Spatiotemporal variation in fish assemblage structure in tropical floodplain creeks

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Synopsis

Biotic assemblages of aquatic floodplain systems have great potential to randomly reshuffle during annual flood periods, and have been described both as stochastically and deterministically assembled. However, only a limited number of studies have been conducted in relatively few habitat types. To evaluate large-bodied fish assemblage structure of floodplain creeks, we used experimental gill nets to sample fishes at sites spaced at even intervals within three creeks in consecutive dry seasons. A total of 60 species were collected, 41 of which were collected both years. The most frequently collected species were piscivores and algivores/detritivores. Multivariate analysis suggested non-random patterns of assemblage structure in both years. Correspondence analysis (CA) of the species abundance-by-site matrix for 2001 suggests species assemblages were most similar among sites within the same creek regardless of depth or longitudinal position. Discriminant function analysis (DFA) correctly predicted 100% of samples based on creek identity, and species ordination scores revealed creek-specific species subsets. In 2002, CA and DFA did not distinguish creeks based on species assemblages. Instead, we observed a significant positive relationship between assemblage composition and site depth and position along the creek longitudinal gradient. Assemblages were most similar among sites of comparable depth and longitudinal position, regardless of creek identity. Predators occurred almost exclusively at mouth and mid-reach sites. Flood duration prior to our 2002 sampling period was prolonged due to abnormally heavy rainfall in November and December 2001 (typically the falling-water period), and may account for the observed inter-annual variation in fish assemblage structure.

Introduction

Both stochastic and deterministic ecological factors are important in structuring freshwater communities (Grossman et al. 1982, 1998, Tonn & Magnuson 1982, Kodric-Brown & Brown 1993), with the relative importance of each often depending on the temporal and spatial scale of investigation (Rahel et al. 1984, Levin 1992, Jackson et al. 2001). Non-random assemblage structure patterns are predictable among years if deterministic factors (e.g. species habitat affinity, habitat-dependent survival, and species-specific predation) outweigh potential stochastic influences. In tropical floodplain systems, the relative influence of stochastic and deterministic factors varies with seasonal water-level fluctuation. Many fish species are adapted to take advantage of seasonal flooding by reproducing at the beginning of the wet season, which allows early life stages to feed and grow within inundated floodplain habitats (Lowe-McConnell 1987). Floodwater recession reduces the availability of aquatic habitats and increases fish densities and biotic interactions (Zaret & Rand 1971, Winemiller 1989, 1996, Rodríguez & Lewis 1997). Although early studies

characterized tropical fish assemblages as stochastic (Lowe-McConnell 1987, Goulding et al. 1988), recent work has emphasized the importance of deterministic mechanisms in structuring floodplain fish assemblages, primarily during low-water periods (Winemiller 1996, Rodríguez & Lewis 1997, Toham & Teugels 1997, Tejerina-Garro et al. 1998, Arrington 2002).

Species-specific habitat associations have been shown to deterministically structure tropical floodplain fish assemblages. For example, differences between water types, such as whitewater (nutrient rich, turbid, pH ~ 7.0) and blackwater (nutrient poor, clear, pH ≤ 4.5) (Sioli 1975), often result in different fish assemblages in otherwise similar habitats (Ibarra & Stewart 1989, Saint-Paul et al. 2000). Reduced levels of dissolved oxygen and differential tolerance to hypoxia (Winemiller 1996), water velocity and substrate composition (Toham & Teugels 1997), and predation mediated by water transparency (Rodríguez & Lewis 1994, 1997, Tejerina-Garro et al. 1998) have also been shown to deterministically affect fish assemblage structure in tropical floodplain systems.

Previous research on the Cinaruco River, Venezuela, has shown deterministic structuring in channel and lagoon fish assemblages (Jepsen et al. 1997, Arrington 2002, Layman & Winemiller unpublished manuscript). Jepsen et al. (1997) observed habitat and dietary partitioning among three predatory *Cichla* species (Cichlidae) in channel and connected lagoon habitats. Layman & Winemiller (unpublished manuscript) observed different prey fish assemblages in lagoons with and without large-bodied predators. An extensive study of littoral-zone assemblages by Arrington (2002) showed that, during the falling-water phase of the annual flood cycle, fish assemblages re-assemble in a deterministic manner based on habitat type (e.g. sand banks, leaf litter, woody debris). These studies suggest tropical floodplain river fish assemblages may be structured based on a combination of habitat variables and predation pressure from large-bodied piscivores.

