Intermittently Closed Estuaries and Tadpole Communities: Influence of Artificial Breaching

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Abstract Naturally or mechanically opening the sand bar of intermittently closed estuaries (ICEs) plays an important role in the proper functioning of these systems. In this study, the impacts of artificial breaching of a coastal lagoon on anuran communities (composition, richness, and abundance) were investigated in the Lagoa do Peixe National Park floodplains, southern Brazil, from 2007 to 2009. The sampling period included two lagoon openings and occurred four times when the lagoon was open and four when it was closed. Artificial opening of the lagoon considerably changed the salinity and availability of temporary ponds in the estuary floodplains. Tadpole species richness and abundance were higher in areas influenced by the sand bar opening than in floodplain areas not influenced by this management. Although salinities were higher when the lagoon was open, only species that do not reproduce explosively occurred in significantly lower abundance. Multivariate analyses demonstrated that anuran species composition differed between areas affected and not affected by the lagoon opening. The composition gradient was associated with conductivity, hydroperiod, and floodplain management. These differences likely relate to individual traits of each species (e.g., habitat preference and reproductive mode). The study suggests that amphibian communities in the Peixe lagoon floodplains are resistant to oligohaline conditions when the lagoon is open. However, projected sea level rise and planned increasing drainage of freshwater wetlands could raise the salinity levels in floodplains to polyhaline or even euhaline conditions. Thus, artificially opening the sand bar for fishery management should be done with caution.

Introduction

Estuary opening is an important component of coastal lagoons in many regions throughout the world (Roy et al. 2001; Saad et al. 2002; Elwany et al. 2003). Intermittently closed estuaries (ICEs) are shallow bodies of water (rivers or barrier lagoons) in which connection to the sea is interrupted by a sand bar formed by sediment deposition. Natural reestablishment of connections between these environments and the sea occurs by increased water levels in the estuary or tidal erosion (Parkinson and Stretch 2007; Netto et al. 2012). Introduced salt water can alter chemical and physical processes in the ICE through changes in salinity, habitat availability, and the direction and flow of water and sediments, due to tides (Gobler et al. 2005; Lill et al. 2011; Barendregt and Swarth 2013). Economic interests such as fishing management, flood prevention, and water quality improvement have led to interventions in the natural dynamics of these ecosystems (Gladstone et al. 2006; Netto et al. 2012; Rolon et al. 2013). Changes in aquatic communities in managed estuaries have been attributed to reduced water volume, increased salinity, and resuspension of sediments (Saad et al. 2002; Suzuki et al. 2002; Crippa et al. 2013). However, reported responses to these disturbances depend on the temporal scale of the study and on taxon-specific traits of the resident fauna and flora (Lill et al. 2011).

Hydroperiod is an important structuring factor for amphibian communities in ponds (Both et al. 2009; Karraker and

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Gibbs 2009; Moreira et al. 2010). The timing and duration of pond surface water should coincide with the reproductive period of species so that egg-laying, hatching, larval development, and metamorphosis are successful (Paton and Crouch 2002; Bunnell and Ciraolo 2010). In short-hydroperiod wetlands, amphibian assemblages are depauperate and low species richness is expected because of exclusion of amphibians with slow rates of development (Babbitt et al. 2003). In permanent wetlands, species are generally exposed to a wide variety of potential predators and competitors (Alford 1999; Werner et al. 2007a). Therefore, larval amphibian assemblages found in temporary environments are often distinct from those that utilize permanent aquatic environments. Human-induced changes in the hydroperiod could cause premature drying of intermittent ponds and affect amphibian larval development and metamorphosis (Bunnell and Ciraolo 2010).

