	0.1 (0.1)	2.0 (0.5)	4.2 (0.9)	1.0 (0.7)	3.5 (0.9)	0.13	-0.75
Clupeiformes	0.3 (0.1)	28.0 (12.6)	2.3 (0.5)	35.2 (10.2)	62.7 (14.4)	30.5 (10.5)	0.45	0.16
Other	0.1 (0.1)	0.2 (0.2)	0.2 (0.1)	3.2 (1.4)	0.9 (0.5)	3.1 (1.5)	0.45	-0.53
Total numerical density	178.9 (13.2)	72.1 (25.6)	185.7 (21.2)	107.8 (54.0)	76.7 (32.7)	57.3 (17.4)	-0.45	0.16
Species richness	27.6 (1.4)	10.8 (3.1)	32.1 (1.0)	28.9 (4.1)	9.0 (2.2)	23.8 (2.1)	-0.20	-0.54

cluster. The shift toward the upper right corner and the convergence between lakes reflect the numerical dominance of the clupeomorphs *R. amazonica* and *A. perezii* and a reduction in the number of species in the lakes during the annual flood (Table 2).

In Lake Terecaya, assemblage structure did not vary much after isolation relative to the marked change that occurred during the flood. In Lake Tineo, considerable change occurred during isolation. In a separate ordination plot for the isolation phase only, Lake Terecaya trajectories for 1987 and for 1988 are separate from each other and run from bottom right to top left (Fig. 5). Separation between years occurs because the 1987 samples had higher relative abundances of *Mylossoma duriventre*, and lower relative abundances of *Poptella longipinnis* and *Metynnis luna*. These three species are deep-bodied characids; *M. duriventre* and *P. longipinnis* are usually found very near the shoreline, in association with submerged trees or deadwood. In Lake Terecaya, *M. duriventre* feeds on aquatic and terrestrial insects and on zooplankton, *P. longipinnis* feeds on aquatic insects, and *M. luna* is a diurnal, pelagic zooplanktivore. Displacement toward the top left corner is caused by a decrease of the characids *Laemolyta orinocensis*, a medium-sized scale-eater and scavenger, and *Acestrorhynchus microlepis*, a small pike-like piscivore, and by increases in the relative abundance of the deep-bodied characiforms. The within-year and among-year variations in assemblage structure were very small in Lake Terecaya compared to the ranges observed in all other lakes. The three samples from comparable dates in 1986, 1987, and 1988 are not sequenced along either axis, as would be expected if assemblage structure oscillated around a set point determined by nondirectional factors that vary little from year to year (Fig. 5, Table 2).

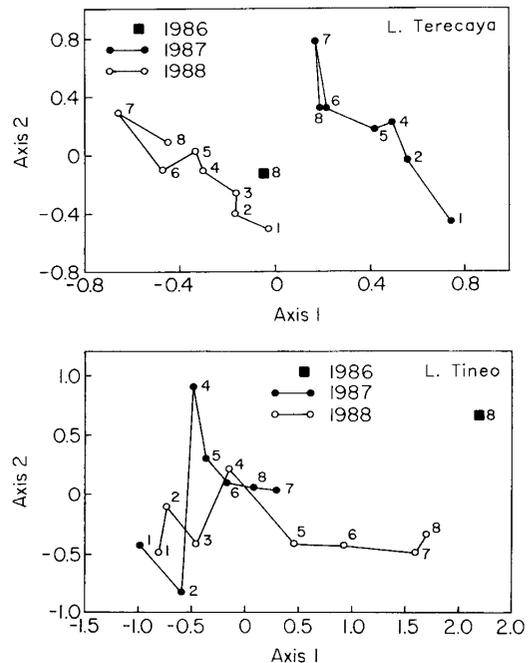


Fig. 5 DCA ordinations showing variation in assemblage structure (species relative abundance) in Lakes Terecaya and Tineo during the isolation phase in 1987 and 1988 with a single sample from 1986 for comparison. Numbered symbols represent samples in chronological order: number 1 is the first sample collected after isolation, early in January. The time interval between consecutive samples is 3 weeks. Neither lake was sampled in mid-February 1987 (number 3)

In the ordination plot for the isolation phase of Lake Tineo (Fig. 5), samples from 1987 and 1988 are ordered along axis 1 in a temporal sequence from left to right. (Axis 2 is not useful; it does not separate the 1987 and 1988 samples from each other, and it does not arrange