Here we report results from an investigation of large-bodied fish assemblage structure in floodplain creeks of the Cinaruco River, Venezuela, during the early dry season of two consecutive years. Our objective was to compare the assemblage structure of large fishes in three ways: (1) among creeks, (2) along creek longitudinal gradients, and (3) between consecutive years.

Methods

Study area

The Cinaruco River is a speciose (>260 fish species, most <10 cm SL) tropical floodplain tributary of the Orinoco River that drains the llanos (savanna) of southern Apure State, Venezuela (6°32′N, 67°24′W). Width of the main channel at the lowest point in the hydrologic cycle ranges from 40 to 200 m. The Cinaruco is an oligotrophic, moderate blackwater river with high levels of dissolved organic carbon and low pH. Seasonal water level fluctuations exceed 5 m, with most rainfall occurring between May and September. Meandering creeks fringed by dense gallery forest drain the floodplain. Creeks investigated in this study flow into floodplain lagoons permanently connected to the river channel. During the dry season, creeks are backwater extensions of adjacent lagoon habitats as water velocity becomes minimal (0–1.0 m s^{-1}). Creek length ranges from approximately 0.6–2 km, and maximum depth varies between 3 and 7 m. Creek habitats are mosaics of sand, leaf litter, cut banks, partially submerged overhanging vegetation, and submerged branches and tree falls.

Sampling methodology

Assemblage structure of large-bodied fishes in three floodplain creeks (Caños Larga, Muchachas, and Mono; Figure 1) was investigated during a 2-week period of January (early dry season) in 2001 and 2002. Multiple sites were sampled in each creek at ~300 m intervals (Figure 2), and the same sites were sampled each year (except site L4 was not sampled in 2001). At each site, fishes were sampled with three monofilament gill nets (25 m × 2 m) with different mesh sizes (2.5, 3.75, and 5 cm). One net of each mesh size was deployed at each site in a random order with 5–10 m maintained between nets. Nets were secured near the creek bank by the float-line and extended perpendicular across the creek channel. We standardized sampling effort by deploying nets for 24 h at each site. Nets were checked at dawn, mid-day, and dusk, and all individuals were measured and identified to species. Undescribed species were labeled by generic name and a numerical identifier (see Table 1). Species were placed into trophic categories based on stomach contents analysis, previously obtained data
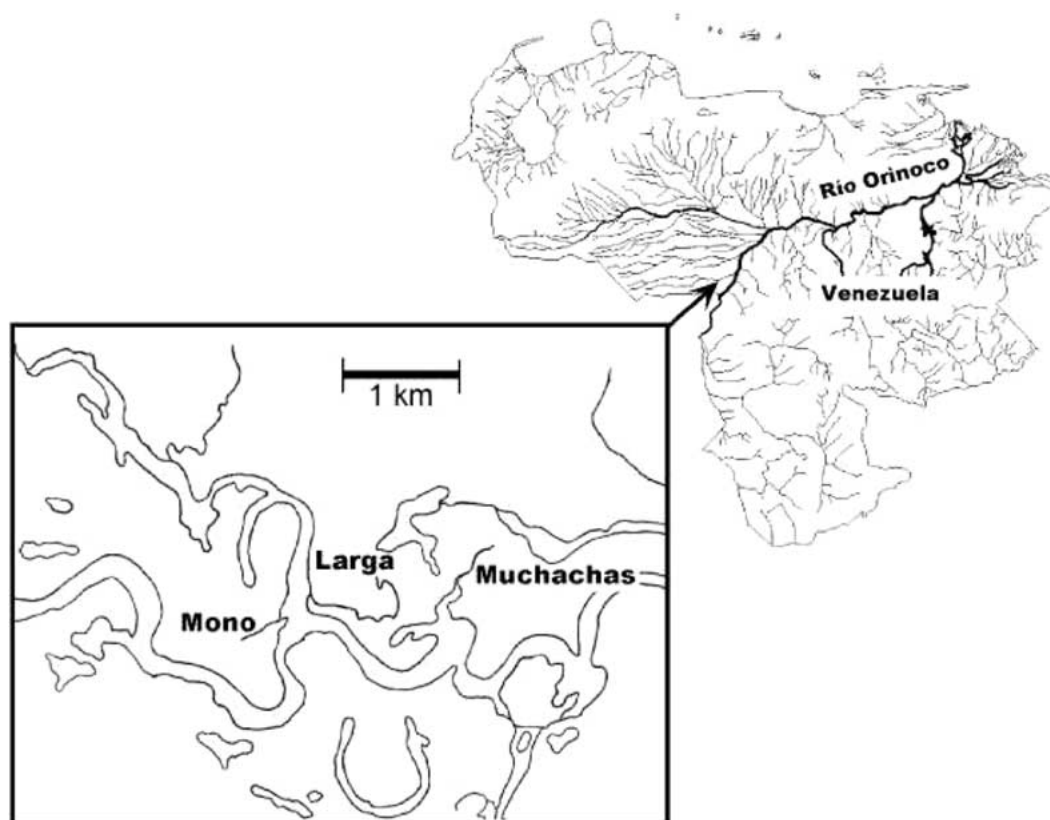
Figure 1. Map of Venezuela illustrating location of the Cinaruco River in the Orinoco River drainage. Expanded section depicts the relative locations of study creeks along the Cinaruco River.
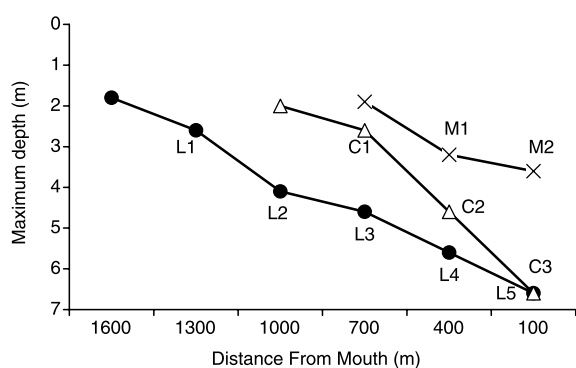

