Dynamic Diversity in Fish Assemblages of Tropical Rivers

KIRK O. WINEMILLER

Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843

I. INTRODUCTION

This chapter examines temporal stability of fish assemblage structure in two tropical rivers and briefly reviews similar information from other tropical rivers. The factors associated with population and assemblage change plus those associated with population persistence and long-term stability of assemblage structure are discussed.

We know that many, and probably most, biotic communities change over time. Changes in community composition and structure are the hallmarks of processes like vegetative succession (Clements, 1949) and ephemeral habitats such as residual pools in the Florida everglades (Kushlan, 1976). Yet much of the basic and applied literature either assumes or strongly implies the existence of stable systems and chronic density-dependence. Traditional fisheries management, in particular, is rife with assumptions of density-dependence and assemblage stability as, for example, in stock indices for small impoundments

(Anderson and Gutreuter, 1983) and the application of stock-recruit models for estimation of optimal yields (critique in Fletcher and Deriso, 1988). The present-day search for indicators of ecosystem health and integrity has resulted in the acceptance of methods that contain strong assumptions about the structure and stability of natural systems. Karr et al.'s (1986) index of biotic integrity (IBI) for North American streams implies that these fish assemblages have regular, stable, and, hence, predictable structures that can be assessed against standards across different settings.

At the same time, however, some ecologists are evaluating the degree of temporal consistency observed in biotic communities. For example, the stability assumption has been questioned for North American stream fish assemblages (Grossman et al., 1982, 1990). When temporal change is observed, it begs the following questions: To what extent are stochastic environmental and demographic factors indicated, and to what extent are deterministic biotic factors indicated? Virtually all of the chapters contained in this volume offer insights into the question of whether communities represent "chance aggregations" or "stable systems" (following Keast's terminology in Chapter 3 of this volume).

Climatic regime and the abiotic environment can directly influence mortality and reproduction. In harsh or unpredictable climates, environmental factors can cause apparent stochastic mortality. This idea dates back at least to Darwin's time and was well articulated by Dobzhansky (1950). Consequently, in more moderate or stable climates, biotic factors that are largely deterministic may have dominant effects on populations and communities. Availability of space and other resources, competition, predation, and other biotic interactions can influence mortality, growth, reproduction, resource use, and niche segregation. However, the contrast between stochastic and deterministic factors can be blurred, as largely stochastic abiotic factors may interact with density-dependent biotic factors. Appleblossom thrips show density-dependent mortality in response to cold temperatures because at higher densities more individuals are excluded from microhabitats that serve as safe havens from freezing (Davidson and Andewartha, 1948).

A. Temperate Fish Assemblages

The assumption of temporal stability of temperate fish assemblages was put to a test by Grossman (1982; Grossman et al., 1982). He found high temporal stability and resiliency in intertidal fish assemblages but not in a Midwestern stream assemblage. Because his interpretations challenged traditional thinking, they promptly received strong challenges (Herbold, 1984; Rahel et al., 1984; Yant et al., 1984). Yet clearly there is much evidence for the disruptive influence of floods and droughts on stream biotas (Harrell, 1978; Matthews, 1986; Resh et al., 1988; Yount and Niemi, 1990; Reice, 1994).

Part of the controversy is due to variation in the scale of analysis (assemblage, space, time) and its influences, but part is derived also from differences in biological interpretation of the patterns. Subsequent research on the temporal stability of North American stream fish assemblages has led to the general conclusion that both stochastic and deterministic factors influence all of these systems, but the degree and scale of their effects differ from place to place and from time to time. For example, Matthews (1986) showed how a stream fish assemblage was changed by flooding yet returned to a more or less consistent structure during a period of relative habitat stability. Several studies highlight how stochastic disturbances alter stream fish assemblages in the short term, though in the longer term assemblages are persistent and relatively stable (Moyle and Vondracek, 1985; Ross *et al.*, 1985; Freeman *et al.*, 1988; Matthews *et al.*, 1988; Yount and Niemi, 1990). Here persistence and stability follow the operational definitions of Connell and Sousa (1983): persistence is indicated by consistent species presence, and stability by consistent patterns of species relative abundance.

B. Tropical Fish Assemblages

Long-term studies of river fish assemblages in tropical rivers are relatively scarce. This is not surprising given the fact that many fish biologists equate the state of ichthyological knowledge of the Neotropics with that of North America during the early nineteenth century. Rapidly changing taxonomy, incomplete biogeographical knowledge, and the paucity of even the most basic faunal surveys over vast regions of the tropics have all contributed to a heavy emphasis on sampling large areas at the expense of repeated sampling within sites. Yet a few exceptional studies can be cited; Lowe-McConnell (1964) was among the first to discuss the temporal dynamics of fish ecology in a tropical region, namely the Rupununi savanna district of Guyana. Although her study did not track the dynamics of a designated study site, she discussed numerous ecological factors associated with wet/dry seasonality, including fish migrations, respiratory adaptations, population dynamics, diet shifts, and species diversity (see also Lowe-McConnell, 1979).

Bonetto *et al.* (1969) were perhaps the first to examine the temporal stability of fish assemblages at fixed locations within a tropical river system. They surveyed assemblage composition of floodplain pools on islands of the Río Paraná in northern Argentina, a region with strong wet/dry seasonality. Their study highlighted the random nature of species strandings in isolated pools but at the same time noted how deterministic processes, especially predation, interact with pool conditions to influence development of fish assemblages subsequent to pool isolation. Welcomme (1969) examined the temporal dynamics of fish populations in a stream flowing into Lake Victoria, Africa. As in Low-McCon-

nell's regional study, Welcomme's findings highlighted strong seasonal dynamics and the importance of longitudinal migrations, especially those associated with wet-season spawning and return to dry-season refugia.

In a similar study, Rodríguez and Lewis (1990) surveyed fish assemblages during two consecutive dry seasons in 20 oxbow lagoons in the floodplain of the lower Río Orinoco, Venezuela. They found much greater variation between lakes within years compared to variation within lakes between years. Species richness and species composition within lakes between years was characterized as strikingly similar, and fish-habitat associations were hypothesized to account for this pattern. Similarly, Chapman and Chapman (1993) analyzed the stability of fish assemblages in residual floodplain pools of the River Sokoto, Nigeria, based on data from a fisheries survey conducted by Holden (1963). They identified some of the same random elements discussed by Bonetto *et al.* but also found a high degree of interannual consistency in the species present in pools; like Rodriguez and Lewis, they postulated habitat selection as a mechanism.

Zaret and Rand's (1971) study of a fish assemblage in a small Panamanian stream was perhaps the first to examine the effect of seasonality on patterns of niche segregation. They observed that most fishes expanded resource use during the wet season when most resources are more abundant and showed a trend to niche compression and segregation during the dry season. Because of its pointed claim to support the "competitive exclusion principle," this study has been widely cited by both fish and non-fish ecologists. Despite the fact that similar patterns have been demonstrated in other tropical fish assemblages (e.g., McKaye and Marsh, 1983; Winemiller, 1989a), several authors have expressed skepticism over Zaret and Rand's study due to their small sample sizes and use of inappropriate statistics for comparing niche overlaps. With a focus on the use of terrestrial resources rather than niche segregation, Goulding (1980) examined seasonal diet shifts among fishes of the Río Madeira in Brazil's Amazon basin. Goulding's study clearly revealed a great reliance by many fishes on food resources of the flooded forest and identified the potential of fishes as seed dispersers for riparian plants.

Several studies associated with international development projects have examined seasonal ecological dynamics (e.g., Lagler *et al.*, 1971) or faunal changes in association with river impoundments (e.g., Balon and Coche, 1974). Zaret and Paine (1973) discussed the changes that occurred in the food-web structure of Lake Gatún, Panama (an impoundment of the Río Chagras in the Canal Zone), following the introduction of exotic *Cichla ocellaris,* a voracious South American piscivore. They noted how the lake's fish assemblage changed over a period of just four years with major effects on non-fish taxa, both aquatic and terrestrial. Recently, Agostinho *et al.* (1992) examined the influence of the Itaipu Reservoir on faunal changes in the Upper Río Paraná and associated wetlands in Brazil. They presented evidence that exotic piscivores, brought in by the sub-

mergence of a natural barrier to upstream dispersal, have contributed to changes in the fish assemblage of the upper Paraná.

Over the past 10 years, I have studied the fish assemblage of Caño Maraca, a swamp creek in the western llanos of Venezuela. Based primarily on data obtained over 12 months of 1984, various aspects of the seasonal dynamics have been published, including resource utilization (Winemiller, 1989a), life-history strategies (Winemiller, 1989b), the influence of respiratory adaptations on population dynamics (Winemiller, 1989c), and food-web structure (Winemiller, 1990, 1996). This chapter examines assemblage stability based on survey data acquired over the full 10-year interval 1984–1994. In addition, I will compare data from fish surveys conducted in the Upper Zambezi River and associated floodplain in Zambia, Africa during 1966 (Kelley, 1968) with those from a very similar survey that I conducted in the same area in 1989 (Winemiller, 1991a; Winemiller and Kelso-Winemiller, 1994).

II. METHODS

A. Study Regions

1. South American Llanos

During January 1984–June 1994, surveys were conducted on the fish assemblage of Caño Maraca, a lowland stream (caño) in the Venezuelan llanos (Fig. 1). The study site is located in the upper reaches where this low-gradient stream has a large, seasonally-inundated floodplain (additional descriptions of the habitat, community, and food-web appear in Winemiller, 1989b,c, 1990). Highly seasonal rainfall produces large within-year variation in the physical and biological attributes of the site. During the harsh dry season (January through early May), many aquatic plants and invertebrates (e.g., diatoms, rooted macrophytes, molluscs, entocostrachans, conchostracans, annual killifishes) survive in sediments in a state of quiescence or arrested early development. During the early stages of wet-season flooding, these populations have very rapid production.

