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Hydrological connectivity in coastal inland systems: lessons from a Neotropical fish metacommunity

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Abstract – We assessed the influence of hydrological connectivity in structuring fish communities through seasonal samplings of environmental variables and fishes in a coastal lagoon and associated pools in the Restinga de Jurubatiba National Park, Brazil. Community structure attributes such as species richness, numerical density and biomass, Shannon–Wiener diversity index and evenness were compared between periods of the lowest and highest hydrological connectivity, while the environmental gradient and fish zonation were explored through ordination techniques. The greater hydrological connectivity established in the rainy season promoted the homogenisation of most environmental variables and fish species, which differed markedly from the arrangement observed in the dry season. Despite variation in fish species composition, community attributes showed non-significant differences between the dry and rainy seasons. The patterns of composition and numerical density in pools were strongly influenced by local factors, especially salinity, dissolved oxygen, total phosphorous concentration and water colour in the dry season, in addition to total nitrogen concentration and depth in the rainy season. Comparable to the role played by flood pulses in river-floodplain systems, the hydrological connectivity in these tropical coastal waterbodies seems to strongly influence fish community structure, and, therefore to determine regional biodiversity.

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Key words: Neotropical fishes; fish community structure; hydrological connectivity; coastal lagoons; metacommunity

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Introduction

The search for an understanding of the dynamic aspects of biological communities in the last decades of the 20th century resulted in the metacommunity concept. Metacommunities are defined as arrangements of communities interconnected by the dispersal of species that potentially interact. In continental aquatic ecosystems, the habitat characteristics and the displacement of organisms in a metacommunity depend on the patterns of hydrological connectivity at various temporal and spatial scales (e.g., daily, monthly, yearly; within or between catchments). Hydrological connectivity is defined as the water-mediated transfer of matter, energy and/or organisms within or between elements of the hydrological cycle (Heiler et al. 1995; Pringle 2003). This concept has been applied as an important conceptual tool at the level of populations, communities and ecosystems in river-floodplain systems worldwide (Amoros & Roux 1988; Petry et al. 2003; Gubiani et al. 2007; Lasne et al. 2007). Generally, these studies have focused on the effects of reduction, extirpation and to a lesser extent, the reestablishment of hydrological connectivity by restoration of flow, especially on fish communities inhabiting floodplains near medium- to large-sized rivers (Okada et al. 2003; Cucherousset et al. 2007). The intensity and duration of hydrological connectivity

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can strongly affect the chemical, physical and biological characteristics of the aquatic environment. Recently, Thomaz et al. (2007) evidenced the role of the main river flood pulses in increasing the similarity of dissolved nutrients (e.g., nitrogen and phosphorous) and chlorophyll-*a* concentrations among Neotropical aquatic habitats.

The great range of hydrological connectivity within South American riverine systems and the seasonality in flooding regimes (especially the tropical ones) stimulated the emergence of concepts such as the Flood Pulse Concept (FPC) (Junk et al. 1989; Neiff 1990). Since the 1990s, the FPC has been widely used as a mechanistic framework for the understanding of how biological processes of riverine ecosystems are affected by the seasonal establishment of hydrological connections during flood events. For productive tropical South American coastal lagoons and nearby aquatic environments such as swamps and pools, however, there is an additional gradient of salinity associated with a specific fish fauna. The flood pulse in these nonriver-associated ecosystems is regulated by the seasonality in the rainfall regime. Although close to the sea, they represent the limits of distribution for several freshwater species that differ greatly in physiological and ecological aspects such as salinity tolerance, which is largely perceived as being related to geographical distribution and taxonomy (Myers 1938; Araújo & Azevedo 2001; de Pinna 2006).

In a seminal work dealing with the biogeography of American fishes, Myers (1938) provided a conceptual framework for the distribution of freshwater fish fauna based on their physiological tolerances to salt water. As that work, freshwater fishes have traditionally been split into three distinct divisions (Myers 1938; de Pinna 2006). Species of the peripheral division typically live in the marine environment, but use the shallow, warm, brackish waters of coastal lagoons and estuaries for feeding, reproduction or as refuges against predators, such as larger fish and marine birds. Although usually restricted to fresh water, fishes of the secondary division are capable of tolerating the salinity of coastal waters for variable amounts of time. In South America, fishes of the secondary division are mainly those of the families Synbranchidae and Cichlidae, and the order Cyprinodontiformes (Myers 1938). Myers hypothesised that the tolerance to higher levels of salinity of fishes of the secondary division is somehow related to their marine ancestry. Alternatively, fishes of the primary division share an inability to survive in marine or even estuarine environments. Therefore, they are strictly confined to fresh water. In South America, fishes of the primary division are those of the Lepidosirenidae and Ostariophysi (Myers 1938), which exhibit an evolutionary history strongly associated with the events of origin and isolation of catchments (Garcia et al. 2003; de Pinna 2006).

Worldwide, coastal ecosystems are strongly threatened by urbanisation and contamination by industrial and domestic sewage (Gelwick et al. 2001; Lorenz & Serafy 2006). In Brazil, the history of settlement and coastal urban development in the last 200 years has contributed to sharp reductions in waterbody surface area (e.g., lagoons, pools and swamps) on the plains of the restingas (bushy vegetation in sand soil) and the surrounding Atlantic forest (for more details, see Dean 1995). These changes in connectivity patterns could be problematic for freshwater biota as the establishment and occurrence of certain species in the community depends on the hydrological cycle (Chase 2007). The richness of fish species in coastal ecosystems in the Neotropics is relatively low compared to that found in waterbodies of similar size and morphometry in floodplains associated with medium- to large-sized rivers (Gelwick et al. 2001; Hollanda-Carvalho et al. 2003; Okada et al. 2003). Among the several factors related to this pattern are the recent geological history of coastal ecosystems, which are not older than 10 000 years, and their harsh environmental conditions, such as drought, extreme temperatures and the influence of sea water. However, the regional diversity may surpass the attested low local richness and mediate species turnover among environments despite differences in the historical distribution, physiological tolerance and environmental requirements of the ichthyofauna. Hydrological connectivity plays an important role in the process of displacement and occupation of the organisms, and thus in the maintenance of regional diversity. These predictions are supported by studies in river-floodplain systems (Gelwick et al. 2001; Damschen et al. 2006; Lasne et al. 2007). However, their effectiveness in coastal ecosystems has never been tested.