Table 3 Summary of MANOVA analyses for the effect of season and year on assemblage properties

Dependent variable	Mean (standard error)				Degrees of freedom, <i>F</i> values, and significance levels of main effects and interaction term						
	Dry season 1987		Dry season 1988		<i>d.f.</i>	Year		Season		Year × Season	
	Early (<i>n</i> = 20)	Late (<i>n</i> = 20)	Early (<i>n</i> = 20)	Late (<i>n</i> = 19)		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Total numerical density ^{a,b}					1,18	1.43	0.25	13.90	0.002	3.48	0.08
CPUE	131.26 (24.12)	59.81 (17.04)	155.36 (32.96)	106.40 (33.98)							
ln(CPUE+1)	4.56 (0.19)	3.60 (0.22)	4.53 (0.27)	4.16 (0.24)							
Numerical density of small tetras ^{a,b}					1,18	3.93	0.06	6.69	0.02	0.02	0.90
CPUE	72.38 (34.19)	13.26 (5.21)	90.57 (26.5)	44.12 (17.93)							
ln(CPUE+1)	2.28 (0.49)	1.23 (0.38)	3.07 (0.48)	1.94 (0.49)							
Total harvested biomass ^{a,c}					1,18	0.79	0.39	4.43	0.05	1.31	0.27
CPUE	4081.0 (482.1)	3004.6 (604.9)	3998.5 (576.1)	4171.7 (858.5)							
(CPUE) ^{1/2}	61.50 (3.97)	49.49 (5.41)	60.49 (4.23)	59.16 (6.11)							
Species density					1,18	0.32	0.58	1.96	0.19	0.28	0.60
No. of species per rarefied sample of 20 specimens	4.78 (0.20)	5.00 (0.27)	4.77 (0.22)	5.17 (0.13)							
Size-class distribution ^d											
< 50	2.91 (0.41)	1.70 (0.31)	3.36 (0.43)	2.62 (0.35)	1,18	2.53	0.13	7.86	0.01	1.46	0.24
50–100	2.90 (0.33)	2.28 (0.24)	2.93 (0.33)	2.72 (0.35)	1,18	0.64	0.43	6.22	0.02	2.34	0.14
100–150	2.84 (0.17)	1.85 (0.22)	2.57 (0.17)	2.42 (0.21)	1,18	0.42	0.52	14.80	0.001	13.27	0.002
150–200	2.11 (0.14)	1.43 (0.17)	1.76 (0.13)	1.65 (0.19)	1,18	0.09	0.77	6.98	0.02	4.16	0.06
200–250	1.36 (0.15)	1.36 (0.18)	1.40 (0.14)	1.54 (0.15)	1,18	0.12	0.73	0.35	0.56	0.29	0.60
≥250	1.23 (0.11)	1.23 (0.14)	1.11 (0.14)	1.25 (0.18)	1,18	0.35	0.56	0.99	0.33	0.15	0.71
Assemblage structure					3,16	1.36	0.29	4.45	0.02	1.04	0.40
PCA axis 1 scores	0.065 (0.080)	-0.161 (0.049)	0.111 (0.116)	-0.015 (0.088)							
PCA axis 2 scores	0.071 (0.072)	-0.112 (0.056)	0.121 (0.091)	-0.084 (0.103)							
PCA axis 3 scores	0.013 (0.085)	-0.076 (0.057)	0.063 (0.092)	0.001 (0.059)							

^a: Means and standard errors are shown for both transformed and untransformed variables. MANOVA was performed on transformed variables

^b: CPUE units are numbers per 1000 s shocker time

^c: CPUE units are g per 1000 s shocker time

^d: Size class intervals are based on standard length (mm). The numerical density for each size class is the total number of individuals falling within the size class (regardless of taxonomic affiliation) per 1000 s of shocker time. Means and SE are for ln(X+1)-transformed numerical densities

the samples in chronological order.) Similar to Lake Terecaya, the late isolation samples from 1986, 1987, and 1988 are not sequential in the Lake Tineo plot; there is a reversal along axis 1 from 1987 to 1988. The displacement toward the right in 1987 and 1988 samples was caused in both years by a decrease in the relative abundances of most characiforms, of cichlids, and of *A. perezii*, together with an increase in the relative abundances of siluriforms (catfishes), of gymnotiforms (knife-

fishes), and of large piscivores (the characids *Hydrolycus scomberoides*, *Rhaphiodon vulpinus*, and *Rhaphiodon gibbus*, and the sciaenid *Plagioscion squamosissimus*).

