Journal of Natural History
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713192031

Factors influencing anuran distribution in coastal dune wetlands in southern Brazil

L. F. B. Moreira[a]; I. F. Machado[a]; T. V. Garcia[a]; L. Maltchik[a]
[a] Laboratory of Ecology and Conservation of Aquatic Ecosystems, UNISINOS, São Leopoldo, Brazil

Online publication date: 21 May 2010

To cite this Article Moreira, L. F. B. , Machado, I. F. , Garcia, T. V. and Maltchik, L.(2010) 'Factors influencing anuran distribution in coastal dune wetlands in southern Brazil', Journal of Natural History, 44: 23, 1493 — 1507
To link to this Article: DOI: 10.1080/00222931003632690
URL: http://dx.doi.org/10.1080/00222931003632690

Journal of Natural History
Vol. 44, Nos. 23–24, June 2010, 1493–1507

Taylor & Francis
Taylor & Francis Group

Factors influencing anuran distribution in coastal dune wetlands in southern Brazil

L.F.B. Moreira*, I.F. Machado, T.V. Garcia and L. Maltchik

Laboratory of Ecology and Conservation of Aquatic Ecosystems, UNISINOS, São Leopoldo, Brazil

(Received 1 May 2009; final version received 18 January 2010)

We investigated the potential role of hydroperiod and habitat structural complexity as explanatory factors defining richness, abundance and spatial and temporal distribution of anurans in wetlands of coastal dunes. This survey was performed in 15 wetlands along the Atlantic coastal zone of southern Brazil. We identified 10 anuran species (nine in the adult and eight in the tadpole stage) distributed in seven genera from five families. The adult richness and abundance varied among the hydroperiod classes, but without temporal variations. Both tadpole richness and abundance varied temporally and both were influenced by hydroperiod. Adult anuran composition was associated with dry months and wetland area, whereas tadpole composition was associated with emergent and floating macrophytes, wetland area and vegetation cover. This study identified the importance of habitat structural complexity and hydroperiod in spatial–temporal distribution models of anurans.

Keywords: anurans; hydroperiod; coastal dunes; habitat diversity; southern Brazil

Introduction

Understanding patterns and factors that influence species distribution and abundance is among the main goals of community ecology and conservation biology (Zimmerman and Simberloff 1996). Many studies have used species distribution along an environmental gradient to infer processes in community structuring (Wellborn et al. 1996; Guerry and Hunter 2002). Anuran amphibians use several ecosystems over their life cycle, from aquatic ones for reproduction and larval growth to terrestrial ecosystems for adults. Larvae of many anuran species are affected by hydroperiod (Kupferberg 1997). Biotic interactions such as predation and competition also exert strong influences on anuran communities, either concerning the survival rate of tadpoles or the choice of reproduction sites by adults (Dayton and Fitzgerald 2001; Zina et al. 2007).

Both habitat diversity and aquatic plant occurrence also affect the tadpole communities in wetland systems (Babbitt and Tanner 1998; Kopp et al. 2006). Wetlands with more complex habitats provide higher numbers of refuges for tadpoles to avoid predators (Rozas and Odum 1988; Kopp et al. 2006). Moreover, heterogeneous environments increase anuran richness because of the higher availability of calling sites (Eterovick and Sazima 2000).

*Corresponding author. Email: leonardobm@gmail.com

ISSN 0022-2933 print/ISSN 1464-5262 online

DOI: 10.1080/00222931003632690
http://www.informaworld.com

Hydroperiod is another environmental parameter that influences the biota in wetland systems, mainly temporary ones. Hydroperiod influences amphibian richness, composition and reproductive success (Semlitsch et al. 1996; Peltzer and Lajmanovich 2004), including the type of tadpole-predator species (Skelly et al. 1999). Interactions among hydroperiod, predation and life history characteristics can be used to build predictive models for anuran community structure (Wellborn et al. 1996). Analogous to the island biogeography theory, an increase in hydroperiod length has had similar effects to those caused by an increase of island area on species richness (Brooks 2000). However, well-defined segregation patterns in anuran distribution under different hydroperiods have rarely been observed in wetland systems (Babbitt et al. 2003).