Figure 2. Graph of the longitudinal gradient for each creek depicting maximum site depth and site designations. Sites are labeled in increasing numerical order starting with the farthest upstream site deep enough to be sampled with gill nets. Legend: Caño Larga (●), Caño Muchachas (△), Caño Mono (×).

(Layman unpubl. data, López-Fernández unpubl. data), and published categorizations (Arrington et al. 2002).

Highly vagile species and species that prey on fish caught in nets (e.g. piranhas) may be overestimated due to high net encounter rates, whereas sedentary species may be underestimated due to low net encounter rates. Morphological characteristics, such as spines, may increase a species susceptibility to collection by gill nets. Although gill nets do not provide an unbiased estimate of species-relative density, standardized samples can be compared within and between years because the same biases can be assumed to operate at each site (see Agostinho & Zalewski 1995, Saint-Paul et al. 2000, Silvano et al. 2000, Tejerina-Garro & De Merona 2001). When comparing gill-net samples, special consideration should be paid to possible effects of seasonality such as variation in mean size of individuals and activity patterns (e.g. migration or nesting). Because we sampled during the same 2-week period of consecutive years, we have no reason to suspect that

Table 1. Trophic classification, and within year rank and relative abundance of species collected in 2001 and 2002.

Species	Trophic class	2001		2002	
		Rank	%	Rank	%
Hydrolycus armatus	P(w)	1	17.67	1	14.85
Semaprochilodus kneri	A/D	2	13.42	2	8.75
Boulengerella lucius	P(w)	3	7.40	4.5	7.43
Leporinus sp. 1	O	4	4.79	4.5	7.43
Leporinus sp. 2	O	5	3.97	11	3.18
Triportheus albus	O	6	3.84	3	8.22
Hemiodus unimaculatus	A/D	7	3.70	9	3.98
Cichla temensis	P(w)	8	3.15	13	2.12
Metynnis hypsauchen	H/F	9	3.01	23	0.80
Serrasalmus manueli	P(c)	10	2.47	9	3.98
Laemolyta taeniatus	O	11.5	2.19	9	3.98
Plagioscion squamosissimus	I/P	11.5	2.19	18	1.59
Hemiodus argenteus	A/D	13	2.05	30	0.53
Curimata vittata	A/D	14	1.78		
Geophagus sp. 1	I	15	1.64	30	0.53
Acestrorhynchus falcirostris	P(w)	17.5	1.51	30	0.53
Curimata incompta	A/D	17.5	1.51	30	0.53
Pristobrycon striolatus	P(c)	17.5	1.51	42	0.27
Serrasalmus rhombeus	P(c)	17.5	1.51	15	1.86
Myleus sp.	H/F	20.5	1.37	23	0.80
Serrasalmus altuvei	P(c)	20.5	1.37	30	0.53
Boulengerella cuvieri	P(w)	22.5	1.23	30	0.53
Chalceus macrolepidotus	O	22.5	1.23	6.5	4.51
Boulengerella maculata	P(w)	25.5	1.10	42	0.27
Pellona castelnaeana	P(w)	25.5	1.10	18	1.59
Pseudoplatystoma fasciatum	P(w)	25.5	1.10	42	0.27