In addition to hydroperiod, amphibians with aquatic larvae are also affected by physical and chemical water characteristics (Wilbur et al. 1990; Boone et al. 2007). However, additive or synergistic effects have also been demonstrated in amphibians (Mann et al. 2009). Among water quality variables, negative effects of increased salinity have been documented in amphibians and other organisms that inhabit freshwater environments such as certain plants, invertebrates, fish, and reptiles (Hart et al. 1991; Grosell et al. 2007). Some effects of exposure to elevated salinity include behavioral and physiological modifications (Karraker et al. 2008; Chambers 2011) and changes in growth and survival rates (Sanzo and Hecnar 2006; Snodgrass et al. 2008; Rios-López 2008). Many freshwater organisms are found in tidal freshwater wetlands with <1,000 μS cm^{-1} or ~0.5 salinity (S_P) and in oligohaline wetlands (around 8,000 μS cm^{-1} or ~S_P 5). Amphibians can rapidly colonize newly formed environments (Eterovick and Fernandes 2002; Patrick et al. 2008) and respond to disturbances such as changes in water quality, prolonged drought, or invasion by fish species, and they may move to different reproductive sites (Petranka et al. 2004; Petranka and Holbrook 2006; Haramura 2008). Thus, coastal areas are potential breeding sites for amphibians, which are limited by the salinity pulse. This pulse reflects the proximity of the connection with the sea and physical and hydrodynamic features of the estuary (Mitsch and Gosselink 2000; Mariani 2001).

Lagoa do Peixe National Park contains a variety of terrestrial, estuarine, and marine ecosystems, and it is the only Ramsar site in southern Brazil. The connection between the Peixe lagoon, an important lagoon in the park, and the ocean has been artificially opened at the end of each winter for at least the past 150 years (Knak 2004). The sand bar has been artificially opened to lower the water level of the floodplain, thereby increasing the grazing area for cattle and allowing the entrance of shrimp. Recent studies of the consequences of this opening have focused on plant and invertebrate communities (Crippa et al. 2013; Rolon et al. 2013). However, the impact of this management on amphibian communities is still unknown, in spite of the great attention paid to declining amphibian populations throughout the world over the last two decades (McCallum 2007; Blaustein et al. 2010).

Our study analyzes the influence of an artificially opened sand bar on anuran richness, abundance, and composition in the Peixe lagoon floodplains. Since hydrology and floodplain formations are highly associated with the opening and closing of the sand bar, and amphibian richness and composition are influenced by hydroperiod and salinity, the following hypotheses were tested: (1) anuran richness and abundance are lower in areas where the sand bar is opened due to exposure to higher salinity; (2) sand bar opening raises salinity levels and anuran richness and abundance decrease during periods that the lagoon is open; and (3) areas influenced by sand bar breaching have a different anuran composition than unmanaged areas and are dominated by species with rapid larval development. We sampled tadpoles because they are more sensitive to environmental disturbances than adult amphibians and entirely dependent on aquatic habitat.

Materials and Methods

The study area is located in the Lagoa do Peixe National Park (LPNP). The conservation unit has an area of 344 km^2 (31° 00′ to 31° 48′ S; 50° 46′ to 51° 09′ W) and includes various environments, such as marshes, coastal lagoons, inland lagoons, and floodplains. Peixe lagoon is one of the few lagoons in southern Brazil where the connection with the ocean has been managed by humans. As a result of these actions, the depth and the duration of intermittent ponds in the Peixe lagoon floodplains are influenced by the lagoon opening process. The lagoon is mechanically opened at the end of winter (August/September), by the creation of a canal that is 200 m long, 40 m wide, and 1.5 m deep. The lagoon closes naturally by the action of wind and waves, generally at the end of summer (February/March). The climate of the study area is moderately humid subtropical, and the average temperature varies between 11 °C in winter and 26 °C in summer, with an average yearly air temperature of 18.5 °C. Annual rainfall varies from 150 to 170 cm year^{-1} (Rossato 2011).