In Lakes Terecaya and Tineo, the assemblage trajectories for isolation showed directional change, with the exception of the late May samples, when the trajectories reversed or halted (samples 8 in Fig. 5). The duration of the isolation phase preceding the flood and the timing and magnitude of the flood had little effect on assem-

blage structure in the dry season. During the study, these hydrological features varied considerably from year to year and reached extreme values relative to historical records (Table 1), yet differences in assemblage structure between 1986, 1987, and 1988 were small relative to within-season differences (Fig. 5, Table 2).

Numerical density

Total numerical density did not vary significantly from year to year, but did change between the early and late dry season for a given year (Table 3); the magnitude and direction of change during the low-water season was comparable across years (i.e., the interaction between factors was not significant). A similar pattern was found for the numerical density of small tetras, but seasonal reduction was stronger for small tetras than for total density (Table 3).

The ratio between total densities early and late in the dry season for 1987 (an 18.1 week interval) ranged among the 20 lakes from 0.10 to 20.33 [mean = 4.52, median = 2.59, and Tukey's M-estimator (Hoaglin et al. 1983) = 2.22]. In 1988, the ratios for a 14.4 week interval ranged from 0.17 to 5.97 (mean = 1.97, median = 1.87, and Tukey's M-estimator = 1.60). Tukey's M-estimator ("biweight" estimator), a robust and efficient maximum-likelihood estimator of central tendency (Hoaglin et al. 1983), indicated that densities decreased by 55% in 1987 and by 38% in 1988. Absolute population sizes decreased more than this because lake surface area decreased during the isolation phase, thereby concentrating the fish (e.g., approximately 10% for Lakes Terecaya and Tineo).

During the isolation phase reproduction was negligible in the lakes, as indicated by the absence of new cohorts in length-frequency distributions and by inspection of gonads (M.A. Rodríguez, unpublished data) thus the average mortality rate can be estimated from the equation $N_f = N_0 e^{-mt}$ (Welcomme 1985), where m is the mortality rate, N_0 is the numerical density (CPUE) in January, and N_f is the final density, adjusted for seasonal reduction in lake area. Total mortalities (pooled across spe-

cies) for the isolation phase were estimated as the mortality at rate m over 26.7 weeks, the average duration of the isolation phase. Total mortality across all lakes was 76% in 1987 and 77% in 1988 (Tukey's M-estimator); the 25–75 interquartile interval was 45–89% in 1987 and 43–81% in 1988. The difference between years was not statistically significant (two-tailed $P = 0.33$; Wilcoxon signed ranks test).

Additional evidence of high mortality rates comes from demographic analysis. Age determinations for 918 individuals (collected mainly in Lakes Terecaya and Tineo during the dry season) showed that most fish were young-of-the-year (24 species in 7 families, mostly characiforms; Table 4). Few individuals lived longer than 4 years. Preliminary examination of catfish otoliths also suggested that individuals older than 4 years were rare (M.A. Rodríguez, personal observation). Although independent calibrations of age determinations from scales and otoliths were not available for these species, previous studies in neotropical river systems have used annuli in hard structures as reliable indicators of fish age (characiforms: Lowe-McConnell 1964; de Godoy 1975; Lilyestrom 1983; cichlids: Lowe-McConnell 1964; Lobón-Cerviá et al. 1993; siluriforms: Reid 1983). In neotropical floodplains annuli generally appear to be formed yearly (but see Welcomme 1985) during the low-water season when growth is slowest.

The most plausible cause of the high mortality appears to be predation by fish; piscivorous fish accounted for 39% of total harvested biomass at low water (average across lakes). Tetrapod piscivores were found in some of the lakes (Rodríguez 1990), but field observations of the abundance and feeding behavior of these piscivores suggest that their impact on fish numbers was low. Piscivorous birds, in particular members of the Ciconiiformes, do not form seasonal aggregations in the region as they do further west, in the internal delta of the Venezuelan Llanos (Ayarzagüena-Sanz et al. 1981).

