Environ Biol Fish (2009) 85:99–108
DOI 10.1007/s10641-009-9466-7

Temporal organization of fish assemblages in floodplain lagoons: the role of hydrological connectivity

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Received: 1 April 2008 / Accepted: 2 February 2009 / Published online: 21 February 2009

Abstract The present study evaluated the hypothesis that after flooding events, non-random patterns of species co-occurrence (segregation) are progressively intensified in fish assemblages inhabiting seasonally isolated lagoons. We sampled lagoons in the upper Paraná River floodplain between 1992 and 1993, and classified them into five hydrological phases, according to their surface connectivity. During the period of isolation (9 months), lagoons depth decreased progressively, but desiccation was reversed after 4 months (possibly due to groundwater infiltration and rainfall). A significant co-occurrence pattern (segregation) occurred in the last phase, supporting our initial hypothesis. However, richness, abundance and composition were significantly correlated with habitat depth, indicating that assemblage structure and organization is closely associated with dynamics of habitat retraction/expansion during isolation. Although environmental conditions of lagoons (absence of prolonged desiccation) prevented an adequate test of our hypothesis, our data suggests that, in addition to the importance of surface floods, the hydrological cycle as a whole has a crucial role shaping the organization of fish assemblages in floodplain lagoons seasonally isolated.

Keywords Assemblage succession · Species co-occurrence · Null model · C-score · Species richness · Neotropical

Introduction

Several hypotheses have been raised to explain the variability of species richness within habitats, including biotic and abiotic factors acting on local and regional scales (Ricklefs 2004). Among these factors, natural disturbances are frequently considered the main force affecting species diversity (Petraitis et al. 1989; Syms and Jones 2000). In fact, a notable generalization of modern ecology is that moderate levels of disturbance maximize habitat diversity and, consequently, species diversity (Connell 1978; Noss 1990). In addition, moderate intensity disturbances may prevent the occurrence of strong biotic inter-

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actions, a situation that affects negatively assemblage diversity (Mouquet et al. 2003). According to Huston's (1979) theoretical model, disturbance intensity and competitive exclusion are the fundamental processes controlling species diversity.

In floodplain-river systems, the seasonal hydrologic pulse is the main natural disturbance controlling the dynamics of aquatic communities (Junk et al. 1989). The flood pulse increases the surface connection among habitats (opportunity for dispersion), the physical space for colonizers and the availability of shelter and resources (Thomaz et al. 2007). Alternatively, during the phase of water retraction (low hydrometric level) alluvial areas with higher elevation become disconnected from other water bodies, and aquatic organisms remain confined within these habitats for different time periods (Lake 2003; Humphries and Baldwin 2003). Crowding of individuals in small habitat patches increases the probability of extinctions events, through both biotic and abiotic stressors. Ward et al. (1999) classified this period as the "phase of biological interaction", because the decreased physical space reduces the size and number of habitats, increases the density of individuals and species and, consequently, intensifies inter/intraspecific interactions.

Marginal lagoons in floodplains remain disconnected for variable periods (weeks to months) during the phase of low hydrometric level. During isolation, stressful abiotic conditions intensify progressively until the following flood (Tockner et al. 2000). At the same time, biotic interactions are expected to become stronger, mainly among individuals confined in habitats of restricted proportions (small lagoons and pools). Therefore, non-random patterns of species co-occurrence (aggregation/segregation) are hypothetically expected between natural disturbance events, basically due to harsh abiotic/biotic conditions that lead some species to local extinctions (Arrington et al. 2005). Marginal lagoons in large floodplains may then represent an interesting environment to study the succession and organization of fish assemblages, considering that the disturbance (flood) is a predictable seasonal event and that lagoons undergo periods of complete isolation, when migration is ceased.