We sampled eight floodplain areas in the park: four not influenced by the lagoon opening (henceforth referred to as natural floodplains) and four areas influenced by this event (henceforth referred to as opened floodplains) (Fig. 1). The minimum distance between the sampling sites was 0.5 km. In each floodplain area, we sampled eight times from November 2007 to October 2009, a period that included two lagoon openings: four times when the lagoon was open (November 2007, August and October 2008, and October 2009) and four
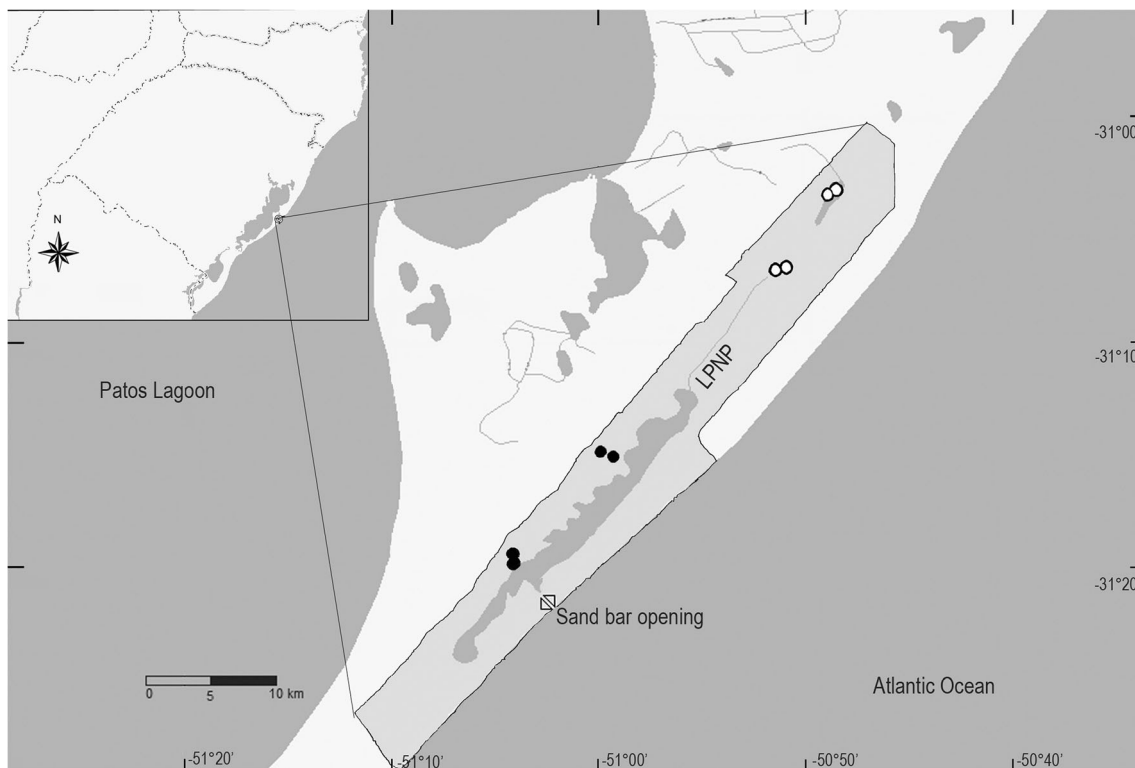
Fig. 1 Map of study area in Lagoa do Peixe National Park, southern Brazil. *Solid circles*, sampling sites under influence of sand bar opening; *open circles*, sampling sites without influence of sand bar

times when it was closed (February and May 2008, March and August 2009). The sampling began in a year in which the sand bar did not close. The lagoon was opened on August 27, 2008 and October 1, 2009. Each area contained 1 ha plots composed of several intermittent ponds (mean depth<40 cm). In each plot, we measured electrical conductivity at seven places with a HORIBA U-222 water quality checker®. Electrical conductivity ($\mu S\ cm^{-1}$ at 25 °C) was used as a proxy for salinity, and samples were taken 15 cm below the water surface. Average values were used for each plot. The sampling locations were classified into four hydrological categories: 0–floodplain without surface water, 1–floodplain with up to ten ponds with surface water, 2–floodplain with >10 ponds with surface water, and 3–floodplain completely covered by surface water.

Tadpole richness and abundance were measured according to the method proposed by Shaffer et al. (1994). Four quadrats (50×50 cm) were placed in ponds at each site. All of the tadpoles in each quadrat were removed with a net (10 cm wide). Each sampling ended after ten consecutive sweeps without tadpoles. The tadpoles were anesthetized with benzocaine and stored in 10 % formaldehyde, then they were identified in the laboratory (Collection license SISBIO n°18576). Voucher specimens were deposited in the herpetological collection of the Universidade do Vale do Rio dos Sinos, Brazil.