Sources of basal ecosystem production differ markedly between seasons (Winemiller, 1990, 1996). During the wet season (late May–August), the vast flooded plain contains very high densities of aquatic and emergent macrophytes. Relatively few invertebrates or fishes feed directly on these plants, but numerous herbivores consume periphyton (diatoms and filamentous algae) attached to macrophytes. Wet-season primary production is transferred to the upper food web via abundant invertebrates and juvenile fishes. During the transition to dry season (September–December), increasing desiccation causes dieback in the accumulated macrophyte biomass. Macrophyte decomposition
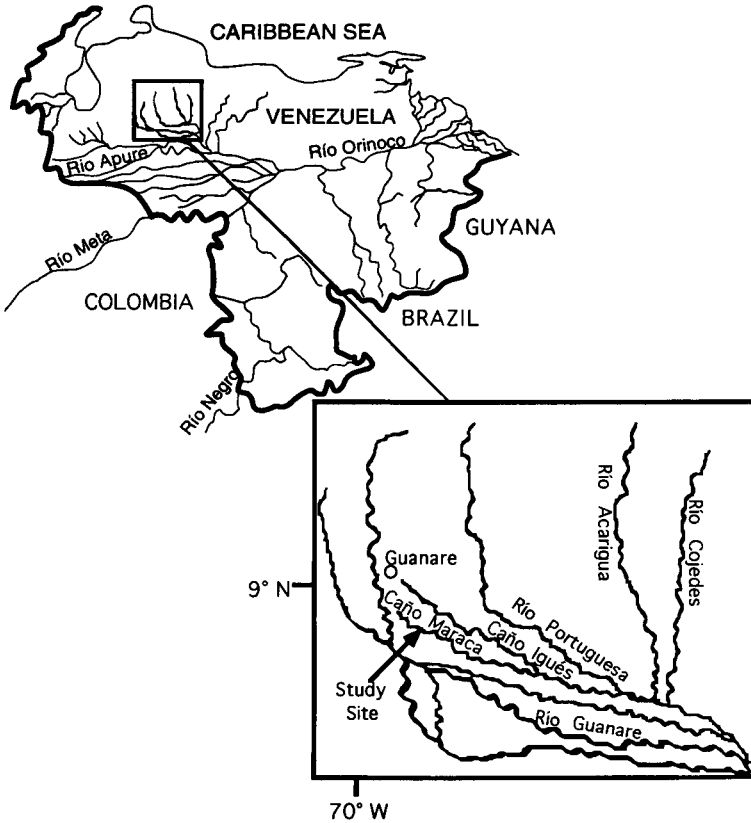
FIGURE 1.   Map showing the location of Caño Maraca within the Río Portuguesa basin of the western llanos in Venezuela.

and the confinement of water in isolated pools and small channels results in reduced dissolved oxygen (DO) and higher concentrations of hydrogen sulfide. Some of the resident fishes survive hypoxia by using special respiratory adaptations and are able to feed and, in some cases, reproduce (Winemiller, 1989b). Detritus from aquatic macrophytes is the principal source of basal production during the dry season. Some fishes have seasonal migrations and leave the site during the onset of harsh dry-season conditions, while other species remain throughout the year; some of these suffer high mortality during the dry season when aquatic macrophyte cover is reduced and fishes are at their highest densities.

Diverse life-history strategies have been documented for fishes at the site (Winemiller, 1989b). Some species remain throughout the dry season and, by virtue of their special respiratory adaptations, survive harsh conditions. Other

populations remain during the dry season, suffer high mortality from hypoxic conditions and predation, but later rebound with a burst of reproduction following the first floods. Other year-round residents suffer high dry-season mortality and rebound during the wet season either by virtue of an opportunistic strategy of rapid maturation and multiple spawnings of small clutches or by way of an equilibrium strategy of less frequent spawning, production of larger eggs, extended parental care, and enhanced juvenile survivorship. Finally, the fishes that leave the site during the dry season return during the floods and spawn large numbers of eggs, usually by scattering them among submerged plants.

2. Barotse Floodplain of South-Central Africa

During April–December 1989, fishes and their habitats were surveyed in the Upper Zambezi River and associated Barotse floodplain in Zambia's western province (Fig. 2). These surveys were comparable to very similar studies performed in the same region during 1966 (Kelley, 1968). Like the llanos, the Upper Zambezi River has a very strong seasonal cycle of flooding and desiccation (additional descriptions appear in Winemiller, 1991a). As in the llanos, aquatic macrophytes, periphyton, and much of the detritus from aquatic plants originate on the floodplain during high water (January–April). Basal production is transferred to the upper food web primarily in floodplain habitats (i.e., lagoons, sloughs, canals), and to a lesser extent within the primary river channel (Winemiller, 1996). During the period of falling water (May–August), there is a massive movement of organisms from the floodplain to the river channel. There, as also in the llanos, detritus assumes greater importance as a basal input, while macrophyte standing stocks decline with falling water levels.

B. Field Surveys

Fish and habitat surveys were conducted at the Caño Maraca site during each month of 1984 and at several irregular intervals thereafter. Methods for habitat parameters are described in detail elsewhere (Winemiller, 1989c). Each survey required one day, used the same sampling methods, and was performed with the same criterion, namely to sample until one hour of sampling yielded no additional (rare) species. In some instances, a representative sample that reflected species' relative abundance rankings was retained and preserved (in place of sacrificing all captured specimens). During each survey, fishes were captured from a "large open pool" area with a 20-m seine (12.7-mm mesh), from "open pool" areas and "vegetation mats" with a 2.5-m seine (3.2-mm mesh), and from "shallow vegetated edge" habitats with a large dipnet (3.2-mm mesh). Total sampling effort varied between dates depending on habitat conditions, but the methods permitted good assessment of species richness without sacrificing

information on relative abundances. Fishes were ultimately fixed in formalin and preserved in ethanol; most specimens were ultimately deposited in natural history collections. During four surveys (in December 1984, January 1988, October 1993, and June 1994), quantitative seine hauls also were made in open water and densely vegetated habitats. These samples permitted comparisons of population densities on a per-unit-area basis between habitats on the same dates, and between dates within these habitats. Except for several large specimens that were identified, measured, and weighed in the field prior to release, fishes from the quantitative samples were retained, and species numbers and biomasses were determined in the laboratory.

During April–December 1989, fishes were surveyed at locations scattered throughout the Upper Zambezi River and Barotse floodplain from Sioma in the South to the juncture of the Kabompo and Zambezi Rivers in the North (Fig. 2). All habitats were targeted, including the main river channel, lagoons, canals, creeks, and flooded vegetation. Fishes in deepwater habitats were captured with monofilament experimental gillnets (50 $\times$ 2 m, containing segments of 5.1-, 10.2-, and 15.2-cm mesh) operated overnight. Angling supplemented some of the river channel samples. Fishes were also captured using seines (30.5 $\times$ 2 m, 25-mm mesh; 6 $\times$ 1.5 m, 6-mm mesh), castnets (25-mm mesh), and dipnets (3.2-mm mesh). Samples of fishes leaving the flooded plain during the early falling-water period (May–July) were obtained by purchasing maalelo catches from local fishermen; maalelo are dams constructed of grass mounds or reed fences that direct fishes into a trap as they attempt to move from flooded grasslands to the permanent water bodies.

Very similar methods were employed by Kelley (1968) to survey the same areas of the Upper Zambezi/Barotse plain during 1966. The goals of the two surveys were to obtain samples representative of fish densities, population size structures, and habitat associations during different seasons. Kelley used a 25-m (12.7-mm mesh) and a 3.3-m (12.7-mm mesh) seine and several 30-m gillnets with meshes ranging between 3.8 and 15.2 cm. Fish abundances were totalled from data reported by Kelley (1968) based on 119 overnight sets of 100 m of gillnet, 43 seine hauls, and nine maalelo samples. His flood-season (March–April) gillnet sets ($N = 40$) caught relatively few fishes. The 1989 abundances were derived from 40 sets of 100 m of gillnet (earliest set was June 28), 40 seine hauls, and two maalelo samples, plus specimens taken by castnet, dipnet, and hook-and-line. Kelley's 1966 survey produced a total of 25,508 specimens, and my 1989 Barotse survey produced 14,504 specimens.

C. Data Analyses

Spearman's rank correlations and Pearson's product-moment correlations were used as estimates of sample similarity based on species abundances. Rank cor-
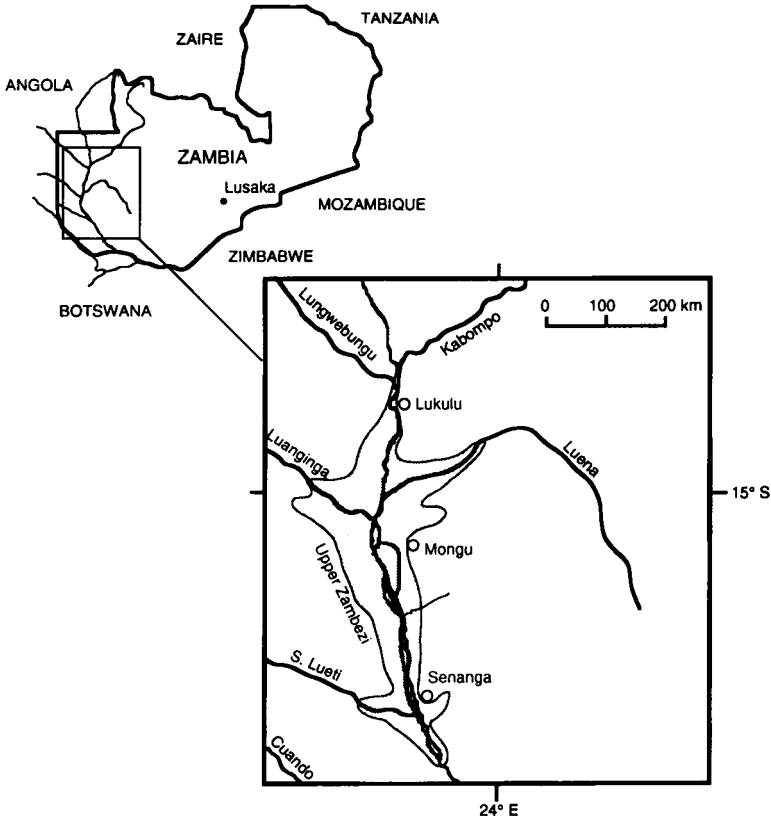
FIGURE 2.   Map showing the location of the Upper Zambezi River and Barotse floodplain in western Zambia.

relation has been used extensively in studies of temporal stability of vertebrate assemblages (Grossman *et al.*, 1990) because it reduces the effects of subtle changes in species abundances that may be influenced by sampling bias. I chose to use rank correlations as a conservative test and also parametric correlation to highlight the effect of the magnitude of differences in species' relative abundances on assemblage similarity. The latter was used primarily in cluster analyses ("average linkage" method) to show hierarchies of assemblage similarities, following the approach of Ross *et al.* (1985).

The criterion (or relative abundance scale) used to exclude rare species influences assemblage patterns and their interpretation (Rahel *et al.*, 1984). No consensus exists for this criterion; most investigators choose either to exclude those species comprising <1% of the total fishes surveyed (e.g., Ross *et al.*, 1985; Bass, 1990), or to examine only the dominant 10 species (Matthews *et*

al., 1988; Chapman and Chapman, 1993). Inclusion of many species that are always rare tends to inflate similarity and estimates of assemblage stability based on correlative methods (Rahel *et al.*, 1984; Grossman *et al.*, 1990). Conversely, to eliminate all but a handful of dominant species imposes a rigid criterion that severely reduces the chance of identifying high similarity based on abundance estimates from field samples. Rather than select a single arbitrary criterion, I examined the influence of scale on assemblage patterns by making comparisons and performing analyses based on several different relative abundance criteria for species inclusion. All available species-abundance data were compiled, and average monthly abundances of species were plotted by rank (Figs. 3 and 4). I looked for inflections in these frequency distributions and analyzed several data sets based on such "natural" breaks. Most of the patterns and interpretations were the same, and therefore results from only two of these data sets are presented here to contrast low and high inclusion criteria: the first inflection that grouped at least 10 dominant species ($N = 14$ for both Venezuela and Zambia studies), and a later inflection that grouped many species, but still eliminated the long tail of the distribution representing very rare taxa ($N = 58$ for Venezuela, $N = 31$ for Zambia). Kelley (1968) failed to report certain species either because they were undescribed at the time and confused with known taxa (e.g., *Serranochromis altus*, Winemiller and Kelso-Winemiller, 1991) or because they were difficult to key out (e.g., *Synodontis* spp.). Thus certain 1989 data had to be combined in order to match the taxonomic units reported by Kelley (e.g., *Synodontis* spp., *Barbus* spp., *Aplocheilichthys* spp.), thereby reducing the number of taxa from 68 to 38 (Fig. 4).
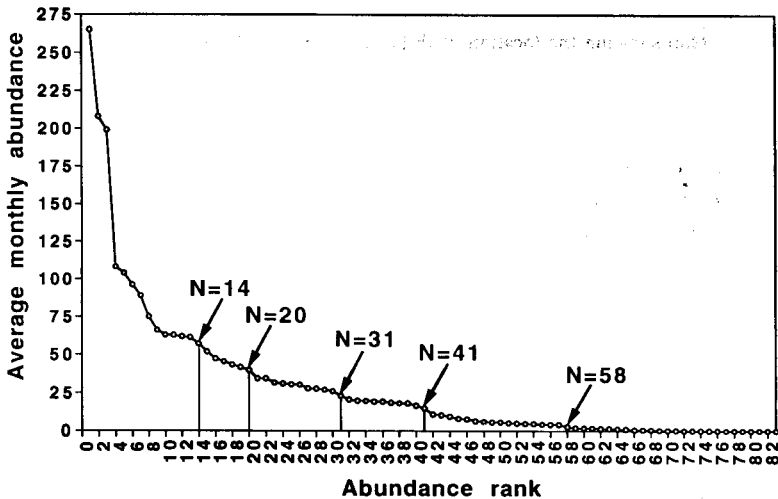