Crustacean parasites, mainly argulids and isopods, were often found on the body surfaces of captured fish. However, fish with symptoms of disease or emaciation were very rare. It was not unusual to find fish wounded and bleeding from bites by other fish, as evidenced by

Table 4 Cumulative percentage of specimens by age class. Ages were read from annuli on scales. With the exception of cichlids (order Perciformes) all families are in the order Characiformes

Family (no. of species examined)	Age class						Number of specimens examined
	0+	1+	2+	3+	4+	5+	
Anostomidae (3)	38.9	65.8	90.2	97.4	100.0		234
Characidae (12)	81.1	95.8	99.7	100.0			380
Cichlidae (3)	50.0	86.8	100.0				38
Curimatidae (1)	15.6	54.9	87.9	98.7	99.6	100.0	224
Erithrynidae (1)	25.0	50.0	75.0	100.0			8
Hemiodontidae (2)	65.0	95.0	100.0				20
Prochilodontidae (2)	50.0	85.7	100.0				14
Total (24)	51.7	77.2	94.2	99.0	99.9	100.0	918

teeth marks on the body and by the semi-circular pattern left on the edge of the clipped fin (M.A. Rodríguez, personal observation). Nip and bite marks on fins, especially the caudal, became increasingly common as the isolation phase advanced; fin and body parts often showed signs of regeneration. Mass mortalities by desiccation, deoxygenation, or hydrogen sulfide poisoning (Brinkmann and de Santos 1973), were never observed in these lakes.

Harvested biomass

Harvested biomass did not vary significantly from year to year (Table 3). Harvested biomass decreased during the low-water season in 1987, but less so than numerical density. No change in harvested biomass group means (unpaired samples comparison) was discernible in 1988 between the early and late dry season (Table 3). Nevertheless, the reduction in total harvested biomass (as for mortality, over a 26.7 week period) calculated across all lakes (paired samples comparison), was 46% in 1987 and 36% in 1988 (Tukey's *M*-estimator); the 25–75 interquartile interval was –5% to 81% in 1987 and –6% to 73% in 1988. The difference in reduction of total harvested biomass between years was not statistically significant (two-tailed $P = 0.47$; Wilcoxon signed ranks test). Reduction of harvested biomass during the dry season was less marked than that of numerical density (more than 25% of lakes showed increases in harvested biomass), which partly reflects biomass addition by individual growth.

Species density

Species density ($E_s(n)$; the number of species represented in a sample with a standardized number of individuals) was calculated by rarefaction for sample sizes of $n = 7, 20, 50,$ and 100 individuals (Heck et al. 1975). Even though the ordering of sites can depend on the sample size (Kempton 1979), in this study the Pearson correlations between E_s values for different sample sizes were high [e.g., $r = 0.97$ for $E_s(7)$ and $E_s(20)$, $r = 0.96$ for $E_s(20)$ and $E_s(50)$, and $r = 0.97$ for $E_s(50)$ and $E_s(100)$]. Analysis of variance for $E_s(20)$ (Table 3) showed that species density did not vary significantly during the low water season or from year to year. Similar results were obtained for $E_s(7)$.

Size-class distribution

The size-class distribution of all fish combined did not vary significantly from year to year (Table 3). Numerical densities of smaller fish (<200 mm) declined during the dry season; this effect was strongest for the smallest size class (<50 mm). The decline in density, at least in the two smallest size classes, must have been primarily due to mortality rather than individual growth, because most

fish in these size classes belonged to species with maximum length less than 100 mm. Density of larger fish (>200 mm) did not undergo detectable seasonal change (Table 3). The high densities recorded for fish under 10 mm and for small tetras (Table 3) suggest that the electrofishing procedure allowed us to obtain representative samples of this size group and probably provided a reliable indicator of changes in their abundance.

Reductions in total numerical density, numerical density of small tetras, harvested biomass, and density of fish under 200 mm were less marked in 1988 than in 1987 (Table 3), presumably because the interval between samples was smaller in 1988 (14.4 weeks) than in 1987 (18.1 weeks). This difference in sampling interval may also explain why the mean values for these properties in 1987 and 1988 showed closer correspondence in the early dry season than in the late dry season (Table 3). Smaller fish underwent stronger seasonal reduction in density than larger fish, which is consistent with the suggestion that mortality by piscivory was the main cause of reduction, as smaller fish generally are more vulnerable to predation (Werner 1986).

Assemblage structure

The repeated-measures MANOVA results for assemblage structure as measured by PCA (Table 3) showed that the year effect and the interaction effect were not significant, but that the season effect was significant. These results indicate that the magnitude and direction of the seasonal change were comparable across years, duplicating the pattern for numerical density, harvested biomass, and size-class distribution. For each effect in the MANOVA, a linear combination of the dependent variables can be constructed that maximizes the fraction of total variance accounted for by that effect; this fraction is a measure of the relative importance of the effect (Tabachnick and Fidell 1989). The percentage of variance accounted for by season (the only significant effect) was 46%.