We performed an ANOVA using permutation analysis to test for differences in amphibian richness and abundance between natural and opened floodplains. Temporal variations are common in anuran assemblages, so we also investigated the effect of the interaction between collection period and type of management of each area. In opened floodplains, we also determined whether the values of electrical conductivity, anuran richness, and anuran abundance differed between the periods that the lagoon was open or closed. All of the ANOVA permutation analyses were performed with the package lmPerm (Wheeler 2010) in R 2.15.1 (R Development Core Team 2012).

A permutational variance analysis (PERMANOVA) was used to assess differences in amphibian composition between natural floodplains and opened floodplains, based on the Bray–Curtis dissimilarity. We used a constrained redundancy analysis (RDA) to evaluate the effects of conductivity, hydroperiod, and floodplain management (natural or opened) on the species composition. Amphibian data were Hellinger-transformed to reduce the influence of outliers (Legendre and Gallagher 2001). We calculated the significance of variance explained by RDAs by performing ANOVA-like permutation tests (1,000 permutations). Analyses were performed using the package vegan 2.0.9 for R (Oksanen et al. 2012).

Results

We collected 1,377 tadpoles belonging to ten different species during the study. Total species richness varied between three and nine species (Table 1). *Rhinella dorbignyi* and *Odontophrynus maisuma* were among the most abundant species and were only found in opened floodplains. *Hypsiboas pulchellus* and *Physalaemus gracilis* occurred in all of the study sites, regardless of management type. Hydrological conditions in opened floodplains ranged from category 0 to 3. Natural floodplains maintained constant hydrological categories throughout the study (category 2).

Anuran richness and abundance differed between natural and opened floodplains (Fig. 2; richness $F_{1,48}=41.667$, $p<0.001$; abundance $F_{1,48}=8.991$, $p<0.001$). There was no significant effect of the interaction between management and collection period on species richness ($F_{7,48}=1.362$, $p=0.243$). However, temporal variations in anuran abundance differed between opened and natural floodplains ($F_{7,48}=2.661$, $p=0.02$). Peaks in the abundance of two species with explosive breeding sensu Wells (1977) (*O. maisuma* and *R. dorbignyi*) were documented in areas influenced by the sand bar opening. Reproduction by these species is associated with heavy rainfall events (>50 mm day^{-1}), when species produce high numbers of eggs (Borges-Martins et al. 2007; Maneyro and Carreira 2012). Since the reproductive behavior of these species could influence variation in abundance, we excluded these two species and reanalyzed the data. Even so, variation in anuran abundance differed between opened and natural floodplains (management $F_{1,48}=8.120$, $p<0.001$; management × collection period $F_{7,48}=4.878$, $p<0.001$).

In the natural floodplains, conductivity ranged from 90 to 310 μS cm^{-1} (0.06–0.2). However, in areas affected by the sand bar opening, electric conductivity was higher when the lagoon was open (Online Resource 1; $F_{1,28}=4.427$, $p<0.04$). Conductivity varied from 145 to 4,000 μS cm^{-1} (0.09–2.6) in areas close to the ocean and from 132 to 3,000 μS cm^{-1} (0.08–1.9) in areas further inland. In fact, when the Peixe lagoon was closed, salinity in the opened floodplains was relatively homogeneous and low (130–600 μS cm^{-1} or 0.08–0.4) due to the flow of freshwater from terrestrial wetlands in the park, and only one sample was taken of oligohaline water. In this study, the sand bar opening events led to an increase in salinity to ~2,900 μS cm^{-1} (or 1.85) in the floodplains. In opened floodplains, anuran richness and abundance did not differ between periods with the bar open or closed (richness $F_{1,30}=0.706$, $p=0.39$; abundance $F_{1,30}=1.953$, $p=0.172$). When we reanalyzed the data without the two species with explosive breeding, average abundance was 2.7 times higher during closed periods than when the lagoon was opened ($F_{1,30}=5.882$, $p=0.021$).