In this sense, the present research investigated the process of temporal structuring and formation of fish assemblages in floodplain lagoons that are seasonally isolated, during a complete hydrological cycle. The work evaluated the hypothesis that, at the patch scale, organization of fish assemblages increases progressively during the phase of spatial isolation, because the main natural disturbance (flood) is absent and the system is not resetting (Thomaz et al. 2007). Under such rationale, we predict non-random patterns of species segregation during the period of disconnection and, as a result of local extinctions, we also expect declines in species richness and remarkable changes in assemblage structure during the isolation period.

Methods

Study area

The present study was conducted in the area of the Upper Paraná River floodplain (in Brazil), located in the Paraná River Basin, the second largest basin of South America. This floodplain comprises the last free-flowing (undammed) stretch of the Upper Paraná River within the Brazilian territory, and lies between the mouths of the Paranapanema and Ivinheima rivers (22° 45'S; 53° 30'W). Its pluvial regime is marked by a wet season from October to February, when the average rainfall is greater than 125 mm monthly (Fig. 1). The flooding period extends from 2 to 4 months, usually between November and May. The dry season occurs from June to September, characterized by an average rainfall less than 80 mm monthly (Fig. 1). Among the seasons, the average variation in

Fig. 1 Daily variation in the hydrometric level (cm; line) of the Paraná River, and monthly average precipitation (mm; bars) during the study period (April 1992 to February 1993)

the hydrometric level is about 2.5 m, with maximum range of 7.5 m in years of extreme floods.

The floodplain is comprised by a mosaic of habitats, including rivers, streams, channels, and marginal lagoons with different degrees of hydrological connectivity. Disconnected lagoons, in particular, are environments that undergo well-marked phases of hydrologic connectivity during a seasonal cycle, which may vary from total desiccation to full connection with the main river. An important ecological aspect is that, between flooding events, these lagoons remain isolated for months, which can promote the progressive desiccation and create stressful biotic and abiotic conditions (Okada et al. 2003). Details on ecological and biological aspects of the study area are presented by Thomaz et al. (2004).

Fish assemblage sampling

To evaluate fish assemblage organization (species richness, assemblage composition and patterns of species aggregation/segregation), sampling was conducted in habitat patches of six lagoons, located on two islands in the main channel of the Paraná River: Porto Rico (Pontal and Canal-do-Meio lagoons) and Mutum (Mutum, Três-Amigos, Porto Rico and Pau-Véio lagoons). These lagoons were small to medium-sized water-bodies, with maximum area ranging from 0.9 to 8.2 ha (Okada et al. 2003).

Fish species were sampled monthly throughout a hydrological cycle, between April 1992 and February 1993. In each lagoon, seining nets (30 m long; 2 m height; mesh size of 0.5 cm between opposite knots) were employed in the littoral zones, only during daytime. All sampled areas were standardized to approximately 100 m^2 (patch), and each habitat patch was considered an independent replicate. A total of three patches were sampled per lagoon in each month ($n=18$ patches/month). In this study, each habitat patch represents an area of 100 m^2 of the littoral zone of each lagoon, in which the effect of the disturbance (flood) is uniform and the following dynamics are expected to be similar. For each sampled patch, maximum depth was measured, all fish species identified (species richness), measured (standard length; cm) and their respective densities recorded. To characterize environmental quality, temperature (°C), oxygen ($mg \cdot L^{-1}$), pH and conductivity ($\mu S \cdot cm^{-1}$) were measured in each patch.