Besides habitat diversity and hydroperiod, other factors such as water chemical variables (Hecnar and Closkey 1996), rainfall and temperature (Prado et al. 2005; Kopp and Eterovick 2006) influence the amphibian community. Whereas in seasonal climates peak activity occurs mainly in the rainy and warm season, in non-seasonal climates anuran activity is distributed throughout the year (Duellmann and Trueb 1994). This segregation is often associated with water availability (Prado et al. 2005; Kopp and Eterovick 2006). The anuran community in Brazilian coastal regions is scarcely known, and just a few studies have been conducted in southeastern and northeastern regions (Carvalho e Silva et al. 2000; Schneider and Teixeira 2001; Rocha et al. 2008). In southern Brazil, studies on anuran ecology in coastal dune wetlands are scarce, and most of them focus on biodiversity surveys of small areas of the Coastal Plain (Loebmann 2005; Loebmann and Vieira 2005; Colombo et al. 2008).

This study analysed factors that affected the anuran adult and tadpole distribution in coastal dune wetlands in southern Brazil. We studied 15 wetlands located close to the coastline in a small area of the Coastal Plain of southern Brazil (*c.* 2500 km^2). The small spatial scale analysed (~ 15 km) and the low spatial variability of temperature and precipitation of the studied area (Rambo 2000) minimized the effects of climate on amphibian richness and species composition among the wetlands. Assuming, therefore, that such variables were relatively constant, we were able to test the following hypotheses. (1) Does hydroperiod affect both spatial and temporal anuran distribution in wetlands of coastal dunes? We expected that amphibian richness would be lower in areas with shorter hydroperiod than in wetlands with longer hydroperiod and that temporal variations in the richness and abundance of the amphibians would be related to water availability; (2) Are similarities in anuran richness and abundance associated with habitat structural complexity? We expected higher similarity in anuran composition in wetlands with similar morphometry and vegetation type.

Materials and methods

Study area

The Coastal Plain is a region in southern Brazil with high aquatic plant diversity (Irgang and Gastal 1996) and wetland concentration (Maltchik et al. 2003). The study area is located in the National Park of Lagoa do Peixe and it is the only conservation unit protected by the Ramsar Convention in southern Brazil. The conservation unit has an area of 344 km^2 (31º02′ to 31º48′ S; 50º77′ to 51º15′ W), 62 km maximum length and with a mean width of 6 km (Loebmann and Vieira 2005). The topography is basically flat, except for a line made by the coastal dunes. The soil is comprised of quartzitic sands of marine origin. With a moist subtropical climate, the mean temperatures range between 14.6°C, in winter, and 22.2°C, in summer, with a mean annual temperature of 17.5°C. The annual precipitation ranges between 1150 and 1450 mm/year, with an annual mean of 1250 mm/year (Tagliani 1995). The absence of hills and the low altitude (less than 20 m above sea level) throughout the study area make the climatic conditions (precipitation and temperature) very similar among the wetland systems of the study (Rambo 2000).

Data collection

Fifteen wetlands were selected from a total of 35 wetland sites recognized from a complete topographic map inventory (1 : 50,000) of the coastal dunes of the National Park of Lagoa do Peixe. The 15 wetlands were selected using the following criteria: (1) occurrence of aquatic macrophytes; (2) distance from the sea no greater than 200 m; (3) wetland area no greater than 3 ha. We sampled anuran amphibians bimonthly for a year (from October 2007 to August 2008) in each one of the 15 wetlands.

Richness and abundance of tadpoles were measured using the methodology proposed by Shaffer et al. (1994). Seven quadrats (50 × 50 cm) were sampled randomly per sampling occasion in each wetland system during the day. The quadrats were placed gently on the water surface so as not to disturb any tadpoles on the pond bed. If any sign of tadpole movement resulting from disturbance was observed, the sampling site was abandoned and another site was chosen. All tadpoles inside the quadrat were removed using a dip net (10 cm wide). Sampling was finished in each quadrat only after 10 consecutive sweeps with no tadpole collection. The collected tadpoles were anesthetized with benzocaine, fixed in 5% formalin and deposited in the amphibian reference collection at University of Vale do Rio dos Sinos (UNISINOS). The tadpoles were identified following taxonomic keys specific to southern Brazil (Machado and Maltchik 2007).