FIGURE 3.   Plot of species' average monthly abundances by abundance rank for Caño Maraca fishes based on 1984 surveys.
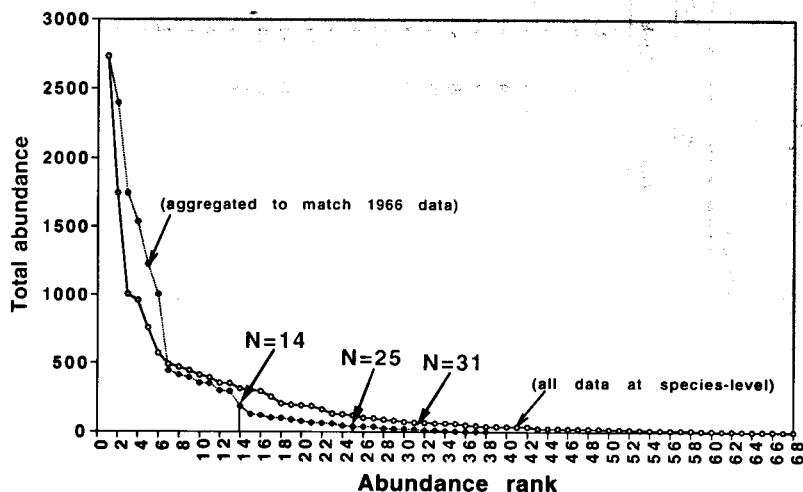
FIGURE 4. Plots of species' average monthly abundances by abundance rank for Upper Zambezi River/Barotse floodplain fishes based on 1989 surveys. One plot contains species aggregations that allow comparisons between the 1989 survey and Kelley's 1966 survey.

Following Winemiller (1989b) and Grossman *et al.* (1990), the coefficient of variation (CV) of monthly population abundance estimates was also used to examine the temporal stability of the Venezuelan fish assemblage. Population CVs (100 · SD/mean abundance) were calculated based on the 1984 monthly samples (to estimate within-year seasonal variation during a typical year) and also based on the full 10-year data set (to estimate overall within- and between-year variation). To examine the relationship between population variability, abundance, and persistence, the CV was regressed against mean abundance and the percentage of samples in which a species was present. In addition, correlations between population abundance estimates and several key environmental variables were performed to examine the influence of habitat conditions on population dynamics.

III. RESULTS

A. Venezuela

Of the 87 species documented at Caño Maraca, characiforms were dominant both in terms of species richness and numbers of individuals, a reflection of their prominent representation in the South American ichthyofauna (Lowe-McConnell, 1975). The nine top-ranked species in overall abundance were all characiforms (Table I, Fig. 3). Based on the 18 samples collected during the

TABLE I   Species Relative Abundance Ranks and Percentage Relative Abundances across Sampling Dates at Caño Maraca

Species	Jan84 Rank	%	Feb84 Rank	%	Mar84 Rank	%	Apr84 Rank	%	May84 Rank	%	June84 Rank	%	Jul84 Rank	%	Aug84 Rank	%	Sep84 Rank	%
Steindachnerina argentea	2	9.23	2	6.94	21	1.43	7	6.71	15	1.06	1	13.60	6	6.79	2	8.47	2	9.47
Odontostilbe pulcher	1	23.70	8	5.88	1	12.41	5	7.84	5	6.45	4	10.65	1	11.07	9	3.74	7	4.88
Ctenobrycon spilurus	3	9.13	3	6.67	1	12.41	2	9.66	23	0.44	2	10.96	4	7.86	3	5.97	1	10.97
Roeboides dayi	8	2.91	26	0.79	32	0.43	32	0.35	15	1.06	10	3.72	7	5.69	1	8.88	8	4.53
Gephyrocharax valenciae	8	2.91	16	1.93	25	1.12	47	0.00	37	0.00	7	5.02	5	7.54	10	3.69	6	5.07
Astyanax bimaculatus	7	3.16	38	0.35	37	0.25	32	0.35	31	0.09	3	10.70	2	9.62	8	3.79	3	8.05
Aphyocharax alburnus	5	4.91	20	1.67	23	1.18	29	0.49	27	0.27	20	0.57	16	2.14	12	3.38	4	6.54
Markiana geayi	11	2.72	43	0.09	33	0.37	36	0.20	37	0.00	5	8.79	8	5.60	14	2.70	5	6.38
Thoracocharax stellatus	15	2.04	5	6.50	5	5.09	34	0.30	37	0.00	50	0.00	47	0.06	29	0.99	29	0.72
Caquetaia kraussii	18	1.70	14	2.02	28	0.87	16	1.87	26	0.35	22	0.52	3	7.98	11	3.58	12	2.41
Triportheus sp.	24	0.78	38	0.35	30	0.56	41	0.10	37	0.00	14	1.29	9	4.43	19	1.92	26	0.99
Bunocephalus amaurus	16	1.94	6	6.23	5	5.09	3	9.62	3	11.40	29	0.26	39	0.22	34	0.73	13	2.39
Aequidens pulcher	4	5.29	14	2.02	10	3.60	25	0.79	19	0.88	22	0.52	10	2.86	5	4.62	10	3.14
Corydoras habrosus	23	0.83	1	7.11	3	6.33	4	8.09	2	16.96	50	0.00	57	0.00	62	0.00	40	0.29
Prochilodus mariae	10	2.87	11	3.42	14	2.23	18	1.78	9	3.71	13	2.12	11	2.73	24	1.45	19	1.39
Otocinclus sp.	6	4.47	9	5.27	7	4.97	6	7.10	1	17.05	36	0.10	43	0.09	41	0.26	40	0.29
Rineloricaria caracasensis	35	0.24	7	5.97	9	3.91	11	2.37	4	6.98	50	0.00	15	2.26	7	3.90	16	1.50
Ochmacanthus alternus	34	0.29	4	6.58	8	4.47	27	0.69	22	0.71	40	0.05	21	0.94	25	1.35	11	3.08
Hoplias malabaricus	17	1.80	32	0.53	22	1.24	22	1.43	37	0.00	8	4.91	14	2.29	6	3.95	22	1.23
Cichlasoma orinocense	22	1.07	20	1.67	18	1.86	17	1.82	17	0.97	9	4.50	26	0.63	13	3.12	36	0.51
Loricariichthys typus	55	0.00	28	0.61	14	2.23	12	2.17	10	3.53	11	3.15	17	1.82	19	1.92	14	2.25
Pyrrhulina lugubris	21	1.31	19	1.76	26	1.06	41	0.10	37	0.00	36	0.10	52	0.03	34	0.73	55	0.03
Pterygoplichthys multiradiatus	49	0.05	12	3.34	14	2.23	15	2.02	7	4.15	6	7.14	18	1.63	21	1.71	50	0.11
Gymnotus carapo	55	0.00	17	1.84	33	0.37	20	1.73	14	2.03	28	0.31	22	0.88	22	1.56	21	1.37
Astronotus ocellatus	29	0.49	24	0.88	37	0.25	25	0.79	31	0.09	36	0.10	43	0.09	4	4.68	55	0.03
Corydoras aeneus	11	2.72	32	0.53	19	1.49	1	10.11	12	2.12	36	0.10	52	0.03	62	0.00	63	0.00
Hypostomus argus	39	0.15	12	3.34	12	2.48	13	2.07	8	3.98	12	2.43	33	0.38	18	1.97	44	0.24

Charax gibbosus	28	0.53	48	0.00	51	0.00	47	0.00	37	0.00	25	0.36	19	1.23	23	1.51	18	1.45
Apistogramma hoignei	19	1.51	10	5.09	13	2.36	24	0.84	20	0.80	50	0.00	52	0.03	41	0.26	47	0.16
Pimelodella sp.2	36	0.19	40	0.18	30	0.56	30	0.44	31	0.09	50	0.00	35	0.28	56	0.05	9	3.70
Microglanis iheringi	20	1.36	17	1.84	26	1.06	8	4.04	12	2.12	33	0.16	27	0.57	15	2.60	24	1.15
Poecilia reticulata	49	0.05	22	1.32	4	5.46	44	0.05	37	0.00	18	0.83	12	2.36	28	1.04	30	0.70
Hemigrammus sp.	44	0.10	43	0.09	48	0.06	47	0.00	37	0.00	30	0.21	47	0.06	16	2.23	15	1.88
Corydoras septemtrionalis	13	2.19	28	0.61	17	2.11	9	3.06	17	0.97	50	0.00	43	0.09	47	0.16	40	0.29
Characidium sp.1	26	0.68	32	0.53	40	0.19	34	0.30	23	0.44	40	0.05	57	0.00	36	0.62	16	1.50
Eigenmannnia virescens	30	0.44	40	0.18	40	0.19	31	0.39	20	0.80	40	0.05	47	0.06	36	0.62	28	0.75
Hoplosternum littorale	31	0.39	23	1.14	11	2.92	10	2.47	6	5.65	25	0.36	40	0.19	47	0.16	63	0.00
Pimelodella sp.3	26	0.68	24	0.88	23	1.18	23	1.04	10	3.53	50	0.00	23	0.72	41	0.26	39	0.35
Pygocentrus cariba	55	0.00	48	0.00	51	0.00	47	0.00	37	0.00	19	0.72	20	1.07	30	0.88	22	1.23
Parauchenipterus galeatus	24	0.78	32	0.53	35	0.31	18	1.78	23	0.44	24	0.41	31	0.41	40	0.47	25	1.05
Tetragonopterus argenteus	55	0.00	48	0.00	51	0.00	47	0.00	37	0.00	50	0.00	35	0.28	62	0.00	19	1.39
Cheirodontops geayi	13	2.19	37	0.44	19	1.49	28	0.64	37	0.00	50	0.00	57	0.00	62	0.00	55	0.03
Rhamdia sp.	44	0.10	28	0.61	44	0.12	21	1.48	29	0.18	16	1.03	31	0.41	46	0.21	37	0.48
Rachovia maculipinnus	55	0.00	48	0.00	51	0.00	47	0.00	37	0.00	15	1.24	13	2.33	27	1.30	45	0.19
Synbranchus marmoratus	44	0.10	48	0.00	44	0.12	47	0.00	27	0.27	33	0.16	29	0.47	31	0.83	30	0.70
Hypopomus sp.1	36	0.19	32	0.53	35	0.31	36	0.20	31	0.09	40	0.05	57	0.00	53	0.10	45	0.19
Schizodon isognathus	55	0.00	48	0.00	51	0.00	47	0.00	37	0.00	33	0.16	37	0.25	47	0.16	27	0.88
Serrasalmus irritans	55	0.00	48	0.00	51	0.00	47	0.00	37	0.00	30	0.21	24	0.66	25	1.35	34	0.64
Leporinus friderici	39	0.15	48	0.00	51	0.00	47	0.00	37	0.00	40	0.05	57	0.00	47	0.16	34	0.64
Serrasalmus medinai	49	0.05	48	0.00	51	0.00	47	0.00	37	0.00	50	0.00	29	0.47	17	2.03	51	0.08
Ancistrus sp.	39	0.15	27	0.70	37	0.25	13	2.07	29	0.18	50	0.00	57	0.00	62	0.00	63	0.00
Hypoptopoma sp.	36	0.19	28	0.61	40	0.19	47	0.00	37	0.00	50	0.00	37	0.25	33	0.78	47	0.16
Bryconamericus beta	55	0.00	48	0.00	51	0.00	47	0.00	37	0.00	40	0.05	24	0.66	31	0.83	47	0.16
Adontosternarchus devananzii	49	0.05	48	0.00	51	0.00	47	0.00	37	0.00	50	0.00	57	0.00	38	0.52	32	0.67
Entomocorus gameroi	49	0.05	48	0.00	51	0.00	47	0.00	37	0.00	50	0.00	47	0.06	41	0.26	32	0.67
Triportheus angulatus	32	0.34	43	0.09	29	0.62	36	0.20	37	0.00	17	0.93	28	0.50	62	0.00	63	0.00
Hoplerythrinus unitaeniatus	55	0.00	48	0.00	40	0.19	39	0.15	37	0.00	25	0.36	57	0.00	56	0.05	63	0.00
Serrasalmus rhombeus	55	0.00	48	0.00	51	0.00	47	0.00	37	0.00	50	0.00	33	0.38	38	0.52	40	0.29
Total sample abundance	2059		1139		1611		2028		1132		1934		3181		1925		3729	