To analyze the relationship between assemblage organization and the dynamics of hydrological connectivity, we divided *a priori* the study period into five different phases (Table 1). Two months were assigned within each phase in order to investigate variations in connectivity and depth along the year, and to increase sample size within phases. Phase 1 represented the period in which all lagoons were connected to the main river, whereas the following phases (2 to 5) represented the period of progressive isolation, when lagoons remained disconnected. Floodplain lagoons in the study area vary independently with respect to connectivity because of differences in geomorphology and altitude, and some may connect earlier or remain isolated for longer periods. Considering this possibility, each lagoon was assigned

Table 1 Hydrological phases (Phases) between April 1992 and February 1993 summarizing variation in hydrological connectivity (surface connection and depth) among lagoons

Phases	Period	Surface connection	Mean depth and range (m)	Sample size	Observation
1	April–May	Yes	2.06 1.45–2.90	19	last months of surface connection
2	June–July	No	1.20 0.55–2.15	30	first months of disconnection
3	August–September	No	0.68 0.37–1.20	36	maximum desiccation
4	October –November	No	1.04 0.45–1.45	30	depth began to increase
5	December–February	No	2.12 1.50–2.55	23	moment that precedes connection

within phases according to their surface connectivity in each month (connected to the main river or disconnected). Consequently, not all 36 patches could be considered in each phase due to differences in surface connectivity among lagoons, what resulted in different sample sizes among phases. In addition, because some lagoons became connected to the river during December 1992 and January 1993, Phase 5 included isolated lagoons sampled in February 1993 to increase sample size. None of the studied lagoons dried out during the period.

Data analysis

Fish assemblage organization

To investigate variation in species richness along the isolation period (e.g. decline), we plotted species richness (mean values and standard error) against hydrological phases. In addition, to investigate variation in fish richness controlling for the effects of patch depth and fish abundance, a multiple regression analysis were performed. Residuals were then plotted against hydrological phases. This procedure was taken because richness is usually correlated with abundance, and because variations in habitat depth may influence sampling efficiency. For all analyses that used fish abundance, density data was corrected following the model proposed by Bayley and Herendeen (2000), which takes into account seine operation, fish size and behavior. This method considers variations in seine efficiency and converts seine captures into unbiased estimates of fish density.

To summarize fish species composition we used a correspondence analysis (CA) with a presence/absence matrix. We considered the scree plot criterion to choose axes for further analysis, and plotted sample scores (mean values and standard error) against hydrological phases to investigate changes in species composition through time. The relationship between assemblage composition (CA scores) and lagoon depth was evaluated through Pearson correlation test.

The level of assemblage organization within patches was evaluated through species co-occurrence analysis, using the C-Score metric (Stone and Roberts 1990). The C-score calculates the average number of checkerboard units for all species combinations, that is, a checkerboard unit represents the number of patches in which species A is present and species B is absent, and vice-versa (Stone and Roberts 1990, 1992). A high number of checkerboards indicates that species distribution is structured by processes that lead to segregation (Gotelli et al. 1997). The C-score of each hydrological phase was calculated from the original matrix of species occurrence (presence/absence).

A null model of species co-occurrence was used to statistically determine if observed co-occurrence patterns could also be obtained by chance. Using the software EcoSim v.7.0 (Gotelli and Entsminger 2001), observed C-scores were compared with a distribution frequency of simulated C-scores, and calculated after 10.000 randomizations of the original data matrix. A sequential swap permutation algorithm was used in all analyses and the sum of lines and columns was fixed (algorithm SIM 9; Gotelli 2000).

Statistical differences between observed and simulated indexes were considered at $\alpha<0.05$. Non-significant C-scores suggest random patterns of species co-occurrence. A significant negative C-score means that species are co-occurring more often than expected by chance, which happens when species are positively associated, e.g. aggregated (Stone and Roberts 1992). On the other hand, a significant positive C-score indicates a lower number of co-occurring pairs than expected by chance, which occurs when species are negatively associated, e.g. segregated (Gotelli and McCabe 2002).

When the C-score analysis indicated non-random patterns of co-occurrence, the species pairs that contributed to produce such pattern were identified. The criteria of identification considered significant all species pairs with number of checkerboards units within the 95° percentile, analyzing the distribution of all possible species combinations.