Adjustment for variation among lakes makes the repeated-measures approach more sensitive for detection of effects than conventional MANOVA, but useful information can be lost if among-lake variation is neglected altogether. Total variation in community structure during the isolation phase can be partitioned into a temporal component (season, year) and a spatial component (among-lake variation). The temporal component results primarily from differential mortality presumably caused by predators during the low-water period (the year effect is not significant), whereas the spatial component is due to assortment of fish among lakes at the onset of the isolation phase and to sampling error. The magnitude of the seasonal effect relative to all other components was estimated by conventional MANOVA. Seasonal change accounted for 14% of the total variation in community structure, indicating that the effect of mortality between sampling periods was small relative to the combined effect of year and among-lake variation.

Fig. 6 DCA ordination showing effect of year and season on assemblage structure (species relative abundance) for 20 floodplain lakes. For clarity, the results of a single ordination that includes the samples from both years are presented in two separate panels. Lakes 2, 3, 5, and 8 are in the Caicara region; lakes 9, 13, 14, and 16 are in the Caura region; the remaining lakes are in the Ciudad Bolívar region. Number 18 corresponds to Lake Terecaya and number 19 to Lake Tineo. In 1988, lake 9 was not sampled in the late dry season

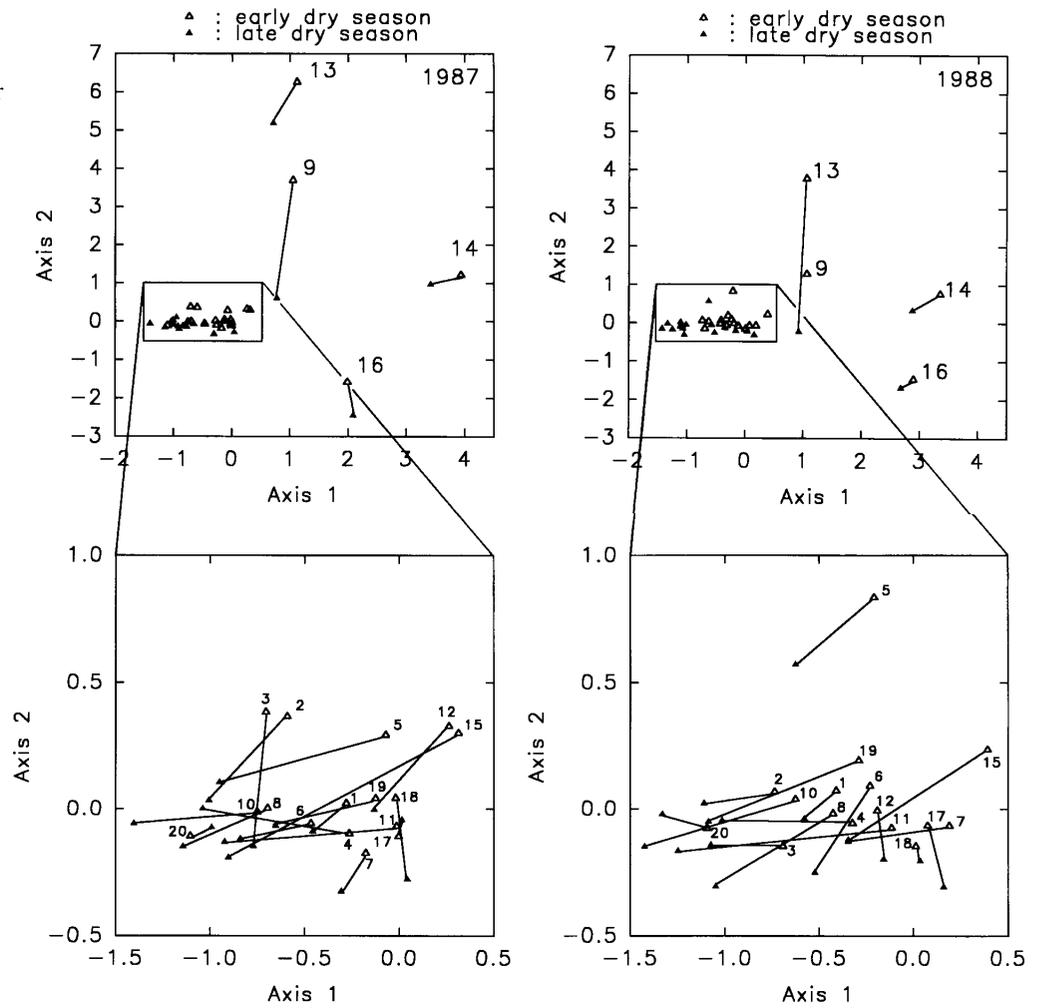


Table 5 Major taxa relative abundance (%), total numerical density (CPUE), numerical density of smaller tetras (CPUE), and water transparency (Secchi depth in cm) for extreme samples in the DCA ordination of all survey samples combined (n = 79) (see

Fig. 6), and Spearman rank correlations of relative abundances, total numerical density, numerical density of smaller tetras, and water transparency with scores of the first two ordination axes

	Mean (SE) for samples with 10 lowest axis 1 scores in the DCA ordination	Mean (SE) for samples with 10 highest axis 1 scores in the DCA ordination	Rank correlation	
			Axis 1	Axis 2
Characiformes	29.0 (4.8)	71.2 (5.6)	0.61	0.01
Siluriformes	43.2 (7.1)	3.0 (1.3)	-0.83	-0.31
Gymnotiformes	16.0 (4.8)	0.0 (0.0)	-0.74	-0.14
Cichlidae	0.6 (0.4)	14.8 (2.9)	0.48	0.16
Clupeiformes	7.9 (3.2)	10.9 (4.0)	0.09	-0.21
Other taxa	3.2 (1.5)	0.0 (0.0)	-0.29	-0.03
Total numerical density	64.6 (16.0)	138.2 (29.0)	0.22	-0.09
Numerical density of smaller tetras	3.0 (1.6)	98.4 (40.1)	0.34	-0.11
Secchi depth	8.50 (1.68)	48.00 (10.63)	0.75	0.33