Table I *continued*

Species	Oct84 Rank	%	Nov84 Rank	%	Dec84 Rank	%	Jan88 Rank	%	Jan89 Rank	%	Jan92 Rank	%	Oct93 Rank	%	Feb94 Rank	%	Jun94 Rank	%
Steindachnerina argentea	3	6.87	4	5.71	1	18.06	7	6.54	11	3.06	2	15.61	1	29.64	4	0.00	17	1.15
Odontostilbe pulcher	1	23.68	3	5.81	2	8.89	1	8.03	3	8.89	3	9.70	2	13.81	4	0.00	4	8.08
Ctenobrycon spilurus	2	10.18	5	5.61	4	5.30	2	7.73	24	0.19	15	1.27	3	13.57	4	0.00	6	5.00
Roeboides dayi	5	6.60	9	3.80	8	2.92	15	2.38	5	7.74	9	3.80	5	9.31	4	0.00	2	15.00
Gephyrocharax valenciae	4	6.79	6	5.34	7	3.87	3	7.44	12	2.77	3	9.70	7	4.17	4	0.00	27	0.38
Astyanax bimaculatus	11	2.37	11	3.19	5	4.21	11	3.51	20	0.38	6	4.64	9	2.12	4	0.00	5	6.54
Aphyocharax alburnus	7	2.84	18	2.12	24	1.32	4	7.14	17	0.86	15	1.27	6	6.41	4	0.00	3	8.85
Markiana geayi	25	0.92	1	6.42	6	3.93	13	2.80	8	3.73	22	0.84	17	0.35	4	0.00	27	0.38
Thoracocharax stellatus	30	0.47	21	1.88	11	2.46	14	2.50	31	0.00	22	0.84	4	11.25	4	0.00	1	16.54
Caquetaia kraussii	10	2.50	10	3.36	17	1.81	8	5.71	2	11.76	5	5.49	10	0.90	4	0.00	11	2.69
Triportheus sp.	19	1.58	2	6.05	3	6.68	44	0.00	6	6.12	30	0.00	8	2.16	4	0.00	9	3.08
Bunocephalus amaurus	6	3.45	13	3.02	20	1.40	25	0.77	20	0.38	25	0.42	30	0.07	4	0.00	36	0.00
Aequidens pulcher	9	2.60	12	3.16	25	1.12	12	3.09	7	5.07	11	2.11	19	0.28	1	83.33	8	4.62
Corydoras habrosus	17	1.74	36	0.57	10	2.49	5	6.84	31	0.00	10	3.38	48	0.00	4	0.00	36	0.00
Prochilodus mariae	13	2.00	25	1.41	12	2.44	5	6.84	28	0.10	30	0.00	38	0.04	4	0.00	14	1.54
Otocinclus sp.	36	0.32	38	0.50	13	1.98	31	0.30	31	0.00	30	0.00	48	0.00	4	0.00	36	0.00
Rineloricaria caracasensis	22	1.24	46	0.24	23	1.38	37	0.12	31	0.00	30	0.00	32	0.05	4	0.00	9	3.08
Ochmacanthus alternus	8	2.82	31	0.94	17	1.81	20	1.61	31	0.00	30	0.00	48	0.00	4	0.00	36	0.00
Hoplias malabaricus	27	0.66	14	2.92	31	0.77	23	1.07	15	1.34	15	1.27	25	0.11	2	8.33	12	1.92
Cichlasoma orinocense	32	0.42	32	0.81	35	0.57	18	2.08	4	8.70	7	4.22	20	0.26	4	0.00	36	0.00
Loricariichthys typus	13	2.00	26	1.31	36	0.54	37	0.12	31	0.00	25	0.42	32	0.05	4	0.00	17	1.15
Pyrrhulina lugubris	20	1.53	8	4.13	9	2.81	19	1.78	14	1.43	1	17.72	11	0.79	4	0.00	36	0.00
Pterygoplichthys multiradiatus	23	1.21	27	1.24	51	0.17	33	0.18	22	0.29	30	0.00	25	0.11	4	0.00	22	0.77
Gymnotus carapo	18	1.66	20	2.02	20	1.40	17	2.14	13	2.10	7	4.22	22	0.16	4	0.00	36	0.00
Astronotus ocellatus	46	0.08	35	0.67	40	0.46	30	0.36	1	24.47	15	1.27	42	0.02	4	0.00	36	0.00
Corydoras aeneus	26	0.76	19	2.08	56	0.09	27	0.59	31	0.00	30	0.00	21	0.25	4	0.00	36	0.00
Hypostomus argus	24	1.05	24	1.44	34	0.63	44	0.00	31	0.00	30	0.00	30	0.07	4	0.00	17	1.15

Species																	
Charax gibbosus	12	2.08	23	1.68	16	1.86	33	0.18	31	0.00	30	0.00	15	0.49	4	0.00	36	0.00
Apistogramma hoignei	38	0.18	28	1.18	45	0.34	9	5.53	24	0.19	14	1.69	12	0.71	4	0.00	36	0.00
Pimelodella sp.2	35	0.37	16	2.65	15	1.89	44	0.00	31	0.00	30	0.00	48	0.00	4	0.00	22	0.77
Microglanis iheringi	32	0.42	40	0.37	46	0.32	33	0.18	24	0.19	30	0.00	48	0.00	4	0.00	27	0.38
Poecilia reticulata	21	1.45	50	0.07	43	0.40	40	0.06	19	0.57	11	2.11	32	0.05	2	8.33	27	0.38
Hemigrammus sp.	15	1.87	44	0.27	29	0.83	10	3.87	18	0.76	30	0.00	48	0.00	4	0.00	27	0.38
Corydoras septemtrionalis	37	0.26	39	0.44	20	1.40	21	1.37	31	0.00	30	0.00	16	0.37	4	0.00	36	0.00
Characidium sp.1	16	1.82	30	1.01	26	1.00	24	0.89	28	0.10	25	0.42	13	0.62	4	0.00	36	0.00
Eigenmannnia virescens	42	0.13	7	4.37	14	1.92	40	0.06	31	0.00	30	0.00	25	0.11	4	0.00	36	0.00
Hoplosternum littorale	48	0.05	42	0.30	32	0.66	26	0.65	10	3.44	15	1.27	42	0.02	4	0.00	36	0.00
Pimelodella sp.3	34	0.39	34	0.74	26	1.00	15	2.38	31	0.00	30	0.00	38	0.04	4	0.00	36	0.00
Pygocentrus cariba	50	0.00	17	2.28	19	1.69	31	0.30	31	0.00	30	0.00	48	0.00	4	0.00	12	1.92
Parauchenipterus galeatus	44	0.11	22	1.78	29	0.83	44	0.00	16	1.15	30	0.00	42	0.02	4	0.00	22	0.77
Tetragonopterus argenteus	27	0.66	15	2.79	28	0.89	44	0.00	31	0.00	30	0.00	28	0.09	4	0.00	36	0.00
Cheirodontops geayi	38	0.18	50	0.07	41	0.43	44	0.00	31	0.00	30	0.00	14	0.51	4	0.00	36	0.00
Rhamdia sp.	38	0.18	41	0.34	49	0.26	29	0.48	31	0.00	22	0.84	48	0.00	4	0.00	36	0.00
Rachovia maculipinnus	50	0.00	54	0.03	68	0.00	44	0.00	31	0.00	30	0.00	48	0.00	4	0.00	27	0.38
Synbranchus marmoratus	31	0.45	44	0.27	56	0.09	27	0.59	31	0.00	30	0.00	22	0.16	4	0.00	36	0.00
Hypopomus sp.1	42	0.13	37	0.54	37	0.49	21	1.37	22	0.29	15	1.27	38	0.04	4	0.00	36	0.00
Schizodon isognathus	49	0.03	29	1.11	46	0.32	40	0.06	31	0.00	30	0.00	48	0.00	4	0.00	36	0.00
Serrasalmus irritans	50	0.00	60	0.00	61	0.03	44	0.00	31	0.00	30	0.00	48	0.00	4	0.00	14	1.54
Leporinus friderici	50	0.00	32	0.81	37	0.49	37	0.12	31	0.00	30	0.00	48	0.00	4	0.00	27	0.38
Serrasalmus medinai	50	0.00	48	0.20	53	0.11	40	0.06	31	0.00	30	0.00	48	0.00	4	0.00	17	1.15
Ancistrus sp.	50	0.00	60	0.00	56	0.09	44	0.00	31	0.00	11	2.11	38	0.04	4	0.00	36	0.00
Hypoptopoma sp.	44	0.11	54	0.03	53	0.11	44	0.00	31	0.00	30	0.00	32	0.05	4	0.00	6	5.00
Bryconamericus beta	46	0.08	54	0.03	56	0.09	33	0.18	31	0.00	30	0.00	24	0.14	4	0.00	22	0.77
Adontosternarchus devananzii	50	0.00	60	0.00	32	0.66	44	0.00	24	0.19	30	0.00	48	0.00	4	0.00	36	0.00
Entomocorus gameroi	38	0.18	54	0.03	41	0.43	44	0.00	31	0.00	30	0.00	42	0.02	4	0.00	27	0.38
Triportheus angulatus	50	0.00	60	0.00	68	0.00	44	0.00	31	0.00	30	0.00	48	0.00	4	0.00	36	0.00
Hoplerythrinus unitaeniatus	50	0.00	60	0.00	68	0.00	44	0.00	9	3.63	15	1.27	48	0.00	4	0.00	36	0.00
Serrasalmus rhombeus	50	0.00	46	0.24	48	0.29	44	0.00	28	0.10	30	0.00	48	0.00	4	0.00	27	0.38
Total sample abundance	3801		2976		3489		1681		1046		237		5661		12		260	

Note. Only the 58 most abundant species are listed (total species = 87).