To compare the degree of assemblage organization among hydrological phases, the standardized C-score was used (SES: standardized size effect). The SES measures the number of standard deviations in which the observed C-score is above or below the mean simulated index (Gotelli and McCabe 2002; Sanders et al. 2003). The standardized C-score measures the degree of non-randomness of assemblage organization, in this case, if fish assemblages of each hydrological phase tend toward segregation or aggregation. Finally, we evaluated the relationship between the standardized C-score and lagoon mean depth through Pearson correlation test.

Results

Lagoon depth showed a quadratic trend along the hydrological phases. It decreased progressively during isolation and reached the lowest value in Phase 3 (Table 1). In subsequent phases, lagoons became progressively deeper. Abiotic conditions in lagoons showed weak variation along the phases (Table 2), and none reached extreme values during the period.

During the study period 54 fish species were captured, summing 8,674 individuals in 139 samples. Twenty one species comprised approximately 98% of the total abundance (Table 3). The list with all captured species and their respective taxonomic position are presented by Okada et al. (2003).

Differently to what our hypothesis predicted, mean species richness in the patches did not decrease along the phases (Fig. 2a). During phases of isolation, richness increased until Phase 3, when it started to decrease. Multiple regression analysis showed that species richness correlated significantly with fish density and habitat depth (R^2=0.33; F=33.20; P< 0.001). Habitat depth showed a negative correlation with richness (β=−0.012; t=−2.49; P<0.01), because it progressively decreased from Phase 1 to Phase 3, when habitats started to become deeper (Table 1). Fish density was positively correlated with richness (β=0.017; t=6.27; P<0.001), and showed the same trend along the phases (Fig. 2b). After controlling for effects of abundance and depth on richness, regression residuals showed a trend similar to species richness along the phases (Fig. 2c).

We considered only the first axis of CA for further analysis, which explained 24.6% of data variability. Similarly to fish richness and density, patterns of species composition (CA scores) showed a nonlinear trend along the phases (Fig. 2d). Composition changed progressively until Phase 4, when similarity between Phase 5 and initial phases increased. Ordination scores were positively correlated with habitat depth ($F_{1;48}$= 11.20; P= 0.002; R= 0.44).

We observed random patterns of species co-occurrence in the phases 1 (C-score=3.82; P= 0.141), 2 (C-score=22.29; P=0.205), 3 (C-score= 21.22; P=0.248) and 4 (C-score=14.30; P=0.189). In Phase 5, a non-random pattern of species co-occurrence was observed (C-score=14.12; P=0.033), indicating a trend of negative association among species. In this case, from 240 possible combinations, only seven species pairs presented a number of checkerboard units within the 95° percentile (Table 4), which influenced the observed C-score. The highest number of checkerboard units was observed between the piscivore *Hoplias malabaricus* (Table 5), and some small-sized fish, what suggests predatory effects. In addition, a high number of checkerboards was also observed among piscivorous species (Table 4), such as *Acestrorhynchus lacustris* against *Cichlasoma paranaense* and *H. malabaricus* (Table 5), suggesting possible competitive interactions.

The standardized C-score (SES) indicated the trend in assemblage organization along the hydrological cycle (Fig. 3). Somewhat similar to what we initially hypothesized (increasing segregation patterns during isolation), significant segregation occurred only in the last phase (Fig. 3). Similarly to fish richness, the degree of assemblage organization was closely associated with mean habitat depth (R=0.86; P<0.05).

Discussion

The present study considered the hypothesis that fish assemblages confined to floodplain lagoons should become progressively more organized between seasonal flooding events. As habitats become spatially reduced, the contact among species may intensify and/or harsh abiotic conditions may develop; in either case, some species may go locally extinct, creating patterns of species segregation. At first, results seemed to support our hypothesis. After disturbance (flood), aggregation increased progressively until the phase of lower depth, when an intense clumping of individuals occurred, as evidenced by fish density data. Theoretically, it should intensify exclusion processes through biotic (competition and predation) and abiotic interactions. In the last phase, a significant negative co-occurrence pattern was observed, and *H. malabaricus*, a voracious predator, showed a high number of checkerboard units with small-sized species. Because these fish (predator and preys) are usually found together in shallow vegetated shores (Table 5), a checkerboard distribution suggests that predation may have a role determining the distribution of small preys during isolation. Some studies and experiments have reported strong effects of *H. malabaricus* upon the spatial distribution and popu-