Semaprochilodus laticeps	A/D	25.5	1.10		
Crenicichla o-lugubris	I/P	29	0.82	42	0.27
Cynodon gibbus	P(w)	29	0.82	6.5	4.51
Hemiodus immaculatus	A/D	29	0.82	12	2.39
Ageneiosus brevifilis	P(w)	33	0.68	42	0.27
Leporinus sp. 3	O	33	0.68	15	1.86
Leporinus y-ophorus	O	33	0.68	18	1.59
Raphiodon vulpinus	P(w)	33	0.68	30	0.53
Satanoperca daemon	I	33	0.68		
Cichla orinocensis	P(w)	37	0.55	42	0.27
Geophagus sp. 2	I	37	0.55	42	0.27
Lorichariichthys brunneus	A/D	37	0.55		
Anodus orinocensis	I	40.5	0.41	15	1.86
Argonectes longiceps	A/D	40.5	0.41		
Hoplias malabaricus	P(w)	40.5	0.41		
Pachypops furcraeus	I/P	40.5	0.41	42	0.27
Brycon pesu	O	43.5	0.27	42	0.27
Mylossoma aureus	H/F	43.5	0.27	23	0.80
Agoniates anchovia	P(w)	48.5	0.14	23	0.80
Brycon falcatus	O	48.5	0.14	30	0.53
Hemiodus gracilis	A/D	48.5	0.14		
Hypostomus argus	A/D	48.5	0.14		
Psectrogaster ciliata	A/D	48.5	0.14		
Pseudanos gracilis	O	48.5	0.14	20	1.33
Rhamdia quelen	I/P	48.5	0.14		
Serrasalmus medinae	P(c)	48.5	0.14		
Dekeyseria scaphirhincha	A/D			23	0.80

Table 1. (Continued)

Species	Trophic class	2001		2002	
		Rank	%	Rank	%
Heros sp.	O			30	0.53
Cichla intermedia	P(w)			42	0.27
Hassar ucayalensis	I			42	0.27
Leporinus fasciatus	O			42	0.27
Leporinus sp. 4	O			42	0.27
Platynematichthys notatus	P(w)			42	0.27
Trachycorystes trachycorestes	A/D			42	0.27
Total		52	100%	49	100%

P(w) = piscivore (consumes whole prey); P(c) = piscivore (feeds on chunks of flesh or fin); I/P = invertivore/piscivore; I = invertivore; O = omnivore; H/F = herbivore/frugivore; A/D = algivore/detritivore.

the biases mentioned above should vary among our two sampling periods.

Similarity and diversity indices

Between-year comparisons of creek assemblage similarity were performed using a modified version of the Morisita–Horn index:

$$C_{mH} = \frac{2\sum(an_i \, bn_i)}{(da + db)aN \cdot bN} \quad \text{in which } da = \frac{\sum an_i^2}{aN^2}$$

a and b are assemblages being compared, an_i and bn_i are the number of individuals of the ith species present in assemblage a and b, and aN and bN are the total number of individuals in assemblage a and b (Wolda 1983, Magurran 1988). C_{mH} values range from 0.0 to 1.0 and can be considered as percent similarities. The Morisita–Horn index is based on species-relative abundances, and therefore is preferential to the widely used Jaccard and Sørensen indices in which all species are given equal weight regardless of their abundance (Smith 1986). Inter-annual creek similarities were calculated using species-relative abundances across all sites within each creek.