This study specifically assesses the influence of hydrological connectivity in fish communities of the Restinga de Jurubatiba National Park, southeastern Brazil. In this system, intense rainfall in summer results in the establishment of higher levels of hydrological connectivity among aquatic environments. Fish communities are dominated by several small-sized and sedentary fish species that differ in their habitat preferences and environmental tolerances, but whose ecological cycles seem to be synchronised with seasonal hydrological events. Our main goal is to evaluate whether the establishment of higher hydrological connectivity (i) promotes the homogenisation of physicochemical characteristics and (ii) increases the similarity of the fish communities among the aquatic environments on the restinga.

Material and methods

Study area

In Rio de Janeiro State, a 14 860-ha mosaic consisting of terrestrial and aquatic ecosystems was established in 1998 as the sole Conservation Unit in Brazil protecting a 'restinga' ecosystem. That Conservation Unit was named the Restinga de Jurubatiba National Park. Approximately 20 lagoons that differ widely in morphometry, physicochemical characteristics and biotic composition are located along a 40-km sandy strip in the Park (Farjalla et al. 2002; Hollanda-Carvalho et al. 2003). From the late-autumn until spring, each lagoon is surrounded by about 30 associated water pools.

The Piripiri lagoon (22°12′08″S; 41°27′53″N) is isolated from the ocean by a sand bar with a width of approximately 30 m, and sea water intakes occur when stormy winds blow from the ocean to the shore, mainly between June and November. The lagoon has an intermediate surface area when compared to other lagoons of the Park (about 1.17 km^2; c.f. Hollanda-Carvalho et al. 2003). Surface area contraction due to desiccation occurs in the dry season from April to September, and expansion of almost twofold occurs with the increase in rainfall in the rainy season, which lasts from October to March. The rainy season also accounts for the highest temperatures.

In August 2006, during the dry season, seven discrete entities with surface areas ranging from 0.19 to 214 m^2, herein called pools and two sampling sites in the main waterbody of Piripiri lagoon, herein called lagoon (Fig. 1) were randomly chosen and sampled. Four plastic stakes 2 m high were attached on the edge of each sampling unit to estimate the surface area and to easily identify the locations during the sampling in the rainy season, in February 2007. At this time, the rise of water levels connected almost all lagoon sampling sites and pools.

In the study region, the climate is warm and humid, with a mean annual temperature of 26.6 °C. The regional rainfall showed pronounced inter-annual variation during the study period. Nevertheless, the sampling in the dry season reflected the minimum annual hydrological connectivity (Fig. 2a). This was caused by the lowest pluviometric index in July, which was slightly larger than the historical average. Consequently, while lagoon 1 and 2 were water-linked to one another, pools were hydrologically disconnected, representing discrete entities. The rainfall in January 2007 exceeded by 10 times the monthly average of the last decade (Fig. 2b). Therefore, the sampling during the rainy season coincided with the maximum annual hydrological connectivity of the system when all sampling sites were completely interconnected, with the exception of pool 9, which remained hydrologically disconnected. Hydrological connectivity varies either between or within seasons, considering that even in the dry season some sampling sites were connected, while others remained disconnected during the flood pulse (see Fig. 1).

Sampling

Four environmental variables (temperature, °C; dissolved oxygen, $mg \cdot l^{-1}$; depth, cm; salinity, ppt) were registered before fish sampling. Water samples were sent to NUPEM (Federal University of Rio de Janeiro) to determine nutrient concentrations (N_{total}, $\mu mol \cdot l^{-1}$; P_{total}, $\mu g \cdot l^{-1}$) and the amount of dissolved humic substances (water colour, nondimensional). A seine net (50 m long, 0.5-cm mesh) was used to enclose the sampling area delimited by the plastic stakes to block fish passage. Inside the sampling area, fish were collected by seine nets and sieves until five successive sweeps resulted in no additional individuals captured. All individuals were identified to species level and weighed (g). In order to avoid problems related to differences in surface area among sampling sites, fish number and weight were expressed as numerical and biomass density [respectively, number of individuals captured in 100 m^{-2} and total weight (g) in 100 m^{-2}].

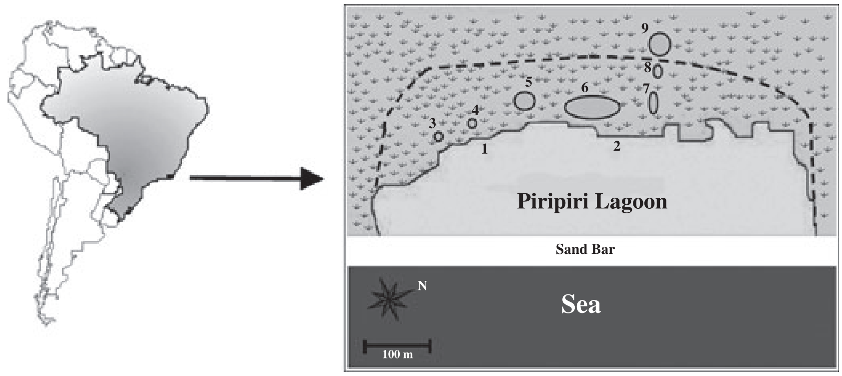

Fig. 1. Schematic representation of sampling sites in the dry season in a complex of coastal lagoon (1–2) and associated pools (3–9) in the Restinga de Jurubatiba National Park. Connected waterbodies in the rainy season are enclosed by the broken line.