10-year study, both persistent and nonpersistent species were common. The frequency distribution of the number of samples in which a species was present was strongly bimodal with approximately half of the species present in 50% or more of the collections (Fig. 5). That so many fishes were represented in so many samples is rather remarkable given that the habitat becomes very harsh during the dry season. During years of unusually low rainfall, the site can dry up completely, as was nearly the condition during the February 1994 visit when only three fish species (*Hoplias malabaricus, Poecilia reticulata, Aequidens pulcher*) were encountered in a single residual pool just 30 cm deep. Recent deforestation in the watershed may be contributing to increasingly harsh conditions during the driest period (March–April), yet subsequent immigration and spawning reestablish a diverse fish assemblage each year.

Within an annual cycle, a direct relationship exists between environmental parameters that indicate the quality of the aquatic habitat and fish diversity and abundance (Fig. 6). Due to the very low relief and gradient of the llanos landscape, the area of aquatic habitat greatly expands with increasing water depth. Depth and pH had the highest correlations with species richness (Table II). Depth and pH covary strongly at this site (Table II), so that high species richness during the wet season probably results from increased water depth and volume rather than low pH. Temperatures can exceed 35°C in shallow dry-season pools, yet many fishes appear to thrive. Dissolved oxygen (DO) is frequently cited as one of the most critical environmental parameters influencing short-term survivorship of aquatic organisms. Yet owing to special respiratory adaptations, diverse llanos fishes can persist in nearly anoxic conditions,
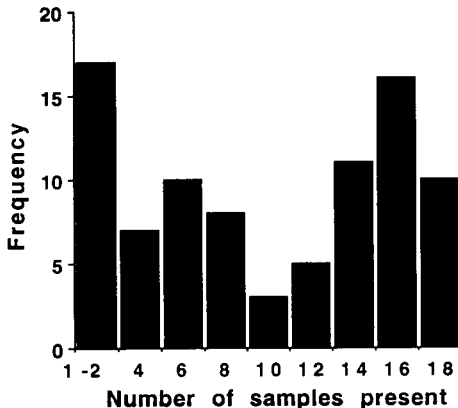
FIGURE 5. Frequency distribution of the number of samples in which individual fish species were present (maximum possible = 18).
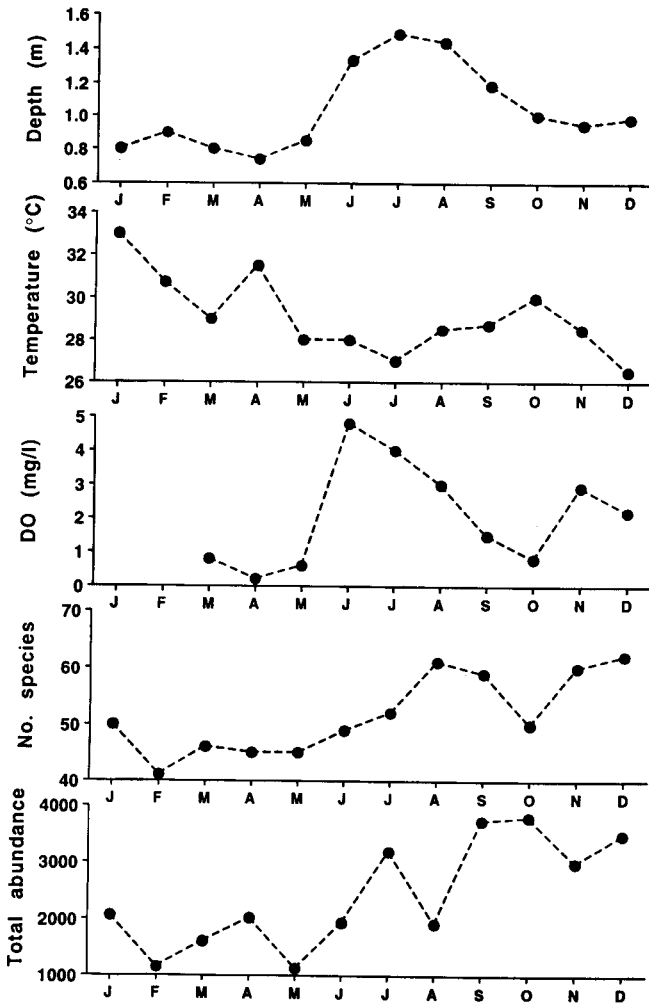
FIGURE 6.   1984 plots of monthly variation in environmental parameters and species and individual fish abundances at Caño Maraca.

and in some cases they are even able to feed and reproduce. For example, the October 1993 sample (surface DO = 0.2 mg/l) contained 47 species and 5661 individuals. Most of the characid fishes sampled had dermal lip protuberances, a morphological response to hypoxia that presumably enhances aquatic surface respiration (Winemiller, 1989c). The low correlations between DO and species richness and abundance (Table II) were influenced by the presence of special respiratory adaptations in a large number of llanos fish species.

TABLE II   Correlations between Environmental Parameters, Fish Species Richness, and Total Fish Abundance Based on 16 Sampling Dates at Caño Maraca

	Depth	Temperature	DO	pH	Velocity	Richness
Temperature	−0.363					
DO	0.614[a]*	−0.508[a]				
pH	−0.764*	0.582*	−0.397[a]			
Velocity	0.806[b]**	−0.383	0.821[b]**	−0.534[b]		
Richness	0.621*	−0.165	0.035[a]	−0.641*	0.178[b]	
Abundance	0.221	0.090	−0.318[a]	−0.188	−0.043[b]	0.025

[a]df = 14 due to lack of field measurement for parameter.
[b]df = 13.
*P <0.025,   **P <0.0001.

Clearly this fish assemblage varies over the short term in response to dynamic changes in habitat driven by markedly seasonal precipitation. The more vexing questions are the following: How do highly persistent species differ from nonpersistent species, and to what extent does the assemblage return to a predictable composition during the late wet season and transition to dry season? The frequency distribution for sample abundance CVs approximates a log-normal distribution, which suggests that very few populations are highly stable, many populations are moderately variable, and many others are highly variable (Fig. 7). The difference between the distribution based on abundant species and that based on all 87 species suggests that extremely large variability is associated with rarity (Fig. 7), but to some extent this is an artifact of
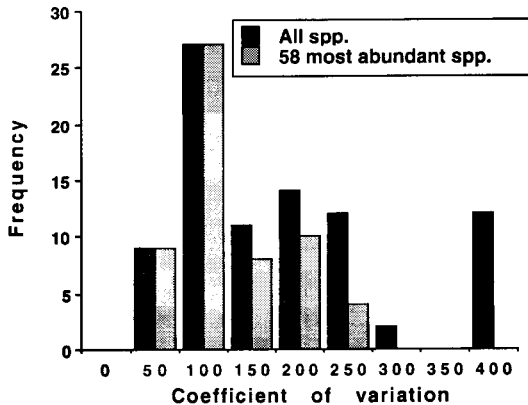
FIGURE 7.   Frequency distribution of the coefficient of variation for species at Caño Maraca based on all species and the dominant 58 species over the 10-year period.

sample size. The relationship between average monthly abundance and the CV was inverse and rather weak for both the data set based on the 12 monthly surveys of 1984 and that based on the full 18 samples from the 10-year survey (Fig. 8). The slope was steeper and the correlation higher for the 1984 data series, an indication that species that tended to remain resident year-round also had lower variability in local density; this pattern is confirmed by the plots in Fig. 9. The most abundant species were the most persistent and also tended to be the least variable over the 10-year study.

Only one species, the cichlid *Aequidens pulcher,* was present in all 18 samples. This fish is a trophic generalist with an "equilibrium-type" life-history characterized by relatively small broods, large eggs, brood defense, and asea-
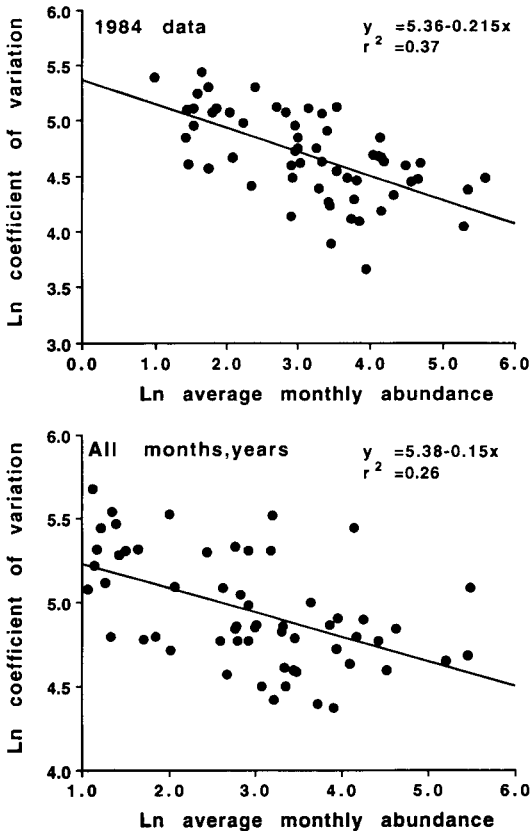
FIGURE 8. Relationship between the average monthly abundance and the coefficient of variation based on the 1984 surveys and on the 10-year survey period.
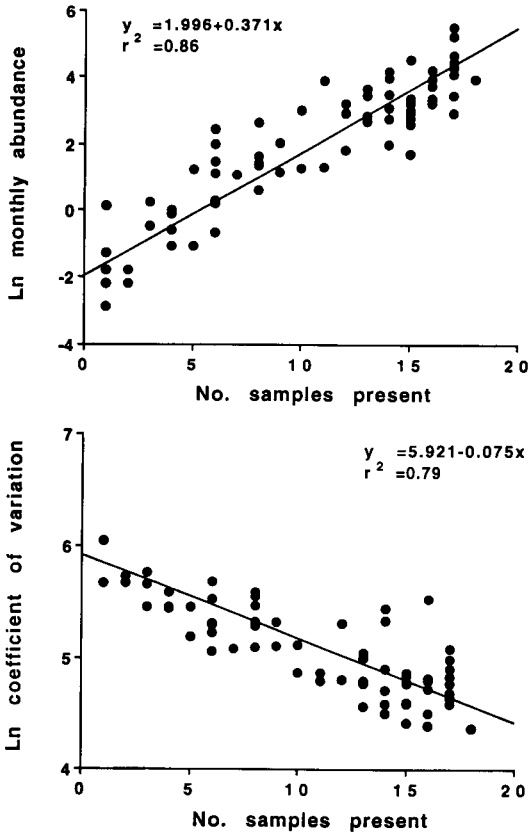
FIGURE 9. The average monthly abundance and the coefficient of variation of sample abundance plotted against the number of samples in which a species was present.

sonal reproduction (Winemiller, 1989b). Because at least some individuals are reproducing during any given period, the population has a strongly persistent size-structure. Of the eight species that were present in 17 of the samples, one characiform has a relatively equilibrium-type strategy (*Hoplias malabaricus*), two characiforms have relatively "periodic-type" strategies (*Steindachnerina argentea, Astyanax bimaculatus*), and five species have relatively "opportunistic-type" strategies (four characids, one poeciliid). Periodic strategists (the "seasonal strategy" of Winemiller, 1989b) spawn only once or twice during the early wet season, shed large clutches of small eggs, and have little or no parental care (Winemiller, 1992; Winemiller and Rose, 1992). Opportunistic fishes mature at small sizes and produce small broods at frequent intervals over extended breeding seasons.