Table 2 Abiotic conditions in lagoon patches along the phases, measured as mean values (±SD) of temperature (°C), oxygen ($mg \cdot L^{-1}$), pH and conductivity ($\mu S \cdot cm^{-1}$)

Phases	Temperature	Oxygen	pH	Conductivity
1	23.38 (1.12)	6.35 (1.68)	6.70 (0.2)	50.84 (13.15)
2	20.21 (1.92)	5.91 (0.94)	6.43 (0.3)	34.17 (13.2)
3	21.52 (0.78)	7.09 (1.11)	6.37 (0.48)	47.44 (33.03)
4	27.70 (1.83)	6.58 (1.44)	6.61 (0.34)	49.22 (16.51)
5	28.13 (1.40)	6.12 (2.19)	6.81 (0.52)	49.22 (13.32)

lation structure of small-sized fish in tropical streams (Fraser and Gilliam 1992; Gilliam et al. 1993; Fraser et al. 2006). However, other results indicated that biotic/abiotic stressors may not be the main causes behind the temporal organization of fish assemblages in the studied lagoons.

The lagoon environment did not reach critical abiotic conditions during the study period, which could limit the permanence of some fish species (Jackson et al. 2001). In this case, lethal levels of oxygen and temperature, for example, were not observed during isolation. In addition, species richness and fish density did not decrease along the phases as previously hypothesized, and showed a negative quadratic relationship with time. These attributes related negatively to lagoon depth, indicating a sequential clumping and dilution of individuals within patches; a likely result of retraction and expansion of habitat size. For example, in the phase of full connectivity and higher depth (Phase 1), we observed the lowest species richness and fish density. With water retraction (Phase 2–3), fish individuals were obligatorily condensed into the patches. Next, with the subsequent increase in depth (Phase 4–5), it is likely that species had opportunities to disperse within lagoons, creating organization patterns toward segregation. In this case, however, the most probable mechanisms that led to segregation was habitat selection (Peres-Neto 2004), differences in the ability to disperse (Schluter 1984; Bradley and Bradley 1985; Peres-Neto et al. 2001), or random movements of fishes among patches (Syms and Jones 2000; Arrington et al. 2005). This idea was even more evident when we analyzed patterns of

Table 3 Most abundant fish species collected in isolated lagoons of the upper Paraná River floodplain, their frequency of occurrence (FO (%)) in the 139 samples, and mean density within patches (coefficient of variation; CV)

Species	Total abundance	FO (%)	Mean density (ind./patch)[a]	CV (%)
Astyanax altiparanae	1,945	74.10	14.85	146.96
Steindachnerina insculpta	1,222	61.15	9.64	197.84
Roeboides descalvadensis	949	46.76	8.49	284.02
Prochilodus lineatus	864	51.80	8.34	278.69
Loricariichthys platymetopon	670	53.96	19.15	235.38
Moenkhausia aff. *intermedia*	615	46.04	4.65	282.34
Hoplosternum littorale	501	28.78	34.33	370.96
Hoplias aff. malabaricus	415	57.55	32.85	187.89
Astyanax schubarti	339	33.81	2.58	265.94
Acestrorhynchus lacustris	231	41.01	2.47	226.83
Cichlasoma paranaense	141	33.09	8.12	265.17
Leporinus obtusidens	125	26.62	1.04	309.51
Schizodon borellii	99	21.58	0.91	331.00
Cyphocharax modestus	82	15.83	1.96	379.77
Satanoperca pappaterra	73	20.14	3.84	258.08
Serrasalmus maculatus	70	23.74	0.58	234.05
Cyphocharax nagelii	44	14.39	0.93	309.24
Laetacara sp.	32	14.39	0.43	280.38
Hyphessobrycon eques	30	13.67	0.50	585.61
Pimelodella gracilis	29	10.79	0.47	453.01
Serrapinnus notomelas	27	12.95	0.72	224.33