Comparison of assemblages between areas showed significant differences associated with sand bar management (PERMANOVA, $F_{1,63}=5.973$; $p<0.001$), however, this association was relatively weak explaining only 9 % of variability ($R^2=0.09$). The RDA corroborated the outcomes of variance analysis. There was a weak but significant relationship ($p=0.001$) between anuran communities and floodplain characteristics. Conductivity, hydroperiod, and floodplain management explained 15 % of the variation in community structure. The first two canonical axes together explained 13.3 % of the total variance in the data, the first axis alone explaining 10 %. The RDA plot (Fig. 3) showed that floodplain management (natural or opened) played an important role along the first axis. Communities with

Table 1 Anuran species record in eight areas of floodplains in Lagoa do Peixe National Park, Brazil, from November 2007 to October 2009. Data correspond to summation of all abundance data on that location

Species	Opened floodplains				Natural floodplains			
	1	2	3	4	1	2	3	4
Bufonidae								
Rhinella dorbignyi	128	269	39	42				
Hylidae								
Dendropsophus minutus					3			
Hypsiboas pulchellus	30	22	9	15	4	2	31	45
Scinax squalirostris		1		2			3	10
Leptodactylidae								
Leptodactylus gracilis	6	2			2			
Leptodactylus latrans			16	20	2			
Physalaemus biligonigerus	45		2					
Physalaemus gracilis	53	118	14	76	23	6	19	8
Physalaemus henselii	3							
Odontophrynidae								
Odontophrynus maisuma	55	211	13	13				