DCA is a valuable complement to MANOVA for evaluating the effects of year and season on assemblage structure, and can also be used to test for robustness of results to choice of technique. Ordination by DCA (Fig. 6) yields results comparable to those of MANOVA. The spatial configuration of points is very similar in 1987 and 1988, as evidenced by the high Pearson correlations between axis scores for 1987 and 1988: $r = 0.97$ for axis 1, and $r = 0.78$ for axis 2. This indicates that year to year variation in the assemblage structure of individual lakes was very small relative to variation among lakes. In both years, the season effect is represented in the plots by a consistent leftward and downward shift from early to late dry seasons, i.e., a decrease along both axes. Lake scores were lower in the late dry season than in the early dry season for 83% of the lakes along axis 1 and for 87% of the lakes along axis 2. The largest increase observed along either axis was relatively small (0.11 units along axis 1 in 1987 for lake 20; Fig. 6).

Although seasonal change in assemblage structure was small relative to difference among lakes (Table 3; Fig. 6), the absolute magnitude of change during the dry season was large and detectable even at the ordinal level;

it reflected a strong reduction in the abundance of characiforms (silver dollars, piranhas, tetras) relative to siluriforms (catfishes) and gymnotiforms (knifefishes) (Tables 5, 6). Because reproduction was negligible and migration was impeded during isolation, change in assemblage structure was due primarily to differences in mortality among species. Given that total mortality was high, even small differences in mortality rate among species greatly changed relative abundance. Trophic guild structure was relatively constant from year to year and showed little seasonal change (Table 6) despite marked change in relative abundance at the specific and ordinal levels. The increase over the dry season of fish that feed on benthic invertebrates (Table 6) reflects an increase in the relative abundance of catfishes and knifefishes (Table 5), many of which fall within this guild. Catfishes and knifefishes were dominant in turbid waters, whereas characiforms and cichlids predominated in more transparent waters (Tables 5, 6).

The results for numerical density, harvested biomass, species density, size-class distribution, and assemblage structure (relative abundance of species, of major taxa, and of trophic guilds) support the notion that these prop-

Table 6 Relative abundance (%) of major taxa and of trophic guilds (based on numerical density with percentages calculated across lakes). Water transparency (Secchi depth, cm) is also presented. n = Number of lakes.