[a] Density values were corrected following the model proposed by Bayley and Herendeen (2000)

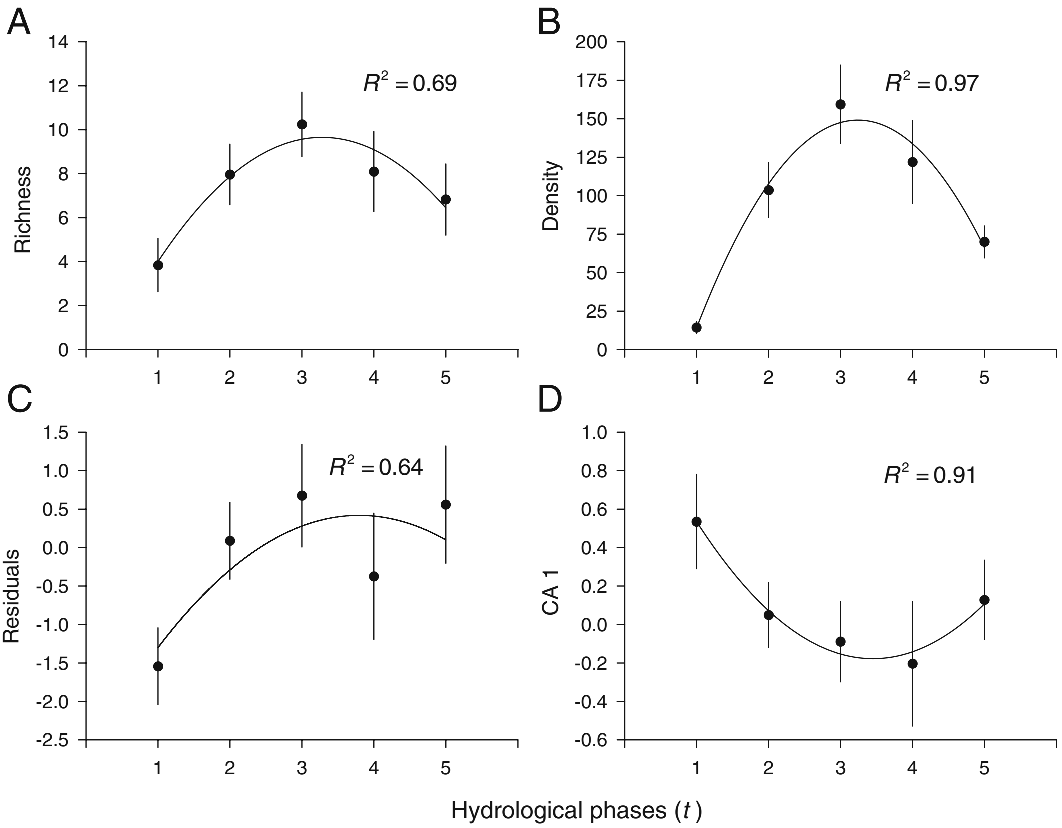

Fig. 2 Trends (mean ± standard error) in species richness (**a**), fish density (**b**), regression residuals (fish richness regressed against fish density and depth; **c**) and CA scores (**d**) in the littoral zone of marginal lagoons, in relation to phases of the hydrological cycle. The polynomial curve describing these relationships was fitted to mean values of richness, density and residuals of each phase, using the Gauss-Newton estimation method ($Richness = -2.04 + 7.13\,(t) - 1.08\,(t)^2$; $Density = -132.92 + 174.02\,(t) - 26.84\,(t)^2$; $Residuals = -2.75 + 1.67\,(t) - 0.22\,(t)^2$; $CA\ 1 = 1.22 - 0.81\,(t) + 0.12\,(t)^2$). Density values are estimates obtained after correcting for seine efficiency (Bayley and Herendeen 2000)

species composition along the phases. In this case, composition in the pre-disturbance phase tended to converge to the structure observed in the period of full connectivity, even though immigration events were absent during isolation. So, our data suggest that changes in composition are unrelated to local extinctions and reductions in richness at the patch scale. Differences in assemblage structure along the phases are probably related to sequential episodes of clumping/dilution of organisms.