Richness and abundance of adult anurans were measured through visual and auditory search procedures (Crump and Scott 1994). Sampling was carried out randomly between 19.00 h and 24.00 h for two consecutive nights. In each sampling, the entire margin of each area was surveyed in 20 minutes. All the individuals located visually or acoustically were registered. Pilot studies have shown that 20 minutes gave enough time for sampling the largest wetland found in the area of the study. Individuals that could not be easily identified in the field were anaesthetized with benzocaine, fixed in 5% formalin to be identified in the laboratory. Specimens collected were deposited in the reference collection at UNISINOS.

Ten descriptors were used to evaluate habitat structural complexity: (1) area; (2) number of droughts; (3) months of drought; (4) richness of macroinvertebrate predators; (5) occurrence of floating macrophytes; (6) occurrence of emergent macrophytes; (7) vegetation cover; (8) type of vegetation at the margins; (9) margin type; (10) contact with the sea. All descriptors were measured in October 2007, except for the number and months of drought. Additional visits (from October 2007 to August 2008) were made monthly in the 15 wetlands studied for assessing the presence or absence of the surface water. Because the majority of the descriptors were computed as present or absent or distributed into classes, quantification occurred only in the period of major activity and reproduction of the amphibians of the region.

The area of the wetland was measured *in situ* using a 50-m measuring tape. The number of droughts was measured as the number of times that the wetland was found without surface water. The dry months were measured as the number of months that the wetland remained without surface water. A dry month was only recorded when two consecutive visits failed to reveal surface water. The richness of macroinvertebrate predators was measured as the number of families of macroinvertebrates classified as tadpole predators (Kopp and Eterovick 2006). Twelve families distributed among three insect orders were included in the analysis: Coleoptera (Dysticidae, Gyrinidae, Hydrophilidae, Noteridae), Heteroptera (Belostomatidae, Naucoridae, Nepidae, Notonectidae, Pleidae) and Odonata (Aeshnidae, Coenagrionidae and Libellulidae). The macroinvertebrates were collected using a dip net (30 cm wide, 250-mm mesh). Three random sweeps of 1 m each were carried out over the several habitats of the littoral zone (detritus, rooted macrophytes and other dominant vegetation), encompassing ~ 1 m^2 of area sampled per habitat. Occurrences of floating and emergent macrophytes (presence and absence) were noticed along the surface water of each wetland. Vegetation cover was classified into two classes: above and below 50% by area macrophyte cover. The margin vegetation (presence and absence) was divided into two types: with and without vegetation of height greater than 30 cm. Margin vegetation was considered to be that not greater than 2 m from surface water. The classification was made with a graduated scale. The margin type was classified into two classes: flat border and angular border. The ponds of angular borders were those whose margins were at least 15 cm higher than the surface water.

Data analysis

Differences in anuran richness and abundance among hydroperiod classes over time were tested using repeated measures analysis of variance (ANOVA). The richness of adults and tadpoles was represented by the number of species of adults and tadpoles observed in each wetland, respectively. Hydroperiod was classified into three classes: permanent, long- and short-term temporary. Permanent were the wetlands that maintained water in all samples; long-term temporary were wetlands that remained with surface water over 3 months, and short-term temporary wetlands were those that had surface water for fewer than 3 months. Anuran abundance was square-root transformed to reduce the heteroscedasticity and to give less weight to the few dominant taxa. The analysis was performed using SYSTAT 12 (Systat 2007).