	Mean (standard error)			
			Dry season 1988	
	Dry season 1987		Early	Late
	Early ($n = 20$)	Late ($n = 20$)	Early ($n = 20$)	Late ($n = 19$)
Taxon (number of species)				
Characiformes (64)	58.4	41.7	56.0	47.0
Siluriformes (25)	13.8 (3.8)	22.0 (4.6)	11.9 (3.5)	25.1 (5.4)
Gymnotiformes (9)	0.8 (0.5)	7.0 (2.6)	1.0 (0.8)	6.6 (2.3)
Cichlids (6)	4.9 (1.2)	6.7 (2.2)	5.7 (1.1)	6.6 (1.5)
Clupeiformes (8)	21.4 (4.9)	19.0 (5.6)	24.4 (5.7)	12.6 (3.5)
Other (4)	0.7 (0.4)	3.6 (1.5)	1.0 (0.6)	2.2 (0.8)
Trophic guild(number of species)				
Piscivores (20)	20.5 (4.2)	18.8 (3.2)	18.1 (3.7)	14.4 (2.4)
Fin and scale eaters (3)	0.3 (0.1)	0.7 (0.4)	0.5 (0.3)	0.3 (0.2)
Zooplanktivores (12)	23.6 (4.6)	23.2 (5.8)	27.0 (5.3)	16.5 (3.6)
Fish that feed on terrestrial invertebrates near the surface (5)	7.5 (3.0)	4.0 (1.7)	3.0 (1.0)	6.0 (2.6)
Fish that feed on aquatic invertebrates associated with substrata (27)	10.6 (2.3)	15.9 (3.3)	7.8 (2.0)	15.2 (2.0)
Algivores-detritivores (27)	21.8 (3.3)	16.5 (3.3)	21.6 (4.0)	23.0 (3.6)
Fish that feed on coarse plant material (3)	0.8 (0.3)	1.1 (0.6)	0.7 (0.2)	1.0 (0.7)
Omnivores (19)	15.0 (2.6)	19.9 (4.3)	21.3 (3.5)	23.6 (3.8)
Water transparency	44.3 (6.6)	24.8 (5.2)	33.5 (6.3)	17.4 (3.6)

ERRATUM. The se for Characiformes were omitted in Table 6. The table should read:

Characiformes (64)	58.4	41.7	56.0	47.0
	(5.8)	(5.3)	(6.2)	(5.7)

erties were regulated. In 1988 all of these properties achieved levels comparable to those of 1987, in spite of the large fluctuation caused by the intervening inundation. Also, the magnitude and direction of changes within the low-water season were generally comparable between years.

Discussion

The present study is probably the first explicitly designed to evaluate the regulation and adjustment stability of fish assemblages in neotropical fresh waters. Although the literature on neotropical freshwater fish assemblages is sparse, the prevailing view is that fish assemblages in floodplain lakes are largely unstructured and unpredictable (Bonetto et al. 1970a,b; Lowe-McConnell 1987; Goulding et al. 1988). Contrasting with this view, in Orinoco floodplain lakes a host of assemblage properties were similar early and late in the dry season in the two years despite the strong fluctuation induced by the intervening flood. The total numerical density, numerical density of small tetras, harvested biomass, size-class distribution, and species relative abundance changed significantly within years (during isolation), and the magnitude and direction of change in these variables was similar from year to year. Recovery of assemblage properties occurred soon after the annual flood deflected these properties far away from their initial state; recovery thus reflected adjustment (resilience), and not simply from great individual longevity coupled with low adult mortality and recruitment (Frank 1968; Warner and Chesson 1985). Because young-of-the-year fish were numerically dominant in these assemblages, and because adjacent lakes often differed greatly in assemblage structure (e.g., Lakes Terecaya and Tineo), recurrence of assemblage properties at the level of individual lakes likely occurred through deterministic regulation by adjustment of recruitment and mortality (Grossman et al. 1990), and not simply through the return of fish older than 1 year or through random movement of colonists in proportion to their abundance in areas adjacent to the lake (Meffe and Sheldon 1990).

Catfishes and knifefishes, which are primarily nocturnal and have sensory adaptations to low light levels (Lowe-McConnell 1964; Bennett 1971; Hara 1971; Fink and Fink 1979), were dominant in turbid waters, whereas characiforms and cichlids, which usually are diurnal and rely on vision (Lowe-McConnell 1964, 1969; Fink and Fink 1979; Goulding 1980) predominated in more transparent waters (Tables 5, 6). The spatial distribution and the differential mortality of fish at low water seemed to be related to water transparency, and presumably can be explained in terms of the importance of vision to predator-prey interactions (Rodríguez 1990). This explanation is consistent with the fact that seasonal assemblage change was detected in the relative abundance of orders but not of trophic guilds, because specific sensory adaptations to optic conditions are readily associated with particular orders but not with trophic guilds.