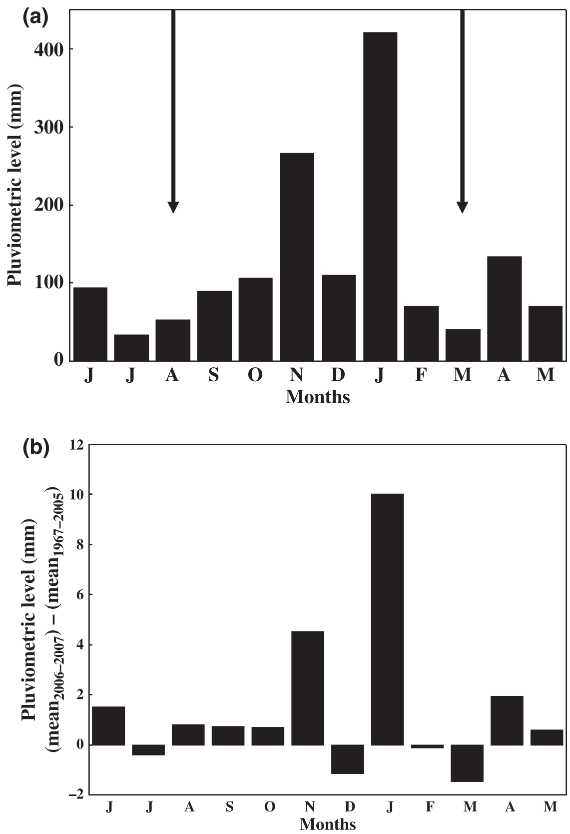

Fig. 2. Monthly variation of regional pluviosity during the period of study (2006 and 2007) (a) and the difference between monthly mean in 2006 and 2007 and the last decades (1967–2005) (b). Arrows indicate the samplings in August 2006 and February 2007. Data supplied by Quissamã Metereological Station.

All variables were log transformed ($\log_{10} x + 1$) to control for the effect of extreme values.

Data analysis

Temporal variation in community structure was tested by paired *t*-test for species richness, numerical density and biomass, Shannon–Wiener diversity index and evenness between the dry and rainy seasons. According to Magurran (1988), these attributes have an empirical value by expressing the ecosystem's well-being. Additionally, they are complementary in the evaluation of how hydrological connectivity influences the fish communities of our study system. Unfortunately, we could not sample pools 7 and 8 in the rainy season due to difficulties in handling the seine nets imposed by the amount of flooded trees and bushes in those areas. Because of this lack of spatial replication, these two sites were excluded from the analysis.

Relationships between fish species composition and numerical density (biotic data) and environmental variables were investigated in a canonical correspondence analysis (CCA) (ter Braak 1986). The CCA is a direct gradient analysis that evaluates how much of the variation in biotic data can be explained by the linear correlations of the physicochemical characteristics. This analysis allows the simultaneous plotting of species and site scores, with environmental variables as arrows. The arrow length indicates the importance of the environmental variable; its direction indicates how well this gradient is correlated with the species composition axes, whereas the angle between arrows indicates the species' environmental preferences (Palmer 1993). In order to determine how hydrological connectivity varies both within a season (spatial scale) and between seasons (temporal scale), we performed separate CCAs for the data matrices of the dry and rainy seasons. Due to methodological limitations imposed by the number of columns of the second matrix, which is larger than the number of lines of the main matrix of CCA, we excluded the temperature, considering its low variation among waterbodies over time.

The statistical significance of the correlations between physicochemical characteristics and biotic variables extracted from the CCA was determined by the Monte–Carlo test, based on 999 permutations. Univariate and multivariate statistical analyses were performed using Statistica™ and PC-Ord, respectively (McCune & Mefford 1999; Statsoft, Inc. 2007). Assumptions of normality (Shapiro-Wilk) and homoscedasticity (Levene) were achieved for the *t*-test, and the level of significance was set at $P < 0.05$.

Results

Environmental patterns

The spatial arrangement of the aquatic environments in the Piripiri system revealed strong differences between the dry and rainy seasons for most of the environmental variables (Fig. 3). Isolated sampling sites closer to the Piripiri lagoon were characterised by oxygenated and brackish to salty waters (pools 3 and 4; 0–8 m from the edge; >3.8 $mg \cdot l^{-1}$; 14.1–23.6 ppt, respectively). The pools most distant from the Piripiri lagoon (pools 5–9; 25–190 m from the edge) are dark coloured, freshwater (<0.4 ppt), and have higher concentrations of P_{total} (Figs 1 and 3, dry season). The flood pulse that enhances the hydrological connectivity among sites in the rainy season promoted the homogenisation of most variables, especially salinity. Higher levels of rainfall in the summer of 2007 probably promoted a dilution effect on the aquatic environments. However, it was insufficient to buffer the spatial gradient of water colour (Figs 1 and 3, rainy season), which is more related to occasional