Fig. 2 Mean values (±SD) of **a** tadpole richness and **b** tadpole abundance in natural floodplains and opened floodplains, across two sand bar openings (2007–2009), in Lagoa do Peixe National Park. *Arrows*, sand opening event; *O*, lagoon opened, *C*, lagoon closed
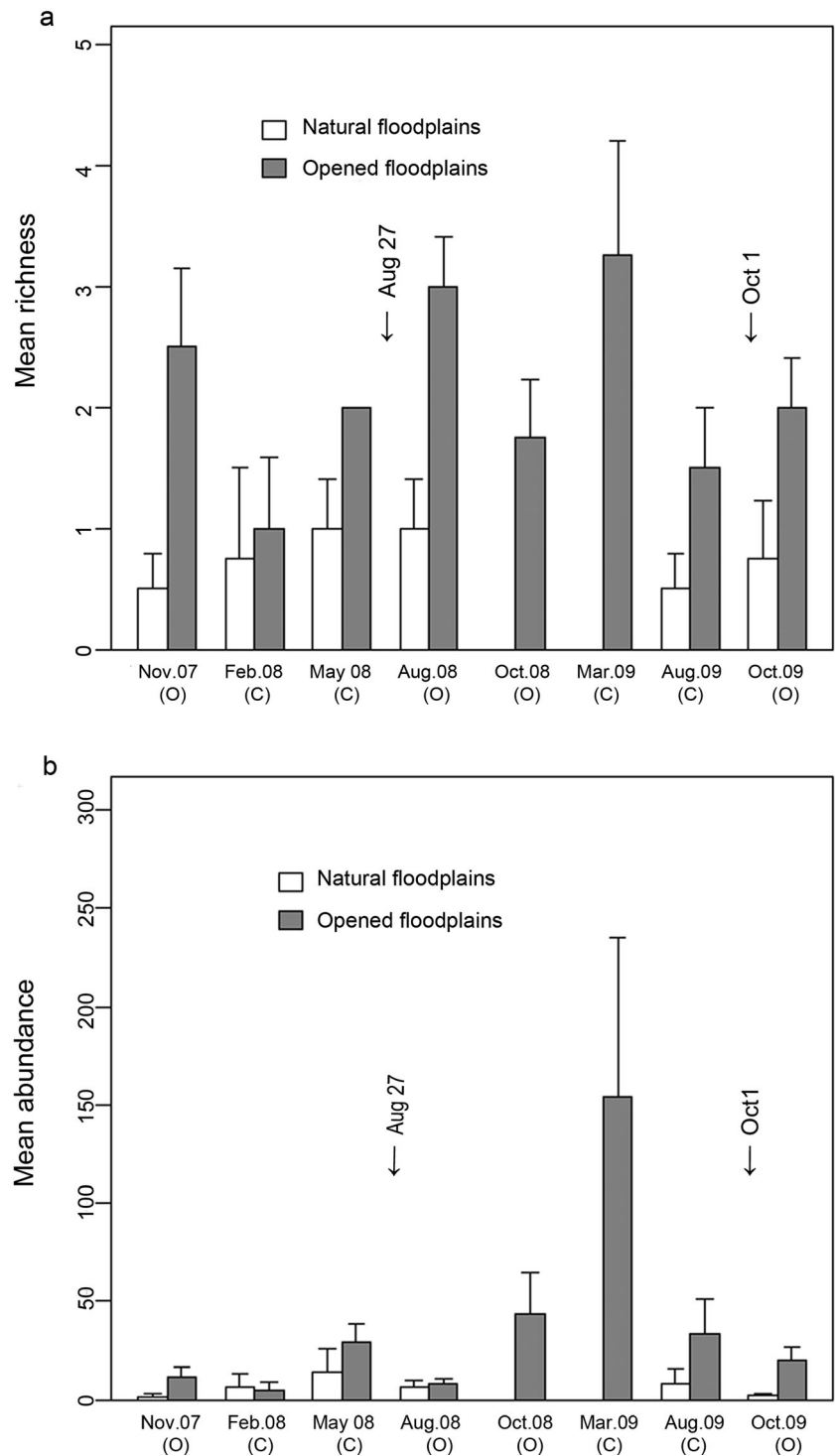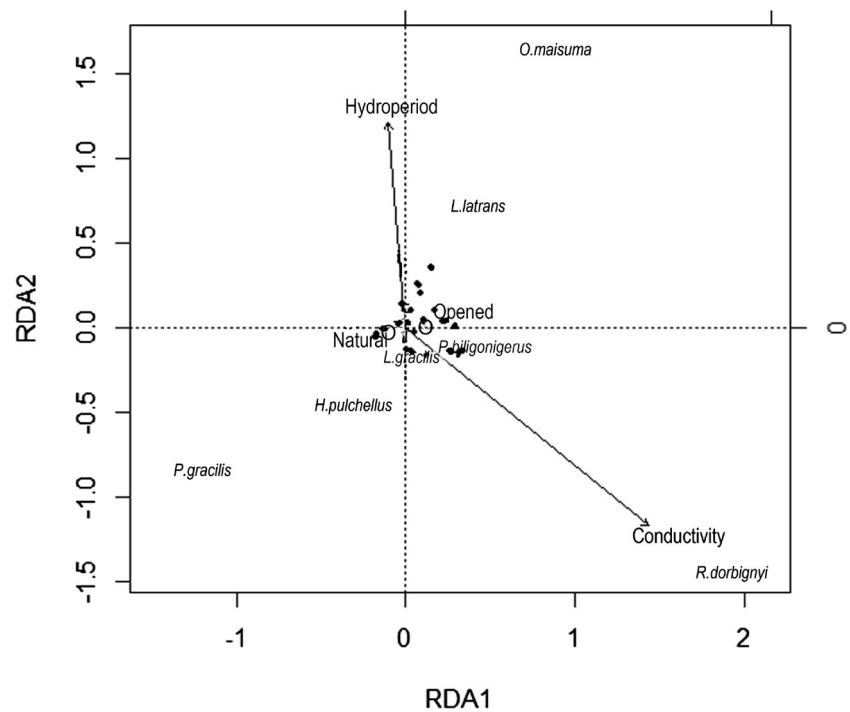

P. gracilis and H. pulchellus were associated with natural floodplains in areas with <10 ponds; communities with *Leptodactylus latrans* and *O. maisuma* were associated with floodplains completely covered by surface water (Fig. 3). Communities dominated by *R. dorbignyi* were associated with floodplains with high water conductivity.