To shed further light on the attributes of stable versus variable fish populations at this site, the effects of one phylogenetic and three ecological variables on average sample abundance and its CV were examined. Assignment of life-history strategies was based on data and patterns reported in Winemiller (1989b) and conform to the following criteria: equilibrium-type (maximum SL >50 mm, mature egg diameter >1.50 mm, with brood guarding), opportunistic-type (maximum SL <50 mm, number of spawning bouts per year ≥2), and periodic-type (all others, with few exceptions species with maximum SL >50 mm, 1 spawning bout per year, egg diameter <1.50 mm, no brood guarding). Species were assigned to trophic guilds (detritivore-algivore, omnivore, invertebrate-feeder, piscivore) based on volumetic dietary data (Winemiller and Pianka, 1990). Fishes were further categorized into two groups: those possessing special accessory respiratory adaptations and those not currently known to possess such attributes. Finally, fishes were segregated based on classification (or not) in the order Characiformes. The results are shown in Table III; neither monthly sample abundance nor its CV were significantly affected by life history, trophic guild, respiratory adaptations, or taxonomic order. The effect of trophic guild on abundance was nearly significant at $P = 0.051$, and a Tukey-HSD test showed that omnivores were more abundant than invertebrate feeders ($P = 0.04$).

The results of Spearman's rank correlations, r_s based on fish abundances among all 18 monthly samples, revealed no general relationship between similarity and duration of the time interval between samples (Table IV). Similarity was nearly as high between-years (especially among samples taken during the same season) as within-years (among samples taken at different seasons) (Table IV). Similar qualitative results were obtained for the 14 and 58 species data

TABLE III   Results of ANOVA and *t*-Tests for the Effects of Life-History Strategy, Trophic Guild, Accessory Respiration, and Taxonomic Order on the Average Abundance and Coefficient of Variation Based on 58 Species at Caño Maraca during 1984

	Abundance			CV		
	F	*df*	*P*	*F*	*df*	*P*
Life-history strategy	0.258	2, 55	0.77	0.942	2, 55	0.40
Trophic guild	2.76	3, 54	0.051	2.30	3, 54	0.09
	t	*df*	*P*	*t*	*df*	*P*
Accessory respiration	1.340	28	0.186	0.723	28	0.47
Taxonomic order[a]	1.122	28	0.27	1.440	28	0.155

Note. Average monthly abundances and CVs were ln-transformed.
[a]Characiforms vs all other orders.

TABLE IV Spearman's Rank Correlations for 10 Selected Sampling Dates at Caño Maraca, Based on Numeric Percentages of the 14 and 58 Dominant Species

	Based on 14 dominant species								
	Jan84	Feb84	Jun84	Oct84	Jan88	Jan89	Jan92	Oct93	Feb94
Feb84	0.157								
Jun84	0.673*	−0.185							
Oct84	0.713*	0.322	0.548*						
Jan88	0.598*	0.372	0.399	0.596*					
Jan89	0.101	−0.443	0.214	0.220	−0.084				
Jan92	0.509	0.212	0.448	0.560*	0.613*	0.308			
Oct93	0.631*	0.176	0.593*	0.534*	0.380	0.117	0.370		
Feb94	0.241	0.000	−0.207	−0.034	−0.103	0.172	−0.035	−0.310	
Jun94	0.380	−0.183	0.100	0.051	0.026	0.099	0.007	0.595*	0.034
	Based on 58 dominant species								
	Jan84	Feb84	Jun84	Oct84	Jan88	Jan89	Jan92	Oct93	Feb94
Feb84	0.598*								
Jun84	0.303*	0.203							
Oct84	0.603*	0.621*	0.469*						
Jan88	0.661*	0.601*	0.356*	0.685*					
Jan89	0.404*	0.295*	0.538*	0.404*	0.452*				
Jan92	0.431*	0.491*	0.400*	0.463*	0.618*	0.670*			
Oct93	0.631*	0.383*	0.344*	0.654*	0.533*	0.421*	0.520*		
Feb94	0.105	0.087	0.191	0.147	0.060	0.236	0.236	0.068	
Jun94	0.242	0.161	0.393*	0.330*	0.182	0.205	0.107	0.322*	0.197

*$P < 0.01$.

sets; the correlation between two r_s matrices containing all possible pairwise combinations among 18 samples was 0.69 ($df = 152$, $P < 0.0001$). The first column of Table IV is selected to provide one example (lower half, results based on 58 species): sample Jan84 was most similar to Jan88 followed by Oct93 and Oct84; aside from Feb94 (the sample from the nearly dry pool), the two early wet-season samples (Jun84, Jun94) were the most dissimilar to Jan84.

The same qualitative pattern resulted from Pearson correlations based on sample abundances; it is illustrated in Fig. 10 by dendrograms using the average clustering algorithm. Based on the dominant 14 species, the four 1984 dry-season samples form a tight cluster on branch D; Jan84, Jan88, and Oct84 cluster on branch H; a combination of wet-1984, transition-, and dry-season samples cluster on branch G; and Jun94 and Feb94 are outliers (see Fig. 10). Based on 58 dominant species, Feb94, Jan89, Jun94, and Jan92 are outliers;
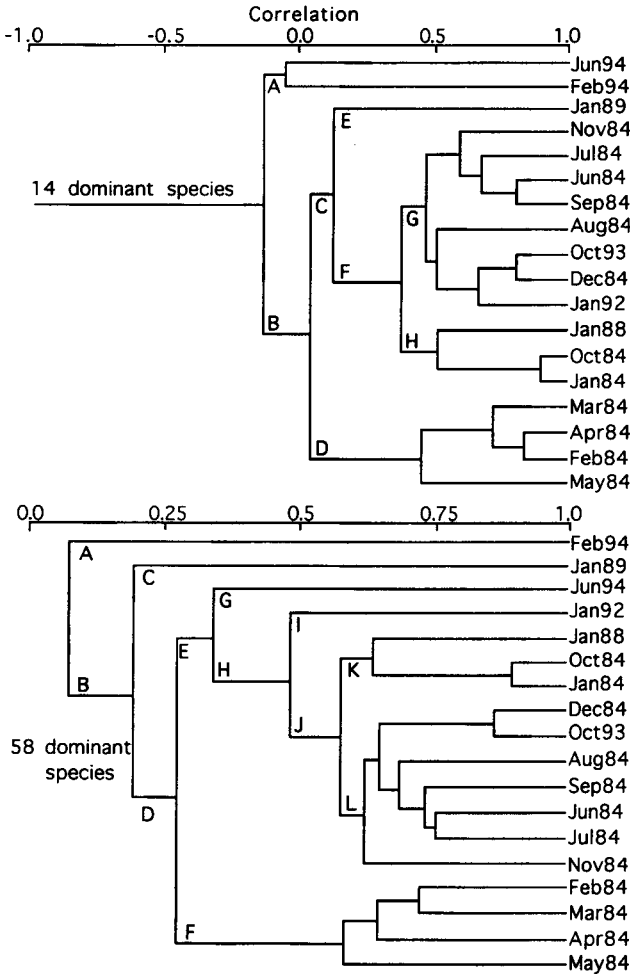
FIGURE 10. Dendrograms showing similarity of fish assemblage structure among surveys conducted over the 10-year period. Top dendrogram is based on the 14 dominant species, and the bottom dendrogram is based on the 58 dominant species. In each case, Feb94, Jun94, and Jan89 are outliers; dry season 1984 samples are grouped; and wet/transition season samples are grouped.

with the four dry-season 1984 samples clustering on branch F; Jan84, Jan88, and Oct84 clustering on K; and all wet season 1984 and the remaining transition-season samples clustering on branch L (Fig. 10).

Absolute fish densities (numbers or biomass/m^2) were estimated for four samples and are plotted in Fig. 11. By either measure, total fish densities were greatest during the transition season (samples Dec84 and Oct93), lower dur-
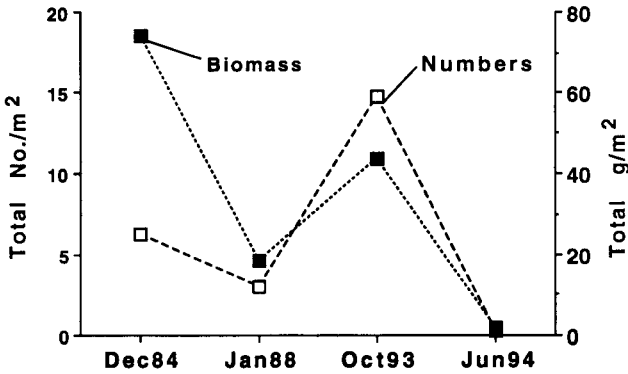
FIGURE 11. The total abundance and biomass of fishes per unit area from four quantitative density estimates performed at Caño Maraca.

ing the dry season (Jan88), and extremely low during the wet season (Jun94). Biomass was larger relative to numbers in the Dec84 sample compared with the Oct93 sample, and this may reflect the influence of piscivory during the transition season. Late transition-season samples, Nov84 and Dec84, contained many large fishes (Table I), some that were piscivores (e.g., *Pygocentrus cariba, Hoplias malabaricus, Caquetaia kraussii*) and others that were non-piscivores but possessing armor or spines (*Hoplosternum littorale, Hypostomus argus*). The abundance of the two dominant fish orders varied greatly in these four density samples (Fig. 12). Characiforms (tetras and related fishes), followed by siluriforms (catfishes), dominated all four periods in terms of numbers, biomass, and species richness. Characiform numbers were greater in sample Oct93 than Dec84, but the reverse trend occurred for biomass density. This trend supports the transition season piscivory hypothesis. Siluriform numbers show a small graded decline from sample Dec84 to sample Jun94, but biomass follows the characiform pattern. Except for the wet-season sample (Jun94), perciform (cichlid) density varied little.