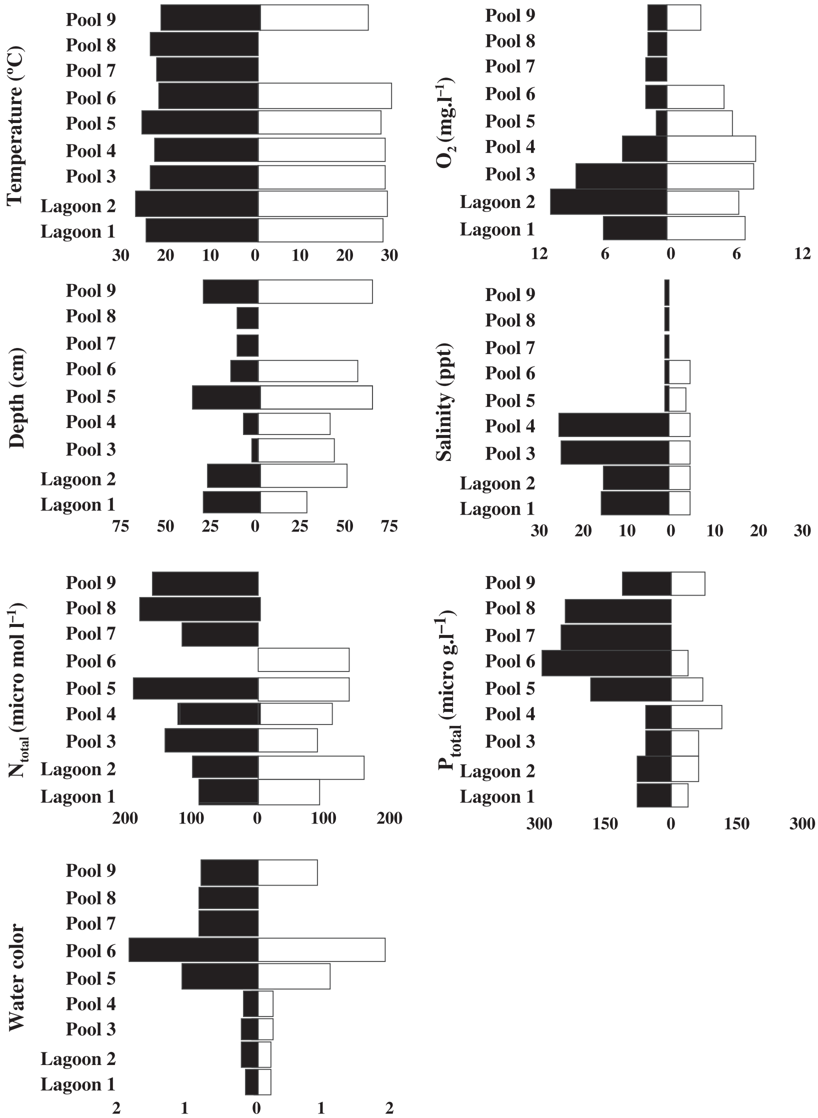

Fig. 3. Environmental variables of the sampling sites [temperature (°C), oxygen (mg·l^{-1}), N_{total} (μmol·l^{-1}), P_{total} (μg·l^{-1}), depth (m), salinity (ppt), colour] in dry (black bars, left) and rainy (white bars, right) seasons, in a complex of coastal lagoon and associated pools in the Restinga de Jurubatiba National Park. Pools 7 and 8 were not sampled in the rainy season.

inputs of fresh-humic waters from the water table. The lowest values of N_{total}, temperature, dissolved oxygen and salinity in the rainy season were registered in pool 9, which is located about 190 m from Piripiri lagoon. This farthest site from the Piripiri lagoon was the only one that was hydrologically disconnected during both seasons (Figs 1 and 3).

Fish patterns

A total of 11 species of fishes were recorded in the nine sampling sites. Bionomical aspects were strongly related to the species distribution patterns in the spatial gradient, especially during the dry season. *Atherinella brasiliensis*, which is a species of the peripheral division of Myers (1938), was restricted to lagoons 1 and 2, which in turn are the sites closest to the ocean among the waterbodies sampled (Fig. 4a). Five species of the secondary division of Myers, namely the cyprinodontids *Jenynsia multidentada*, *Phalloptychus januarius* and *Poecilia vivipara*, the cichlids *Geophagus brasiliensis* and the exotic *Tilapia rendalli*, were captured in sites near the Piripiri lagoon (<35 m) (Fig. 4b). Among those, *P. vivipara* occurred in sites that differed greatly in salinity (0.1–23.6 ppt). Five species of the primary division, the otophysans *Hyphessobrycon bifasciatus*, *H. luetkenii*, *Callichthys callichthys*, *Hoplias malabaricus* and *Hoplerythinus unitaeniatus* were restricted to the sites that did not show any influence of sea water (Figs 3 and 4c). This pattern of relative segregation of fish species, which reflects Myers' divisions, was absent in the rainy season, when *A. brasiliensis*, *G. brasiliensis* and *T. rendalli* dispersed from the lagoon to the aquatic environments of the restinga. Alternatively, higher densities of *H. malabaricus* and *H. bifasciatus* were found in Piripiri lagoon. *Poecilia vivipara* and *H. bifasciatus* were the most frequent species (100%