Abiotic variables other than transparency, such as oxygen deficiency, hydrogen sulfide poisoning, and high temperatures, have been shown to affect the distribution of fish in Amazonian floodplain lakes (Brinkmann and de Santos 1973; Junk et al. 1983; Welcomme 1985). However, these variables did not appear to explain assemblage changes in the Orinoco lakes. In contrast with the Amazon lakes, the Orinoco lakes were generally well oxygenated during isolation, with percent oxygen saturation near the bottom falling below 25% in only 4 of the 79 survey samples (M.A. Rodríguez, personal observation). Although specific physiological adaptations to low oxygen concentration can be associated with particular taxonomic groups (e.g., the Root effect is strong in characiforms and nearly absent in catfishes; Farmer et al. 1979; Powers et al. 1979), other physiological adaptations, as well as a variety of morphological and behavioral adaptations, are broadly distributed among major taxa (Kramer et al. 1978; Powers et al. 1979; Junk et al. 1983; Welcomme 1985), and there appears to be no evidence suggesting that catfishes and knifefishes systematically differ from characiforms and cichlids with respect to tolerance to hypoxia or to high temperature. A canonical correspondence analysis (program CANOCO; ter Braak 1988) of species relative abundance and environmental data found no significant effect of oxygen concentration and water temperature on fish assemblage structure, but pointed to water transparency (among 23 environmental variables) as the best predictor of assemblage structure (Rodríguez 1990).

The perception of assemblage stability depends on the chosen level of taxonomic and numerical resolution (Rahel 1990). When numerical resolution is coarse (presence/absence, rank abundance indices), assemblages may seem not to change significantly even when individual species undergo wide stochastic fluctuations (Ebeling et al. 1990; Rahel 1990). Such constancy may be interpreted as deterministic regulation when in fact it reflects bounded stochastic variation (Connell and Sousa 1983; Ebeling et al. 1990; Rahel 1990). Detection of assemblage change also is more difficult when taxonomic resolution is coarse (relative abundance of higher taxa or foraging guilds) than when it is fine (species relative abundance) (Rahel 1990). In the present study similarity in assemblage structure between years was found at various taxonomic levels (species, orders, guilds), at the most precise level of numerical resolution (relative abundance) commonly used in ecological studies. Reduction of ecological "noise" by use of only the first axes of PCA and DCA ordinations (see Methods and study area) further increased the precision of between-year comparisons. This pattern suggests that assemblage recovery cannot be interpreted simply in terms of bounded fluctuations, and thus that deterministic mechanisms probably explain regulation.

Mechanisms of regulation in Orinoco fish assemblages may differ from those operating in other systems. In temperate streams, species-specific habitat preferences, coupled with high fish mobility, have been proposed as a

mechanism for assemblage regulation (Meffe and Sheldon 1990). Potential mechanisms for deterministic structuring of coral-reef fish assemblages include habitat preference in larval recruitment to the reef and habitat-dependent survival after settlement (Jones 1991). Determinism in intertidal fish assemblages may result from food resource partitioning (Grossman 1986b).

Plausible mechanisms of regulation in Orinoco fish assemblages include (1) site-dependent winnowing or culling of prey species by piscivores, (2) habitat selection by young-of-the-year and older fish when floodwater recedes, and (3) selection of spawning sites by mature females. The available evidence is consistent with the notion that differential mortality by piscivory strongly modifies species relative abundance during the dry season, but additional data (consumption rate and selectivity for major piscivores) would be required to demonstrate the proposed role of piscivory. In addition to the presumed direct effect of piscivores over the low-water period, piscivores could affect assortment (mechanisms 1 and 2) indirectly by influencing site selection by prey. At high water, fish may use environmental cues to select spawning sites and habitats that will reduce the likelihood that they or their offspring occupy an unfavorable lake at isolation. Selection for such behavior could be strong given the high mortality during the dry season. The key element insuring regulation and adjustment stability would appear to be that processes strongly influencing relative abundances during isolation, such as behavioral decisions (choice of spawning sites or of habitat before isolation), or the outcome of predator-prey interactions, are connected predictably to lake features having limited year-to-year variation, such as water transparency.

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