In three samples the fish density data were segregated by two major pool habitats, open water ("open") and dense vegetation ("veg"). Clusters based on correlation between the numerical versus biomass densities of the dominant 58 species were different (Fig. 13). Open water samples from the three periods formed a tight cluster (branch C) when the analysis was based on biomass data. Clustering based on numerical densities had the veg-Dec84 sample most similar to open-Jan88, and the two Jun94 samples clustered together (Fig. 13). The differences between the two dendrograms is due to the influence of the Jun84 sample. The early wet-season sample (Jun94) contained mostly small juvenile fishes, most of which used dense vegetation both as a foraging sub-
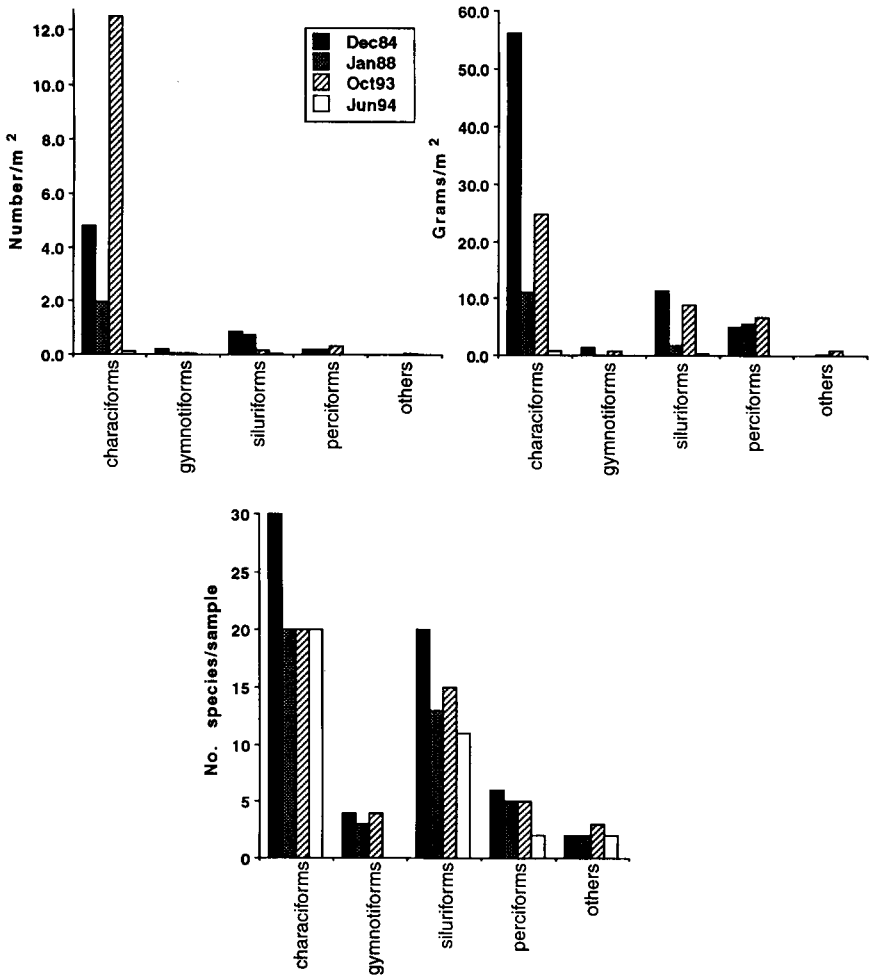
FIGURE 12. The numerical, biomass, and species densities of fish orders from four quantitative density estimates performed at Caño Maraca.

strate containing microcrustacea and other juvenile food resources and as a refuge from predators. Growth is rapid, and many species undergo ontogenetic niche shifts involving less frequent occupation of vegetation and greater feeding on terrestrial arthropods, detritus, seeds, or fishes (Winemiller, 1989a). The habitat affinities of adult size classes were very predictable for many species. For example, most of the knifefishes (weakly electric gymnotiforms) reside almost exclusively in vegetation, whereas redbelly piranhas, *Pygocentrus*

TABLE V   Comparison of Species Abundance Ranks and Percentage Relative Abundances
between Year-Long Surveys during 1966 and 1989 on the Upper Zambezi/Barotse Floodplain

Species	1966		1989	
	Rank	% abundance	Rank	% abundance
Pseudocrenilabrus philander	1	21.707	1	18.829
All Aplocheilichthys spp.	2	11.185	4	10.597
Schilbe mystus	3	8.633	3	12.038
All Barbus spp	4	8.527	2	16.526
All Synodontis spp.	5	8.515	5	8.432
Tilapia sparrmanii	6	6.143	6	6.922
All Clarias spp.	7	4.046	12	2.055
Marcusenius macrolepidotus	8	3.438	7	3.075
Hydrocynus forksahli	9	3.356	10	2.441
Serranochromis macrocephalus	10	3.289	13	2.020
Tilapia rendalli	11	3.266	9	2.716
Micralestes acutidens + Rhabdalestes maunensis	12	2.799	24	0.407
Pollimyrus castelnaui	13	2.070	8	2.847
Oreochromis andersonii	14	1.937	27	0.255
Serranochromis codringtoni	15	1.529	11	2.427
Petrocephalus catastomus	16	1.501	16	0.820
Serranochromis altus + S. angusticeps	17	1.494	20	0.531
Ctenopoma multispinis	18	1.407	21	0.455
Serranochromis giardi	19	1.353	19	0.607
Hemichromis elongatus	20	1.015	17	0.696
Hepsetus odoe	21	0.533	14	1.276
Pharyngochromis darlingi	22	0.423	28	0.248
Serranochromis robustus	23	0.388	18	0.683
Auchenoglanis ngamensis	24	0.369	33	0.083
Labeo lunatus	25	0.243	30	0.145
Oreochromis macrochir	26	0.216	22	0.427
Serranochromis carlottae	27	0.204	26	0.262
Mormyrus lacerda	28	0.141	15	0.869
Hemigammocharax multifasciatus	29	0.125	32	0.124
Hemigrammocharax machadoi	30	0.074	38	0.007
Chiloglanis sp.	31	0.043	37	0.014
Brycinus (=Alestes) lateralis	32	0.016	34	0.076
Hippopotamyrus discorhynchus	33	0.012	25	0.303
Ctenopoma intermedium	34	0.004	23	0.414
Tilapia ruweti		0.000	29	0.159
Afromastacembelus frenatus		0.000	31	0.138
Amphilius uranoscopus		0.000	35	0.041
Serranochromis longimanus		0.000	36	0.028
Hippopotamyrus ansorgii		0.000	39	0.007
Total sample abundance		25,508		14,504

<0.0001 in each case). The correlations were even greater for Pearson correlations using ln-transformed sample abundances (0.90 with 14 species, 0.91 with 25 species, and 0.92 with 31 species, where P <0.0001 in each case). Whereas some shuffling of species' abundance ranks has occurred, the high correspondance between these large-scale surveys conducted nearly a quarter of a century apart is rather remarkable, especially in the presence of artisanal and commercial fishing. Abundance does not seem to be related to phylogeny, life history, trophic niche, or body size; representatives of all these categories are well dispersed throughout the rankings in Table V. The greatest drops in abundance rank were *Micralestes acutidens* (from 12th in 1966 to 24th in 1989) and *Oreochromis andersonii* (from 14th to 27th). *Micralestes acutidens* might have been undersampled in 1989 since this small schooling characid appeared to favor shallow water areas between sand ridges along the edge of the river channel. Most of Kelley's *M. acutidens* came from river channel samples, and this habitat was not extensively seined during 1989. *Oreochromis andersonii* should have been captured just as effectively as other large tilapine cichlids within lagoons, river edge habitats, and flooded terrain. Large tilapine cichlids are among the most valued fishes, but why this species alone might have suffered reductions from overharvest is unclear.

IV. DISCUSSION

A. The Influence of Seasonality on Assemblage Patterns

The annual changes that occur in the abiotic environment of floodplain rivers are very predictable in tropical regions (Lowe-McConnell, 1975, 1979; Welcomme, 1979; Junk *et al.*, 1989). Strongly unimodal patterns of annual precipitation (or bimodal patterns in some equatorial regions) result in sheet flooding followed by gradual recession of waters until the only aquatic habitats that remain are permanent stream channels, lagoons, and isolated floodplain pools. Primary production is strongly correlated with initial flooding and the area of aquatic habitat. Secondary production, both in the form of invertebrates and algivorous fishes, rapidly follows suit; degradation of aquatic habitats ensues with the onset of the dry season, with profound effects on fish assemblages.

In the Venezuelan llanos, high temperatures, aquatic hypoxia, habitat reduction, and isolation contribute to a general reduction in local fish populations in the dry season, with changes in assemblage structure and, in many cases, niche shifts (Winemiller, 1989a,b, 1990). Despite the fact that many species possess adaptations for survival under extreme hypoxia, fish mortality is very high during the llanos dry season. Occasionally all aquatic habitat may

be eliminated locally, as was nearly the case in sample Feb94; if this happens, the subsequent wet-season assemblage is reconstructed entirely from immigration. At least two Caño Maraco fishes, an annual killifish (*Rachovia maculipinnis*) and a swamp eel (*Synbranchus marmoratus*), can survive for several months in the absence of surface water.

The Caño Maraca fish assemblage showed its greatest changes in association with seasons. In terms of species' relative abundances, the assemblage was more similar within seasons over periods separated by as much as 10 years than it was between seasons during the same year. Species biomass distributions between open water and dense vegetation habitats were conserved between seasons and years. Species' relative abundance patterns at Caño Maraca indicated that the assemblage was persistent from year to year, especially during the late wet season and transition (falling water) season. Despite recent deforestation in this watershed, it appears that the species composition of this assemblage can be predicted with a high degree of accuracy each year, especially during the transition period (August through December). But since the timing of hydrological events in the llanos cannot be predicted with great accuracy, it would be naïve to assume that the assemblage will return to the same composition and structure each year on the same month. For example, December and January seem to be pivotal months in the transition to dry-season conditions, during which the habitat is shrinking but pools are not yet isolated nor severely degraded.

Within the seasonal progression, late September through October is an unusual period each year in that hypoxic conditions appear for a few weeks then disappear until the peak dry season (February through April). This circumstance occurred during both 1984 (Fig. 6; Winemiller, 1989c) and 1993, and it seems to result from a pulse of microbial respiration associated with the decomposition of aquatic macrophytes that die en masse as large tracts of higher terrain are drained. Because of the brief occurrence of dry-season features within the middle of the transition season, October samples tended to cluster with January (the early dry season) in Fig. 10.

Reproduction by most fishes is strongly tied to precipitation and hydrology, and even those species that spawn year-round have bursts of spawning activity during the early wet period. This pattern of seasonal reproduction has been described for tropical floodplain regions throughout the world (Lowe-McConnell, 1964; Welcomme, 1969; Winemiller, 1989b, 1991a). It is actually rather surprising that any fishes would attempt to reproduce under the crowded conditions of the transition season (see following discussion) or the harsh conditions of the dry season. Nonetheless, small opportunistic fishes, such as the guppy and annual killifishes, maximize their lifetime fitnesses and population growth rates by adopting a strategy of rapid maturation and continual high reproductive effort. Some species with brood guarding also spawn during

the dry season (e.g., the cichlids *Aequidens pulcher* and *Caquetaia krausii*). In the Upper Zambezi/Barotse system, many of the mouth-brooding cichlids spawn once just before the beginning of the flood period (Winemiller, 1991a). Presumably, mate selection is facilitated by high fish densities during the low water period, and developing eggs and larvae can be transported onto the flooded plains by the brooding parent. The large eggs of these species allow the larvae to develop from endogenous reserves for many days while protected inside the parent's mouth, so that exogenous feeding can be delayed whenever floods come later than usual.