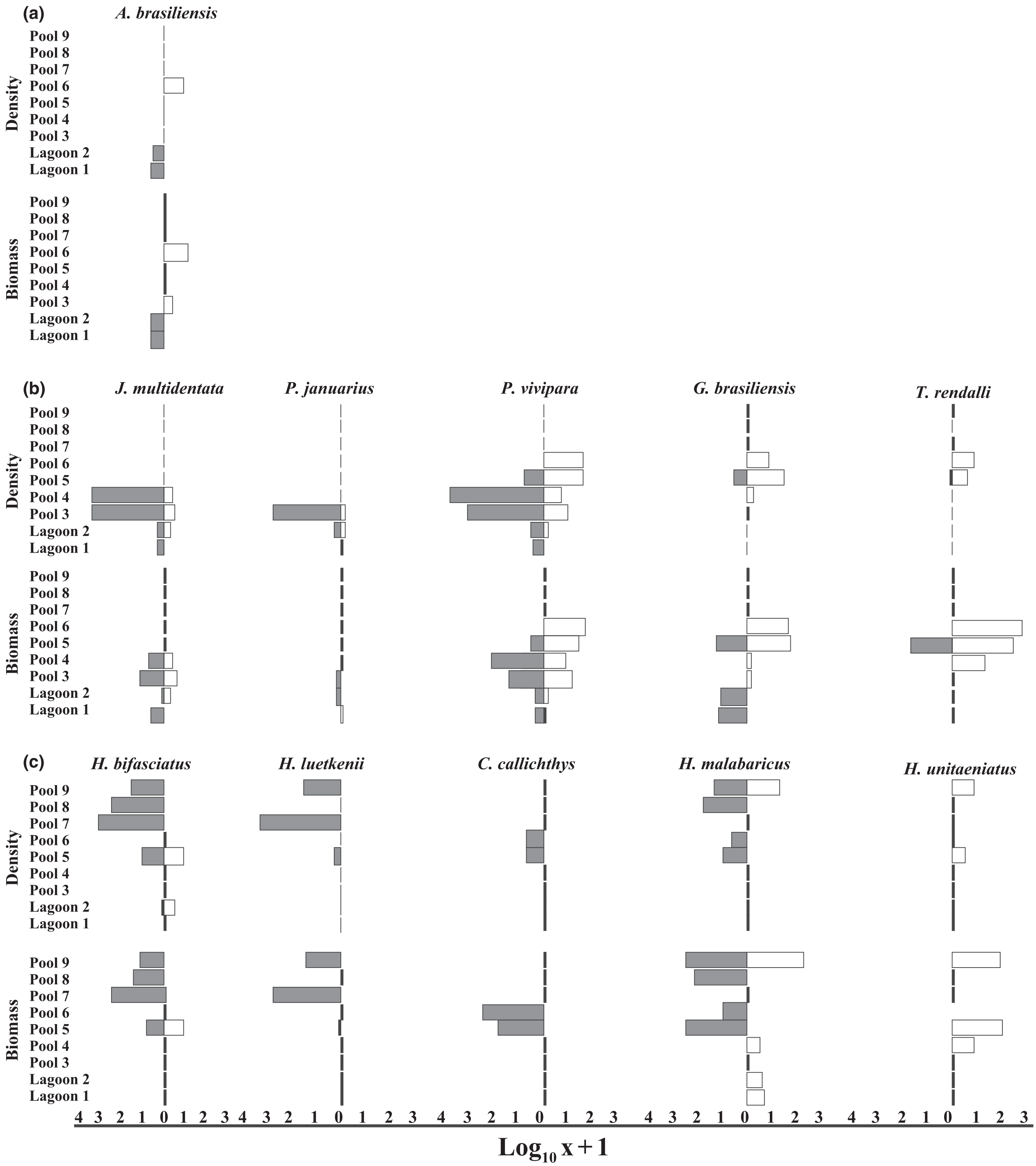

Fig. 4. Numerical density (upper) and biomass (lower) of fish species belonging to peripheral (a), secondary (b) and primary (c) division in dry (black bars, left) and rainy (white bars, right) seasons, in a complex of coastal lagoon and associated pools in the Restinga de Jurubatiba National Park. Pools 7 and 8 were not sampled in the rainy season.

and 82% of samples, respectively) in both seasons, and communities achieving higher species numbers were observed mostly in the rainy season (Fig. 4; Table 1).

The diversity in this metacommunity overall was similar between the dry and rainy seasons (ten and nine species, respectively). On a local scale, however, species number varied greatly among pools compared to the Piripiri lagoon in the dry season, and species from the primary division account for most of this variation (Fig. 4c). Despite the low species numbers of most pools, typically ranging between two and three species, there was a high spatial turnover of species

Table 1. Fish community attributes [species richness (S), numerical (individuals 100 m^{-2}) and biomass (g 100 m^{-2}) density, Shannon's Diversity Index (H') and evenness (E)] in a complex of coastal lagoon and associated pools in the Restinga de Jurubatiba National Park during dry and rainy seasons (mean ± SE) in August 2006 and February 2007 respectively.

		S	Density	Biomass	*H'*	*E*
Lagoon 1	Dry	6	1.77	2.14	1.53	0.85
	Rainy	5	0.89	1.59	1.46	0.90
Lagoon 2	Dry	6	1.81	1.97	1.62	0.91
	Rainy	6	1.46	1.66	1.50	0.84
Pool 3	Dry	3	4.45	2.52	1.10	1.00
	Rainy	5	1.98	2.25	1.03	0.64
Pool 4	Dry	2	5.09	3.10	0.69	1.00
	Rainy	9	1.76	2.63	1.47	0.67
Pool 5	Dry	7	2.49	3.61	1.79	0.92
	Rainy	5	2.96	3.76	1.50	0.93
Pool 6	Dry	2	1.95	3.40	0.68	0.98
	Rainy	4	2.78	3.96	1.35	0.97
Pool 7	Dry	2	4.39	3.85	0.69	1.00
Pool 8	Dry	2	3.45	3.19	0.68	0.99
Pool 9	Dry	3	2.86	3.44	1.10	1.00
	Rainy	2	2.43	3.43	0.67	0.97
	Dry	3.67 ± 2.06	2.14 ± 1.26	2.02 ± 0.66	2.00 ± 0.45	0.99 ± 0.05
	Rainy	5.14 ± 2.12	1.04 ± 0.74	1.75 ± 0.98	1.46 ± 0.32	0.90 ± 0.14

from the primary division among pools. Pool 5 and the sampling sites in Piripiri lagoon registered similar species numbers (seven and six, respectively), but the pool and lagoon differed largely in fish species composition. All five species from the primary division were observed at pool 5, and only *H. bifasciatus* occurred in the Piripiri lagoon (Fig. 4; Table 1). Small-sized with a short, sedentary life cycle, viviparous species such as *P. vivipara* and *J. multidentata*, together with *H. bifasciatus*, composed 80% of the numerical density, but only 7% of the biomass. *Hyphessobrycon bifasciatus* was extremely abundant in the freshwater pools (pools 5, 7, 8 and 9), whereas *P. vivipara* and *J. multidentata* were more abundant in the brackish sites located closer to the lagoon in the dry season (pools 3 and 4) (Fig. 4). When the mean fish densities were compared among sampling sites, all population sizes were at least two times greater in the isolated pools than in the lagoon, with the exception of *G. brasiliensis*. Almost all community attributes were, on average, higher in the dry season (Table 1). However, the greater variability among sites determined the absence of significant differences between the dry and rainy seasons for species richness ($t_6 = -0.38$; $P = 0.72$), numerical density ($t_6 = 1.54$; $P = 0.17$), biomass ($t_6 = 0.88$; $P = 0.41$), Shannon–Wiener diversity index ($t_6 = -0.38$; $P = 0.72$) and evenness ($t_6 = 1.64$; $P = 0.15$) (see SE, Table 1).