Measures of β diversity are useful because they provide a single value that characterizes differences (or similarities) in species composition among all sites along an environmental gradient (e.g. creek longitudinal gradient). We calculated β diversity for each creek during both years using Whittaker's measure:

$$\beta_W = (S/\alpha) - 1$$

where S is the total number of species present along the gradient (γ diversity), and α is average sample diversity measured as species richness (Magurran 1988).

Higher values of β_W correspond to a longitudinal gradient with sites of dissimilar species composition, and lower values represent similar species composition at all sites. A comparison of various β diversity measures found Whittaker's measure to be the most effective while having the fewest restrictions (Wilson & Shmida 1984).

Multivariate analyses

Species abundance-by-site matrices for 2001 and 2002 were analyzed by correspondence analysis (CA) using CANOCO (Version 4, Microcomputer Power). CA is an indirect gradient technique that simultaneously ordinates sample and species scores obtained by reciprocal averaging (Quinn & Keough 2002). In our analyses, we down-weighted rare species and selected Hill's scaling option, which scales the axes in units of standard deviation (SD) (ter Braak & Šmilauer 1998). A half turnover of species in samples occurs in 1 SD, and full species turnover occurs in 4 SD. Linear regressions were performed using SigmaStat (Version 2.03, SPSS Inc.) to determine relationships between CA axis scores for sites and corresponding measures for depth, species richness, and total abundance. Additionally, we performed linear regressions to determine if depth was significantly correlated with species richness or total abundance. Multivariate analysis of variance (MANOVA) and discriminant function analysis (DFA) were conducted using the statistical package JMP (Version 4.04, SAS Institute Inc.). Both analyses were conducted using 'creek' as a categorical variable and sample scores obtained from CA. DFA predicts creek of origin for each sample, with the null hypothesis equal to the percentage of correct predictions expected by chance. These analyses

determined whether samples are significantly grouped by creek.

Results

Nearly twice as many individuals were caught in 2001 (n = 730) as in 2002 (n = 377); however, only three more species were collected in 2001 (Table 1). A total of 60 species were collected, of which 41 were collected in both years. The most frequently collected species were piscivores and algivores/detritivores (Table 1). In both years, the number of species (S) and individuals (N) collected was significantly and positively related to water depth at the sampling location (S_{2001}: $R^2 = 0.50$, p = 0.033; S_{2002}: $R^2 = 0.45$, p = 0.035; N_{2001}: $R^2 = 0.56$, p = 0.020; N_{2002}: $R^2 = 0.45$, p = 0.034). Species-relative abundance patterns were fairly similar between years, especially for the most common species (e.g. *Hydrolycus armatus*, *Semaprochilodus kneri*, *Boulengerella lucius*; Table 1). Species assemblage structure for each creek in 2001 was most similar to the composition of the same creek in the following year (Table 2a). Although β diversity was positively associated with creek length in both years, values were higher in 2002 than in 2001 (i.e. higher species turnover among sites within creeks in 2002; Table 2b). Relative spacing of samples in CA ordinations for 2001 and 2002 illustrate greater local assemblage dissimilarity in 2002 (samples are spaced relatively farther apart on axes scaled in units of standard deviation; Figure 3).

CA revealed different patterns of assemblage composition in 2001 and 2002. CA ordination for 2001 suggests local assemblages were most similar within a given creek (Figure 3), and MANOVA revealed a significant creek effect ($F_{4,10} = 13.37$, p < 0.001). Using the first four canonical axes derived from CA, DFA correctly classified 100% of 2001 samples

according to creek. Inspection of species ordination scores revealed that site composition consisted of a subset of species with similar relative densities at all sites in each creek (e.g. *H. armatus*, *S. kneri*, *Leporinus* sp. 1, *Leporinus* sp. 2, *Cichla temensis*, and *Plagioscion squamosissimus*), and a species subset with taxa that predominantly occurred in only one creek (e.g. *B. lucius*, *Hemiodus unimaculatus*, and *Laemolyta taeniatus* in Caño Muchachas; *Curimata incompta*, *C. vittata*, and *Acestrorhynchus falcirostris* in Caño Mono; and *Serrasalmus manueli* and *S. rhombeus* in Caño Larga).