Discussion

Areas affected by opening the Peixe lagoon to the sea had higher amphibian richness and abundance than areas not affected by this management. The two areas also differed in their species composition. Our analysis demonstrated that tadpole composition was related to floodplain characteristics

Fig. 3 Redundancy analysis
(RDA) ordination describing the
relationships between tadpole
communities and floodplain
characteristics. *Solid circles*
represents sampled sites. *Open
circles* represents centroids of
levels of factor variables
(floodplain type). Only species
away from origin are labeled.
Species not labeled are:
D. minutus, P. henselii, and
S. squalirostris. See Results for
full species names

(floodplain management, conductivity, and hydroperiod). Some species (*H. pulchellus* and *P. gracilis*) were strongly associated with the most natural floodplains. After sand bar breaching, saltwater intrusion changed most of the freshwater environments to oligohaline conditions in the opened floodplains. Although salinity was higher when the lagoon was open, we only observed differences in the abundance of species when taxa with explosive breeding were omitted from the analysis. Salinity inputs may explain differences in the presence of tadpole species through the effects on (1) spawning site selection; (2) the presence of predatory macro-invertebrates; and (3) food sources.

Studies evaluating the effects of salinity on amphibians have produced conflicting results according to the species studied. The range of salinity in which metamorphosis occurs seems to be great, and eggs and larvae generally tolerate oligohaline water (Smith et al. 2007; Alexander et al. 2012). Contrary to the proposed hypothesis, both tadpole richness and abundance were higher in areas subjected to sand bar opening. The presence of tadpoles in ponds or pools relies, in the first instance, on the location selected for egg-laying by adults. We know that salinity can be used, at least in part, as an oviposition cue by some species (Haramura 2008); however, anurans may also have to deal with abiotic factors not related to marine water intrusion when selecting oviposition sites. At Lagoa do Peixe National Park, anuran assemblages are composed of a pool of species with prolonged calling activity and slow larval development (e.g., *H. pulchellus* and *Pseudis minuta*) and explosive breeders with fast larval development (*Rhinella arenarum, R. dorbignyi, O. maisuma,* and

Elachistocleis bicolor) (Moreira and Maltchik 2012). It is not surprising that explosive and prolonged breeders would select different breeding ponds, according to specific preferences, such as vegetation cover, hydroperiod, or the risk of predation (Both et al. 2009; Moreira et al. 2010).

An explanation not associated with the selection of egg-laying sites is the indirect effect of sand bar opening on tadpole predation pressure. In temporary environments, predation by aquatic invertebrates can play an important role in shaping tadpole community richness and composition (Van Buskirk 2005; Both et al. 2009; Nomura et al. 2011). In our study area, there is evidence that opened floodplains have different aquatic invertebrate compositions than natural floodplains (Crippa et al. 2013). Aquatic insects that can prey on tadpoles, such as dragonfly larvae (Aeshnidae and Coenagrionidae), giant water bugs (Belostomatidae), and predaceous diving beetles (Dysticidae and Noteridae) are common in unmanaged floodplains. This is in contrast to the slightly saline environments of the Peixe lagoon opened floodplains, where crustaceans (Anostraca and Cladocera), nematodes, and freshwater snails dominate numerically. In fact, common benthic components in other ICEs (Chironomidae larvae, mollusks, and oligochaetes) are mainly collectors and shredders (Gladstone et al. 2006; Lill et al. 2011; Netto et al. 2012). A plausible new hypothesis is that tadpoles in temporary areas of ICEs are less threatened by predation by aquatic invertebrates.

A fundamental difference between freshwater wetlands and brackish parts of an estuary is the mineralization of organic matter (Weston et al. 2006). Salinity intrusion increases