A large amount of the variance in the biotic matrix in the dry and rainy seasons was explained by environmental variables on CCA, which are approximately 76% and 92% respectively. The correlations between fish species and physicochemical features were high and significant in the dry and rainy seasons (dry season: first axis $P < 0.01$; rainy season: first three axes $P < 0.01$; tested with 999 permutations). The higher eigenvalue of the CCA axis in the dry season reveals a high degree of correspondence between species and sampling sites and unimodal responses of the species to the long and strong environmental gradient determined by the low hydrological connectivity within this season (Table 2).

In the dry season, the distribution of species and samples formed two main groups along the first CCA axis, one at the left of zero score with the connected and isolated pools, at or near the Piripiri lagoon and another at the right with the isolated pools, determined by salinity, dissolved oxygen, colour and P_{total} (Fig. 5a). A single strong environmental gradient in the dry season, determined by the characteristics mentioned above, influenced the composition of communities by species that are closely related: communities consisting of the cyprinodontiforms *P. januarius*, *J. multidentata*, *P. vivipara* and the atherinopsid *A. brasiliensis* were associated with salty and more oxygenated sites (lagoons 1 and 2, pools 3 and 4). On the other hand, communities located farther from the lagoon were dominated by the otophysans *H. luetkenii, H. bifasciatus* and *H. malabaricus*. Those sites are hypereutrophic, oligohaline and have low levels of dissolved oxygen (pools 5–9). Differently from the dry season, phylogenetic relatedness does not seem to influence species distribution in the rainy season along the first three CCA axes. These were determined mostly by N_{total}, salinity, depth, colour, dissolved oxygen and P_{total} to a lesser extent. More than a single strong environmental gradient determined by the characteristics mentioned above influenced the composition of communities by species in the rainy season. The first three axes of CCA were necessary to encompass most of the variation in species data (Fig. 5b–d). Overall, communities consisting of *A. brasiliensis*, *T. rendalli*, *G. brasiliensis*, *P. vivipara*, *J. multidentata*, *P. januarius* and *H. bifasciatus* were associated with nitrogen rich, salty and shallow hydrologically interconnected sites

Table 2. Results of canonical correspondence analyses of fish communities and physicochemical characteristics in a complex of coastal lagoon and associated pools in the Restinga de Jurubatiba National Park.

	Canonical correspondence dry season			Canonical correspondence rainy season		
	CCA1	CCA2	CCA3	CCA1	CCA2	CCA3
Eigenvalue	0.921	0.470	0.260	0.770	0.310	0.227
Species variance data						
% of explained variance	42.3	21.6	11.9	54.4	21.9	16.0
% cumulative	42.3	63.9	75.9	54.4	76.3	92.3
Monte–Carlo test for eigenvalues (999 permutations)						
Pearson correlation for species – environmental variables	1.000	0.983	0.979	1.000	1.000	1.000
P-value	0.002	0.065	0.139	0.003	0.004	0.005

Eigenvalues obtained after 24th, 17th and 19th iteration, respectivelly for axis 1, 2 and 3 of dry season and after 16 th, 41th and 4th iteration, respectively for axis 1, 2 and 3 of rainy season.

(lagoons 1 and 2, pools 3–6). The community that remained hydrologically disconnected was dominated solely by *H. malabaricus* and *C. callichthys*, which were associated with the deeper and freshwater pool 9 (Fig. 5b and c). Sampling sites' positions along the most important CCA axes (CCA1 and CCA2) evidenced a strong hydrological connectivity effect even between seasons: with the exception of the isolated pool 9, the discrete units of sampling sites placed apart at low hydrological connectivity (dry season) were closer to each other at high hydrological connectivity (rainy season).