B. The Influence of Biotic Interactions on Assemblage Patterns

Biotic interactions influence the structure of tropical floodplain fish assemblages throughout the year, but they seemingly play the largest role during the transition season. During the wet season, large fish populations and biomass build up as a result of immigration, reproduction, and rapid growth in the vast and productive aquatic environment. As floodwaters recede, this fish biomass and diversity are concentrated in ever increasing densities; at the same time, many food resources become more limited. For example, there are fewer submerged surfaces for the attachment and growth of algae and associated benthic fauna, and a reduced water surface area results in fewer terrestrial insects and seeds reaching the aquatic system. For most fishes, resource competition becomes more intense with the progression of the transition season. Most benthic algivores shift to detritivory (Winemiller, 1990, 1996), and numerous invertebrate feeders and omnivores show increased food and habitat segregation (Winemiller and Pianka, 1990). Even piscivores increase interspecific segregation by diet during the transition season, and this despite the fact that fish prey should be more available in the shrinking habitat (Winemiller, 1989a). Ontogenetic diet shifts are largely responsible for this pattern, with wet season diets strongly influenced by juveniles feeding on invertebrates, and transition season diets dominated by specialized piscivory by juveniles and adults both (Winemiller, 1989a).

Theoretically, the fish assemblage should reveal the greatest between-year similarity during the transition season because this is the period when biotic interactions should eliminate vagrant or fugitive species and adjust the relative abundances of the resident species that are well suited to the local conditions. Conversely, dry-season assemblages should be determined to a greater extent by stochastic abiotic factors like pool strandings. Determination of wet-season assemblages, especially during early flooding, should contain a large random element associated with the timing of immigration and spawning. Transition-

season samples were similar within and between years (Fig. 10, Table III). Dry-season samples formed a tight cluster within the year 1984; however, there was relatively low between-year clustering of dry-season samples (Fig. 10, Table III). With the exception of the June 1994 sample (very early wet season), wet-season samples tended to be similar to transition-season samples, particularly early transition season, and to those from the same year.

It would be misleading to suggest that the fish assemblage of Caño Maraca is completely determined by ecological factors such as habitat selection, competition, and predation. Several surprises were encountered during the later surveys. For example, the large cichlid, *Astronotus ocellatus,* was a common but not dominant species in the 1984 transition-season samples; in the Jan89 sample, *Astronotus* was the most abundant fish. No explanation for this apparent explosion of the local *Astonotus* population can be provided. Likewise, only a few *Pseudoplatystoma fasciatum* (Pimelodidae), a large piscivorous catfish, were captured at the site during 1984 surveys. This species did not reproduce at the site and occurred in only one sample; it can be classified as a vagrant species. *Pseudoplatystoma* was never again encountered at Caño Maraca (although it occurs in the channel several kilometers downstream), but several individuals of another large piscivorous catfish, *Pseudopimelodus apurensis* (Pimelodidae), were captured at the site in October 1993. Many of these *Pseudopimelodus* were dead or in distress from hypoxia. Presumably, both of these large catfishes migrated from downstream into the estero region of the creek where they fed on the abundant fishes. In the case of *Pseudopimelodus,* many individuals failed to exit prior to the hypoxia that occurs each October. Quite likely, even a relatively small number of these large predatory catfishes could have a significant impact on the local fish assemblage. It is very doubtful that a few vagrant omnivores or algivores have any influence at all on the ecosystem. Another somewhat unpredictable source of mortality is piscivorous wading birds such as ibises, egrets, herons, and storks. These birds congregate each year in greatest numbers during the late transition and dry seasons, and they certainly have an impact on llanos fish populations.

C. An Integrated View of Tropical Fish Assemblage Dynamics

Tropical freshwater fish assemblages are, taxonomically and ecologically, among the most diverse vertebrate assemblages anywhere in the world (Roberts, 1972; Lowe-McConnell, 1975; Goulding et al., 1988). The underlying basis for phylogenesis is geographical and historical, but the generation and maintenance of physiological, morphological, and behavioral diversity associated with this phylogenetic diversity is largely a function of ecology and

history (Roberts, 1972; Lowe-McConnell, 1975; Winemiller, 1991b; Lundberg, 1993). Perhaps we can never fully understand the biogeographic/ecological histories that produced extant regional fish assemblages. However, we can begin to develop a model of the factors that interact to produce local assemblage patterns on much shorter ecological time scales. The combination of predictable, seasonal abiotic factors; short-term, unpredictable abiotic factors; and responses by a diverse biota make tropical floodplain fish assemblages rich systems for study.

Lowe-McConnell (1975) provided one of the first conceptual models of fish responses to tropical floodplain ecosystem dynamics. This model has been elaborated upon by Welcomme (1979) and Junk *et al.* (1989), among others. The model assumes a strong unimodal pattern of annual precipitation, as would be encountered in the llanos or Barotse floodplain. During the annual floods, nutrients enter the aquatic ecosystem from the adjacent and newly submerged terrestrial landscape, and this drives a sustained pulse of aquatic primary production in the form of aquatic vegetation and microbes. In some areas, water quality may be poor, even hypoxic, during the initial stages of inundation when microbes process newly flooded detritus (Lagler *et al.*, 1971). Many fishes migrate from rivers and lagoons onto floodplains where a burst of spawning takes place. Others spawn in the channels of larger rivers, and eggs and larvae drift into floodplain habitats, some perhaps located many kilometers downstream from the spawning site. Many fishes, larger species in particular, migrate long distances for spawning.

Each fish species seeks a particular kind of local habitat within the floodplain drainage basin, and species vary greatly in their degree of habitat selectivity. Some species move farther up tributaries to small floodplain habitats (like Caño Maraca); others seek particular environmental conditions in flooded areas and lagoons along major river channels (e.g., Upper Zambezi; see also Rodríguez and Lewis, 1990; Chapman and Chapman, 1993). Most locations also contain a population of year-round residents, mostly smaller species, many possessing accessory respiratory adaptations.

Microcrustacean and aquatic insect production is very high on the flooded plains, and this serves as a food resource for juvenile fishes. Terrestrial arthropods, terrestrial vegetation, and seeds are important food resources for many tropical river fishes, and these are more available to fishes during the annual floods. During the initial stages of the flood season, fish survivorship is high because encounter rates with predators are low within the vast habitat with its complex matrix of submerged macrophytes.

As flood waters recede, fishes are concentrated at higher densities, and many migrate back into permanent river channels. During this time, predatory fishes and birds often congregate at major points of entry to larger rivers. The migratory fishes of the larger rivers may swim hundreds of kilometers to find

optimal habitats. During this transition season, young-of-the-year continue to grow, encounter rates with preferred food resources decline, and encounter rates with competitors and predators increase. Mortality gradually increases, especially for small fishes. Local floodplain habitats may experience acute hypoxia as water recession results in the death of aquatic macrophytes (as described for Caño Maraca). Biotic interactions during this period impose selection for efficient use of space and food resources, as well as effective means for predator avoidance and defense. Members of diverse piscivore assemblages probably gain a very significant fraction of their annual food intake during this period, and this places a premium on efficient foraging, even when fish prey are relatively abundant. In many regions (like Caño Maraca and the Upper Zambezi), densities of small fishes are greatly reduced by piscivores within a period of just 3–4 months [see Jackson (1961) for a discussion of the influence of piscivores on African river fish ecology].

The major changes that unfold in floodplain ecosystems during the falling water period do not result in random fish assemblages; rather, selection for ecological performance results in local assemblages with similar structures year after year. The intensity of this selection and associations between optimal habitat conditions and fixed geographical locations probably vary from year to year depending on the timing and height of the floods. To some extent, fishes must respond to a moving target on these highly heterogeneous floodplain landscapes. Ultimately, many aquatic organisms become trapped in isolated pools or channel segments, where peak dry-season conditions cause deterioration of water quality and the death of large numbers of fishes. Within these isolated dry-season habitats, physiological stress interacts with predation as a major mortality agent. Whereas strandings contain a large random element, interspecific variation in resistance to degraded conditions and predation is nonrandom, and this creates a degree of stability in the composition and structure of dry-season fish assemblages.

V. SUMMARY

Fishes in tropical floodplain habitats respond to changes in their abiotic and biotic environments, many of which are predictable on a seasonal or annual basis but unpredictable in the short term. The fish assemblage and habitat characteristics of a seasonal creek and its floodplain in the Venezuelan llanos were examined over 10 years. Each year, aquatic populations undergo massive die-offs and emigrations in response to the drying of the floodplain. Each year, the rainy season causes extensive flooding and a renewal of aquatic habitats and populations. Levels of variability in the structure of the fish assemblage were similar within and between years, and this was true when comparisons

were based on either the dominant 14 or 58 species. Hierarchical clustering tended to group assemblages based on season rather than year. Species richness was positively associated with water depth, and the persistence of individual species varied widely. The most persistent species tended to be the most abundant with the least variability. Persistence and abundance were not significantly associated with life history, trophic niche, accessory respiratory adaptations, or taxonomic order. Species biomass distributions between open water and dense vegetation habitats were conserved between seasons and years. Fish assemblages of the Upper Zambezi River and floodplain in Zambia were compared between surveys conducted in 1966 and 1989. Assemblage structure was highly correlated, with only two species showing large shifts in relative abundance ranks. The patterns from both areas indicate that tropical floodplain fish assemblages are structured by a blend of deterministic and stochastic processes operating across a broad range of temporal and spatial scales. Fish assemblage variability is increased by the short-term unpredictability of precipitation and stochastic mortality associated with dry season conditions. Interannual variation is reduced by habitat selection during wet-season colonization, population resiliency, and species interactions during the late wet season.

References

Agostinho, A. A., Julio, H. F., Jr., and Borghetti, J. R. (1992). Considerações sobre os impactos dos represamentos na ictiofauna e medidas para sua atenuação. Um estudo de caso: Reservatório de Itaipu. *Rev. UNIMAR; BB14*, Suppl., 89–107.

Anderson, R. O., and Gutreuter, S. J. (1983). Length, weight, and associated structural indices. *In* "Fisheries Techniques" (L. A. Nielsen and D. L. Johnson, eds.), pp. 283–300. Am. Fish. Soc., Bethesda, MD.

Balon, E. K., and Coche, A. G. (1974). "Lake Kariba, a Man-made Tropical Ecosystem in Central Africa," Monogr. Biol., No. 24. Dr. W. Junk, The Hague, The Netherlands.

Bass, G. D., Jr. (1990). Stability and persistence of fish assemblages in the Escambia River, Florida. *Rivers* 1, 296–306.

Bonetto, A., Cordiviola de Yuan, E., Opignalberi, C., and Olivieros, O. (1969). Ciclos hidrológicos del rio Paraná y las poblaciones de peces contenidas en las cuencas temporarias de su valle de inundación. *Physis (Buenos Aires)* 29, 213–223.

Chapman, L. J., and Chapman, C. A. (1993). Fish populations in tropical floodplain pools: A re-evaluation of Holden's data on the River Sokoto. *Ecol. Freshwater Fish* 2, 23–30.

Clements, F. E. (1949). "Dynamics of Vegetation." Hafner, New York.

Connell, J. H., and Sousa, W. P. (1983). On the evidence needed to judge ecological stability or persistence. *Am. Nat.* 121, 789–824.

Davidson, J., and Andewartha, H. G. (1948). The influence of rainfall, evaporation and atmospheric temperature on fluctuations in the size of a natural population of *Thrips imaginis* (Thysanoptera). *J. Anim. Ecol.* 17, 200–222.

Dobzhansky, T. (1950). Evolution in the tropics. *Am. Sci.* 267, 76–82.

Fletcher, R. I., and Deriso, R. B. (1988). Fishing in dangerous waters: Remarks on a controversial