Local assemblages did not significantly group by creek in 2002 (MANOVA $F_{4,12} = 0.56$, p = 0.693; Figure 3). DFA correctly classified only 50% of samples by creek. Instead, CA axis I was significantly related to site depth ($R^2 = 0.59$, p = 0.010), and axis II separated headwater samples from mid-reach and mouth samples (Figure 3). Piscivores (e.g. *B. maculata*, *B. cuvieri*, *A. falcirostris*, *Platynematichthys notatus*, *Pseudoplatystoma fasciatum*) were caught almost exclusively at mouth and mid-reach sites.
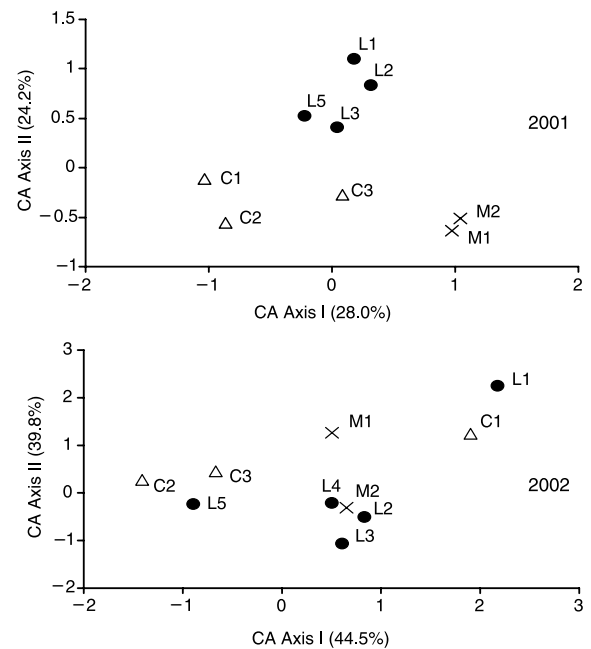

Figure 3. CA ordination of creek sites in 2001 and 2002 based on species abundances. Axes are scaled in units of SD, with a 50% turnover in species composition occurring in 1 SD and a full turnover of species composition in 4 SD. Legend: Caño Larga (●), Caño Muchachas (△), Caño Mono (×). Refer to Figure 2 for site designations.

Table 2. Morisita–Horn index (C_{mH}) values of inter-annual assemblage similarity (a), and Whittaker's measure (β_W) of beta diversity (b).

2002		2001	
	Larga	Muchachas	Mono
(a) Larga	**0.870**	0.731	0.620
Muchachas	0.681	**0.823**	0.592
Mono	0.748	0.599	**0.671**
(b) 2001	1.087	0.800	0.268
2002	1.803	1.214	0.625

Discussion

In tropical floodplain creeks, non-random patterns of assemblage structure are most likely to occur during the low-water period when increasing fish densities intensify biotic interactions (Winemiller 1989, 1996). We observed non-random assemblage structure during the early dry season in consecutive years, although the pattern differed between years. In 2001, large-bodied fish assemblages significantly grouped by creek, whereas assemblage structure in 2002 was correlated with maximum site depth and location along the longitudinal gradient. Specific creek assemblages in 2001 may be partially explained by dominant habitat characteristics. Both of the curimatid species (detritivores) collected during the sampling period occurred predominantly in Caño Mono, a shallow creek with a dense accumulation of decomposing leaves. *S. manueli* and *S. rhombeus*, large piranha species commonly collected in deep habitats of lagoons and the main river channel (Layman unpubl. data), were predominantly collected in Caño Larga, the deepest creek studied. Fishes in the herbivore/frugivore trophic category were most frequently collected in Caño Muchachas, perhaps reflecting the composition of the surrounding gallery forest. In 2002, predators were congregated at mid-reach and mouth sites, presumably for access to prey moving toward deeper habitats as water recedes from the floodplain (Agostinho & Zalewski 1995, Fernandes 1997). The dominance of piscivores in downstream locations is similar to a conceptual model proposed by Schlosser (1987) for small warm-water streams. However, the variation in piscivore distribution among years suggests that the observed pattern is tied to a temporally variable aspect of the system, rather than increased habitat heterogeneity or stability as proposed in Schlosser's model.