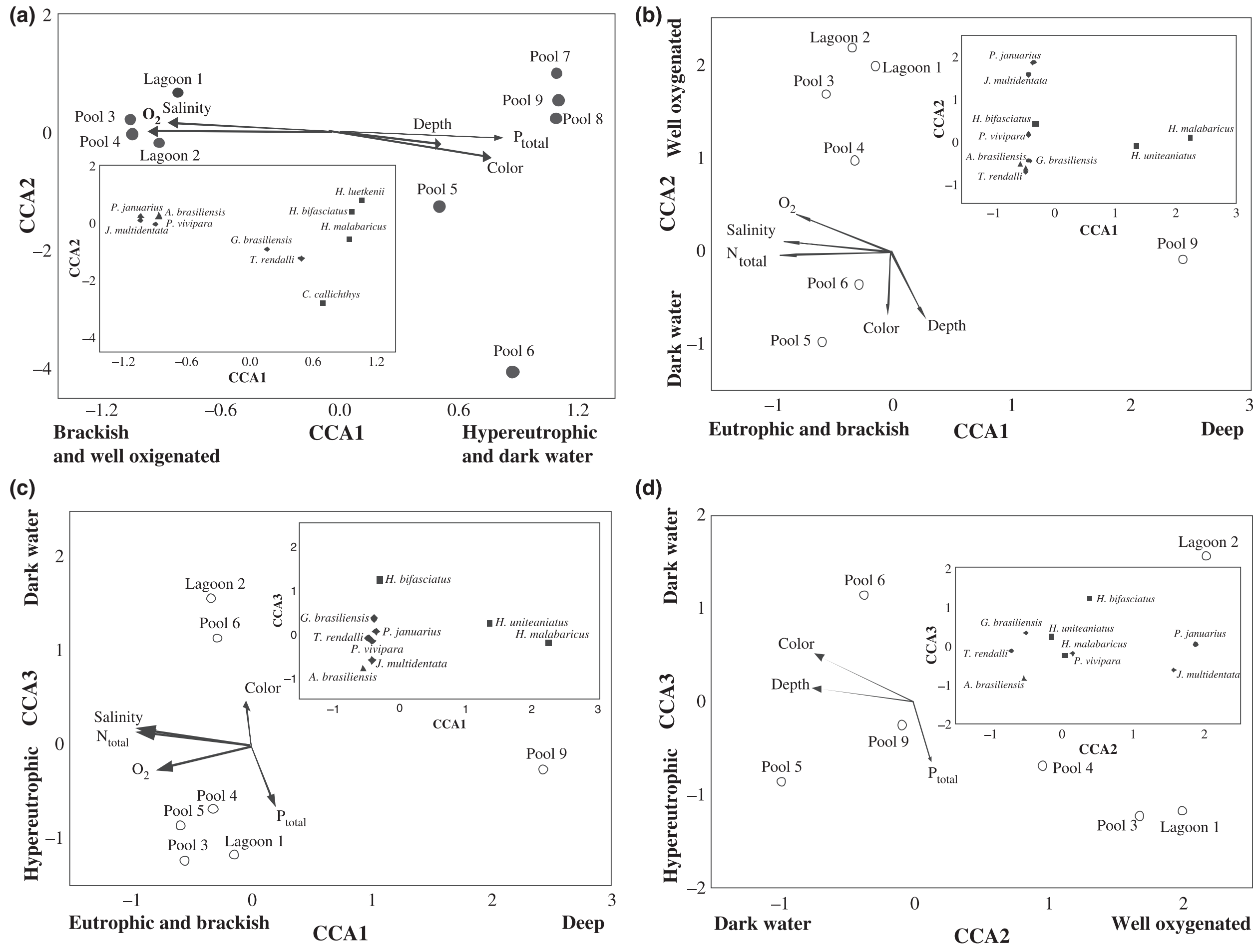

Fig. 5. Ordination of sampling sites in dry (a) and rainy (b, c and d) seasons and fish species [(peripheral (triangle), secondary division (diamond) and primary division (square)] along the axes of the canonical correspondence analysis (CCA) in relation to environmental gradients (arrows) in a complex of coastal lagoon and associated pools in the Restinga de Jurubatiba National Park. Only significant axes (determined by the Monte–Carlo test) and variables with correlation coefficients >0.5 were shown.

Discussion

Environmental patterns

Small-sized and shallow aquatic environments are strongly influenced by local driving factors (*sensu* Thomaz et al. 2007). As a result, the adaptations and life history of the biota may reflect the temporal environmental modifications determined by the seasonal flooding (Capone & Kushlan 1991; Cucherousset et al. 2007; Davey & Kelly 2007). The present study provides evidence that the high hydrological connectivity established during the flood pulse in the rainy season helps to homogenise the biotic and abiotic components of a coastal system previously subjected to local factors in the dry season. The modifications in the physicochemical characteristics with the establishment of hydrological connectivity in our coastal ecosystem are comparable and in accordance with the driving force exerted by flood pulses on tropical floodplains (Junk et al. 1989; Petry et al. 2003; Thomaz et al. 2007).

The establishment of greater hydrological connectivity among the sites in the rainy season buffered the gradients of salinity and dissolved oxygen. In spite of the diluting effect of the flood pulse, some variables, such as water colour, were less temporally affected. In the Restinga de Jurubatiba National Park, the dark waters are rich in dissolved humic substances from degradation processes of autochthonous and allochthonous organic plant matter, such as aquatic macrophytes and surrounding vegetation (Farjalla et al. 2002). Therefore, the poorly vegetated Piripiri lagoon and nearby pools in the dry season were less affected than the most distant pools by the humic substances carried by rain from the restinga towards the lagoon in the rainy season.

Fish patterns

In spatially heterogeneous landscapes such as those investigated in this study, the temporal variability of among-site accessibility and environmental conditions related to hydrological connectivity influences the processes of local extinction and colonisation (Gelwick et al. 2001; Okada et al. 2003; Davey & Kelly 2007; Jocqué et al. 2007), resulting in markedly different community structure (Capone & Kushlan 1991; Cucherousset et al. 2007). This pattern, however, was not observed here due to (i) the permanence of some heterogeneity in limnological conditions among waterbodies even in the rainy season and (ii) the overall dominance of small-sized species in both the rainy and dry seasons.

The low degree of hydrological connection of the aquatic environments promoted spatial heterogeneity and environmental gradients that regulate the fish distribution according to the habitat preference and/or tolerance of each species. Some environmental variables effectively filter out species. The close phylogenetic proximity of the species in the examined sites suggests that the patterns of fish distribution in the dry season are not stochastic (Chase 2007). After the colonisation process throughout the last hydrological connection, the salinity influenced the maintenance of species in the lagoon and associated pools in the Restinga de Jurubatiba National Park. This may explain the high species turnover observed in the dry season. The seasonal isolated sites distant from the lagoon play the role of refuges for species of fishes more sensitive to salinity, such as those of the primary division, in spite of the low concentrations of dissolved oxygen in the water of those isolated sites (*sensu* Magoulick & Kobza 2003). Furthermore, as evidenced by the higher fish density in pools than in the Piripiri lagoon, these peripheral pools allow the persistence of most species within this metacommunity.

Continental aquatic environments subjected to drying episodes are among those with the highest variations in dissolved oxygen concentrations (Okada et al. 2003). Thus, it is not surprising that some species of the primary division of our metacommunity bear morphological and physiological adaptations that maximise survival in harsh environmental conditions during hydrological disconnection (Lytle & Poff 2004). Among these, *H. malabaricus* and *H. unitaeniatus* exhibit physiological acclimation to hypoxia and air breathing, respectively (Driedzic et al. 1978; Rantin et al. 1992). However, the enhancement of hydrological connectivity in the rainy season enables these species to disperse. The biozonation detected in the dry season between the restinga aquatic environments and the lagoon contrasted with the co-occurrence of most fish species in the rainy season. Depending on their dispersal abilities and environmental preferences, fish species could then occupy the recently created environments in the rainy season. Furthermore, they could then reach those pools with the most favourable conditions for survival in the dry season, as suggested by the patterns of distribution of *H. bifasciatus*, *H. malabaricus*, *T. rendalli* and *G. brasiliensis*. The gradient analysis supported the hypothesis that these processes take place in the rainy season in the Piripiri system, when all hydrologically connected sites were more similar in terms of composition of species of fishes. In summary, the greater hydrological connectivity caused by the flood pulse in the rainy season allowed the dispersion of organisms and promoted homogenisation of communities in terms of fish species composition.