Table 4 Species pairs that contributed to the highest checkerboard units (within the 95° percentile) in Phase 5. The mean number of checkerboard units (observed C-score) in this phase was 14.12

	Cichlasoma paranaense	*Hoplias aff. malabaricus*	*Moenkhausia aff. intermedia*
Acestrorhyncus lacustris	36	36	–
Astyanax schubarti	–	36	–
Serrapinus notomelas	–	39	–
Hyphessobrycon eques	–	–	48
Laetacara sp.	–	44	–
Roeboides descalvadensis	–	45	–

Table 5 Ecological aspects of fish species that created checkerboard distributions in Phase 5

Species	Ls (cm)	Trophic guild	Habitat preference
A. lacustris	11.8 (5.6–24.7)	Piscivore	open water–surface
C. paranaense	5.1 (1.2–10.5)	Piscivore	vegetated shores–bottom
H. malabaricus	13.3 (3.9–32.7)	Piscivore	vegetated shores–bottom
A. schubarti	4.7 (2.2–6.9)	Herbivore	open water–vegetated shores
S. notomelas	3.1 (2.3–3.4)	Algivore	vegetated shores
H. eques	2.9 (1.3–4.0)	Invertivore	vegetated shores
Laetacara sp.	2.9 (0.42–5.0)	Invertivore	vegetated shores–bottom
R. descalvadensis	4.7 (1.1–8.5)	Invertivore	vegetated shores
M. intermedia	4.8 (1.6–6.2)	Invertivore	open water–vegetated shores

Information on trophic guilds and habitat preferences were obtained from Machado-Allison (1990), Casatti et al. (2003), Petry et al. (2003), Suzuki et al. (2004), Hahn et al. (2004), Pelicice and Agostinho (2006), and field observations. Ls = mean standard length (min.–max.)

In addition, the only non-random co-occurrence pattern (Phase 5) was remarkably influenced by rare species in number and occurrence (*Laetacara* sp., *Serrapinus notomelas*, *Hyphessobrycon eques*, *C. paranaense*; Table 3), and by species geographically segregated across sampled lagoons and islands (restricted to Mutum Island: *S. Notomelas*, *A. lacustris* and *Hoplosternum litoralle*; rare in Mutum lagoon: *Moenkhausia intermedia* and *Astyanax schubarti*). Peres-Neto (2004) stressed that rare species and those geographically segregated may inflate the number of checkerboard units and create spurious non-random patterns. Relationships suggesting strong biotic interaction, such as *H. malabaricus* (predator) versus *Roeboides descalvadensis* and *A. schubarti* (small preys), also seemed influenced by geographic distribution before isolation. These species are widespread in many environments of the floodplain, but *R. paranensis* and *A. schubarti* were absent and rare, respectively, in Mutum lagoon over the study period. Similarly, competitive interactions, as suggested by checkerboard distributions among piscivores, may not be the case; these species do not overlap in microhabitat use. *Acestrorhynchus lacustris* shows preference for open water habitats, whereas *H. malabaricus* and *C. paranaense* live in close association with aquatic macrophytes or bottom structures (Table 5). Therefore, it is very likely that the negative co-occurrence pattern observed during the pre-disturbance phase resulted from the past biotic drift before isolation, the distribution of rare species, plus differences in habitat preference.