Observed inter-annual variation in assemblage structure may be explained by the duration of floodplain inundation prior to the sampling period. Wet-season water level data for the Río Cinaruco are unavailable; therefore regional rainfall data obtained from the National Oceanic and Atmospheric Administration National Climate Data Center (NOAA NCDC) for the Orinoco drainage basin were used as a surrogate. Abnormally high rainfall occurred during November and December of 2001 (a period typically associated with falling-water levels), resulting in a substantially longer period of floodplain inundation prior to our 2002 sampling period (Candido García, pers. commun.). Using average monthly precipitation from 1979 to 2002 as a baseline for comparison, regional measurements for November and December 2001 were as much as 175 and 200 mm above average, respectively (depending on location in the Orinoco drainage basin). Regional precipitation measurements for November and December 2000 approximated baseline values. Prolonged inundation of the Cinaruco River floodplain could result from direct local rainfall, or indirectly through discharge from upstream locations or decreased local discharge due to flow retardation caused by elevated water levels in the Orinoco (or some combination of the three).

Longer sustained periods of floodplain inundation may affect fish assemblage structure in two ways: (1) by affecting species-specific survival rates, or (2) by affecting the phenology of ecological phenomena. First, longer periods of sustained inundation may differentially affect survival rates of predator and prey species. Increased duration of floodplain inundation allows prey species and juveniles longer periods in refuge and nursery habitats which may increase survival (Lowe-McConnell 1987, Agostinho & Zalewski 1995). Additionally, many predators increase foraging rates during the post-inundation period when per-unit-area prey densities increase in shrinking aquatic habitats (Lowe-McConnell 1987, Winemiller 1996, Winemiller et al. 1997, Jepsen et al. 1999). Extended periods of inundation may therefore negatively affect predator survival by decreasing or delaying foraging opportunities. Agostinho & Zalewski (1995) observed decreased predator density, and increased prey density in the Parana River, Brazil in a high flood-level year. However, they hypothesized that lack of recruitment from previous low flood-level years was responsible for the decrease in predator density, whereas increased food and refuge availability combined with fewer predators resulted in increased prey density. In our study, species-relative abundances were fairly similar between years and observed variation was not related to species trophic classification, suggesting that the extended period of inundation did not differentially affect survival of predator or prey species.

Second, assemblage structure of fishes in floodplain creeks may vary predictably with time following the floodplain inundation period. Rodríguez & Lewis (1994, 1997) observed stochastic colonization of Orinoco floodplain lakes during the wet season (prior to isolation), but as the dry season progressed (isolating floodplain lakes from the river channel) assemblage structure became more predictable. Extended periods of floodplain inundation may delay the intensification

of ecological interactions that structure assemblages in floodplain creeks. Although we sampled over the same 2-week period in both years, our 2002 sampling directly followed the prolonged inundation period caused by late seasonal rainfall in 2001. In 2002, assemblage structure was correlated with water depth and position along the creek longitudinal gradient, in part due to predators congregating at creek mouths, possibly to consume prey moving toward deeper habitats. As water levels continue to fall, intense biotic interactions (i.e. predation, competition) might exclude some species from certain creeks, resulting in creek-specific assemblages (as observed in our 2001 samples).

Some studies have characterized tropical floodplain fish communities as stochastic assemblages, often citing continuously changing water levels as a primary factor (Lowe-McConnell 1987, Goulding et al. 1988, Jepsen 1997, Saint-Paul et al. 2000). Several factors may influence the outcome of investigations of assemblage structure in tropical floodplain systems, including spatial and temporal scale of investigation (Rahel et al. 1984, Levin 1992, Crook et al. 2001, Jackson et al. 2001), and phase of the hydrologic cycle (Zaret & Rand 1971, Winemiller 1989, 1996, Rodríguez & Lewis 1997, Arrington 2002). Mechanistic understanding of how specific processes structure floodplain fish communities likely requires a combination of descriptive investigations conducted on extensive spatial and temporal scales, along with experimental investigations. Our results suggest duration and timing of floodplain inundation may strongly influence large-bodied fish assemblage structure in floodplain creeks during the subsequent low-water period.

Acknowledgements

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