The ordinations of species and samples along the environmental gradients evidenced that fish were distributed along a one-dimensional axis in the dry season and multi-dimensional axes in the rainy season. Especially in the dry season, the overall lower local species richness was associated with the tolerance of species that differ markedly in physiological limits imposed mostly by salinity and dissolved oxygen levels. Our results on Piripiri lagoon and associated pools reinforce trends described by other authors concerning the exacerbated effects of these variables in structuring fish communities, even in coastal ecosystems (Gelwick et al. 2001; Garcia et al. 2003; Okada et al. 2003; Lorenz & Serafy 2006). *Atherinella brasiliensis* occurs in costal zones from the north to the southeast of South America (Dyer 2003). This marine species may reach coastal lagoons by larval drift during sea water intrusion events over the continent, which occur with greater intensity in southeastern Brazil between July and October. The sampled cichlids and cyprinodontids species are typical inhabitants of south and southeast Brazilian coastal lagoons (Araújo & Azevedo 2001). They are able to withstand variable conditions of salinity (i.e., eurihaline), while characins, erythrinids and callichthids are more sensitive to the strong salinity gradient (i.e., stenohaline) in the system.

As predicted by MacArthur & Wilson (2001) in the Island Biogeography theory, factors such as the absence of dispersal ways, area and isolation can negatively affect colonisation rates. These factors may have implications for the maintenance of fish populations on the investigated *aquatic islands* of the Restinga de Jurubatiba National Park in the dry season. In that sense, the alterations promoted by global warming in phases of the hydrological cycle reinforce the concern about ecosystems where hydrological connectivity operates as a mechanism of species coexistence. According to recent forecasts, in the upcoming decades, southeast Brazil will experience a decrease in the rainfall indices of 10–20% and the rising of sea level (IPCC 2007). In this sense, scenarios of reductions or even the absence of hydrological connectivity, such as those that might result from prolonged drought, a sequence of unusually dry summers or the rising of marine intrusions, may cause first local and then secondarily regional extinctions. These processes are supposed to have a greater impact on species of fishes of the primary division, such as the Otophysi. Therefore, several diversity components, such as local and regional diversity, can potentially be reduced in the Restinga de Jurubatiba National Park. Recently, a strong positive correlation was found between the importance of seasonal alternation of periods of higher and lower hydrological connectivity and diversity of species of amphibians, which obviously bears on their conservation (McMenamin et al. 2008). Similar trends were confirmed for other groups of plants and animals in terrestrial and aquatic ecosystems (e.g., Capone & Kushlan 1991; Cottenie et al. 2003; Penczak et al. 2004; Adler et al. 2006; Damschen et al. 2006; Cucherousset et al. 2007; Davey & Kelly 2007; Jocqué et al. 2007; Lasne et al. 2007). Thus, the persistence of the several species of fish fauna in this coastal system probably depends on the maintenance of seasonal pulses of hydrological connectivity. As evidenced by the ordination of species and samples, the increase of hydrological connectivity reduces spatial heterogeneity, enables the displacement of individuals and seems to minimise pressures of competition. A decrease of hydrological connectivity, on the other hand, promotes spatial heterogeneity, the recovery of distinctive properties of local habitat features and promotes the assembly of organisms sharing similar physiological tolerances to salt water and life-history strategies.

We are aware of the methodological limits of our pioneer study in these Neotropical coastal waters. Despite the low number of species of fishes in these coastal lagoons and associated pools, studies replicated in space and time are necessary since several aspects of their lifespan, reproductive period and feeding ecology are still or partially unknown. Difficulties in accessibility and the distance between lagoons limited an appropriate replication at the lagoon level. Sampling sites varied largely in surface area and reflect the real complexity of the coastal waterbodies in terms of size. However, the sizes of those discrete waterbodies could not be considered as a quantitative variable in our statistical analysis due to their physical continuity in the rainy season. In order to overcome this limitation, we analysed both the numerical and biomass density of fish species. Despite our efforts, it is possible that this standardisation was insufficient to lessen the effects of the water level rising with the flood pulse on fish community attributes, such as estimation bias. Therefore, this study does not allow generalisations to all similar habitats. Our results are preliminary. Further studies, which should take into account the methodological questions we detected herein, are needed. However, it is also possible that the absence of significant differences between the dry and rainy seasons for all community attributes results from the extended effects of local driving factors over the low regional species diversity, even after the establishment of hydrological connectivity (Cottenie et al. 2003). On the other hand, the gradient analysis highlighted the effects of hydrological connectivity, or the absence thereof, on the metacommunities in either the dry or rainy seasons in our coastal ecosystem.

Despite the limitations of this study, we concluded that the flood pulse influences both spatial, or within season, and temporal, or between season, scales of fish metacommunities in the Piripiri system. That situation is probably caused by variations in the degrees of hydrological connectivity of different waterbodies. As far as we know, this is the first report of influences of flood pulses on aquatic metacommunities in ecosystems other than river-floodplain or lake-floodplain. Therefore, the flood pulse might have a greater influence in aquatic ecosystems than previously hypothesised, and coastal lagoons and their surrounding ponds might be considered alternative ecosystems to test the FPC predictions. We suggest extending this approach to other independent lake-ponds systems to validate the patterns observed here. Furthermore, studies aiming to better identify the influences of local and regional factors on fish metacommunities in these systems are also desired.

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