nitrogen and phosphorus release, changing sediment microbial processes from methanogenesis to sulfate reduction. In addition to changes in microbial communities, salt stress contributes to increases in phytoplankton biomass (Van Meter and Swan 2014), which can reduce periphyton biomass through shading effects. Changes in pond salinity can also result in distinct zooplankton assemblages (Cottenie et al. 2003; Van Meter and Swan 2014). Historically, tadpoles have been regarded as suspension-feeding herbivores and detritivores (Altig et al. 2007). More recently, there is growing evidence that anuran larvae feed selectively and consume substantial amounts of animal food and epilithon (Schiesari et al. 2009; Whiles et al. 2009; Costa and Vonesh 2013). Fatty acid and stable isotope analyses show that plant detritus and bacteria are the major components of the diets of tadpoles with short larval development times, although these studies underscore the potential for spatiotemporal variation in tadpole diet. Molluscs and microcrustaceans (mainly copepods, cladocerans, and ostracods) were consumed and assimilated by species with larval periods of 1–3 months, such as *Agalychnis callidryas* (Costa and Vonesh 2013), *Lithobates pipiens* and *Lithobates sylvaticus* (Schiesari et al. 2009), *Pseudacris crucifer* (Whiles et al. 2009), and *Rana aurora* (Hamilton et al. 2012). Despite the general lack of information on many Neotropical amphibian larvae, changes in the abundance and/or species composition of zooplankton and epilithon can have strong impacts on tadpole abundances. Like other explosive breeders, tadpoles of *O. maisuma* and *R. dorbignyi* may adopt alternative feeding strategies based on food availability. Species with longer developmental times may also benefit from seasonal changes in food quantity and quality. Tadpoles that consume animal material develop faster than conspecifics under the same conditions that do not consume animal material (Heinen and Abdella 2005).

Estuarine environments are characterized by fluctuations in environmental conditions at different temporal scales (Barendregt and Swarth 2013) and adult amphibians can move between upland habitats, tidal freshwater wetlands, and entirely aquatic habitats. These multiple habitats can be beneficial to most anuran species, because they provide habitat complementation (Pope et al. 2000). The main expected change after breaching an ICE is the intrusion of marine waters, but the impacts of higher salinity will depend on the frequency of sand bar openings and freshwater inflow. In addition, an increase in the number and persistence of temporary ponds in the floodplains is expected when the sand bar is closed due to an increase in the groundwater level. Thus, floodplains would constitute a favorable environment for the development of species with longer larval stages. Species with a short larval phase (around 2 months), such as *L. latrans* and *Physalaemus biligonigerus*, were associated with opened floodplains. *H. pulchellus* was the only species with a long development time (3 to 6 months), and it was associated with natural floodplains with few ponds. The abundance of *H. pulchellus* was similar between natural and opened floodplains, although the occurrence frequency was higher in the natural floodplains. The hydroperiod in the opened floodplains may be suitable for species with a long development time, but this will depend on the capacity of the anuran species to respond to habitat variation. Species of amphibians can reduce the time to metamorphosis in response to a reduced volume of water (Wells 2007), but we cannot be sure that this is the case with *H. pulchellus*.

Distribution patterns of anuran communities inhabiting temporary coastal ponds are mainly attributed to gradients in hydroperiod (Beja and Alcazar 2003; Moreira and Maltchik 2012). Despite the significant differences in the tadpole composition, the axis related to hydroperiod only explained 3.34 % of the total variance. This result was not unexpected because the constraints of hydroperiod appear to be temporary and interact within a spatial context (pond connectivity) (Werner et al. 2007a; Werner et al. 2007b). In floodplains of the LPNP, pond connectivity was affected by the surface flooding dynamics, which depends on sand bar openings and freshwater inflow. This effect may weaken the developmental constraints imposed on tadpoles by hydroperiod length.

Although we expected a reduction of anuran tadpoles in the opened floodplains related to marine intrusion, the sand bar breaching appeared to have a positive effect. It remains unclear which mechanisms linked with the dynamic conditions in opened floodplains favored tadpoles, but the effects of sand bar breaching seem to be related to individual traits of species (habitat preferences, dietary plasticity, and reproductive modes). Regardless of the actual mechanism, a clear difference in tadpole species was related to breaching and artificially opening the sand bar should be done with caution. Our results showed that estuarine amphibian species were able to cope with slightly oligohaline floodplains. However, reductions in the freshwater inflow could raise the salinity in floodplains to polyhaline or even euhaline conditions. Increasing drainage of freshwater wetlands, especially for rice production and pine silviculture, could result in more widespread saltwater intrusion during opened sand bar conditions in the Peixe lagoon floodplains. For amphibians, these changes would be particularly important when combined with projected sea level rise due to climate change. Understanding the processes regulating tadpole abundance and diversity in estuaries and coastal ponds will help to elucidate the possible effects of one of the most likely consequences of global warming (Nichols and Cazenave 2010).

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