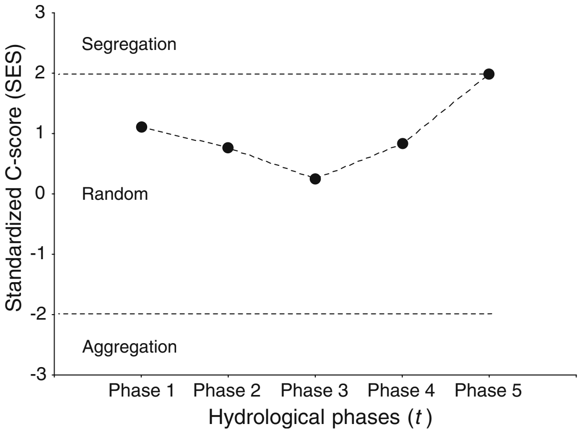

Fig. 3 Standardized C-score (SES) indicating the level of organization (random, aggregation and segregation) of fish assemblages throughout the hydrological cycle

It is worth noting, however, that environmental conditions of lagoons prevented an adequate test of our hypothesis. In the case, lagoons remained isolated for more than 9 months, but they did not experience prolonged desiccation; a basic assumption to investigate the raised hypothesis. In fact, mean depth of lagoons began to increase approximately 4 months before the surface connection with the Paraná River, a phenomenon in close association to variations in the hydrometric level and rainfall (Fig. 1). As a consequence, lagoons did not develop harsh abiotic conditions, and strong biotic interactions probably prevailed during a short period among seasons. Our results, therefore, cannot decisively support nor reject the hypothesis of progressive organization, since lagoons diverged from the expected desiccating trend. We presume that such hypothesis can be tested when the seasonal hydrological regime is modified, as a result of flow regulation by dams (Piana et al. 2006; Pompeu and Godinho 2006) or during years of severe drought (Magalhães et al. 2007). In addition, it can be investigated in other floodplain environments, such as drying ponds or lagoons permanently disconnected. These water bodies may significantly dry out, and predation pressure, competition for space or limiting abiotic conditions may prevent the permanence of some species (Okada et al. 2003).

Apart from hypothesis testing, the present results suggest that other factors interrupt successional dynamics in marginal lagoons prior to surface connectivity. Although the concept of hydrological flood pulse is based on surface floods as the major force (Junk et al. 1989), connectivity in some environments may start earlier from other sources, such as rainfall and infiltration of groundwater (Tockner et al. 2000; Malard et al. 2002). River-floodplain systems can be considered as “pulsing” systems (Ward et al. 1999; Tockner et al. 2000; Malard et al. 2002), with contraction phases and hydrological expansions. For instance, Tockner et al. (2000) classified the hydrological connectivity between the Danube River and its floodplain into three phases, each associated to different ecological processes: (1) disconnected phase, (2) connected phase by water infiltration, and (3) phase of surface connection. In the Upper Paraná River floodplain, groundwater may create lagoons or expand those desiccated in periods that precede floods (Souza Filho and Stevaux 2004). The rising waters after 4 months of isolation illustrates this process, an event that influences the amount and quality of habitats, may redistribute fish assemblages, and mediate the strength of biotic interactions and stressful abiotic conditions.

Our data, therefore, suggest minimal changes in fish assemblage organization in these lagoons during the isolation period; changes observed are probably related to sequential episodes of clumping/dilution of organisms within patches. This natural hydrological regime may have a role in maintaining fish diversity in floodplain lagoons along the seasons, since desiccation is shortly reversed. As a consequence, the hydrological regime as a whole, along with the isolation processes at the local scale, must be invoked to explain the temporal organization of fish assemblages in these environments.

Acknowledgements The authors are especially indebted to Edson K. Okada, which kindly supplied all data analyzed in the present study. The authors also thank PEA, NUPELIA and Maringá State University for providing ideal conditions and logistical support. CNPq provided a scholarship for the first author.

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