We evaluated the importance of 10 biotic and abiotic variables in the composition of adult and tadpole assemblages using the Canonical Correspondence Analysis (CCA). In CCA, correlated variables should not be included in the same model because the relationship between species and predictors is maximized (Ter Braak and Smilauer 1998). For this reason, the choice of the variables is crucial in CCA. We submitted the variables to a forward procedure and selected them manually on the basis of additional explained variation. The significance of each variable was tested by the Monte Carlo test (with 1000 permutations). This procedure excludes the redundant variables (Palmer 1993). The variables tested were wetland area, number of droughts, months of drought, richness of macroinvertebrate predators, occurrence of floating macrophytes, occurrence of emergent macrophytes, vegetation cover, type of vegetation at the margins, margin type, and contact with the sea. In the environmental matrix, occurrence of floating macrophytes and emergent macrophytes, type of vegetation at the margins, margin type, and contact with the sea were represented by dummy variables. All ordination and permutation tests were performed using PC-ORD 4.20 software (McCune and Mefford 1999).

Results

A total of seven wetlands dried out during the study period. Only the permanent wetlands remained with surface water in December. The number of droughts and the number of dry months varied between studied wetlands (Table 1). Macroinvertebrate

Table 1. Location, wetland attributes, environmental parameters and macroinvertebrate families of 15 coastal dunes wetlands in southern Brazil.

Geographic location	Vegetation cover	No. of droughts	Months of drought	Macrophytes	Area (m^2)	Macroinvertebrate predators
31º09′44″ S; 50º49′03″ W	>50%	2	2	Floating	152	5
31º11′26″ S; 50º50′43″ W	>50%	0	0	Floating, emergent	1680	8
31º11′53″ S; 50º51′08″ W	<50%	0	0	Floating	795	3
31º21′20″ S; 50º51′19″ W	>50%	2	3	Emergent	1200	1
31º12′33″ S; 50º51′53″ W	<50%	3	5	Emergent	240	1
31º12′33″ S; 50º51′53″ W	>50%	0	0	Floating, emergent	175	3
31º13′11″ S; 50º52′31″ W	>50%	0	0	Emergent	700	6
31º13′13″ S; 50º52′28″ W	<50%	0	0	Floating, emergent	180	5
31º13′28″ S; 50º52′47″ W	>50%	0	0	Emergent	120	1
31º13′24″ S; 50º52′47″ W	>50%	0	0	Emergent	1078	5
31º13′24″ S; 50º52′43″ W	>50%	2	2	Floating, emergent	2431	6
31º15′24″ S; 50º55′00″ W	<50%	0	0	Floating	228	1
31º15′59″ S; 50º55′38″ W	<50%	1	9	Emergent	1650	0
31º15′59″ S; 50º55′43″ W	<50%	1	1	Emergent	1800	1
31º16′03″ S; 50º55′45″ W	<50%	1	9	Emergent	1000	1

Table 2. Anuran species recorded in 15 coastal dune wetlands in southern Brazil, from October 2007 to August 2008.

Species	Short-term temporary		Long-term temporary		Permanent	
	Adults	Tadpoles	Adults	Tadpoles	Adults	Tadpoles
Bufonidae						
Rhinella arenarum (Hensel, 1867)	0	0	4	12	2	0
Rhinella dorbignyi (Duméril and Bibron, 1841)	0	0	0	0	0	2
Cycloramphidae						
Odontophrynus maisuma Rosset, 2008	2	0	4	0	0	0
Hylidae						
Hypsiboas pulchellus (Duméril and Bibron, 1841)	35	7	65	63	175	158
Pseudis minuta Günther, 1858	5	1	34	2	404	11
Leiuperidae						
Physalaemus biligonigerus (Cope, 1861 "1860")	7	0	6	12	0	6
Physalaemus gracilis (Boulenger, 1883)	18	0	50	18	126	71
Pseudopaludicola falcipes (Hensel, 1867)	2	0	0	0	9	0
Leptodactylidae						
Leptodactylus gracilis (Duméril and Bibron, 1841)	13	0	17	0	14	6
Leptodactylus ocellatus (Linnaeus, 1758)	5	0	12	92	111	0

richness varied from zero to seven, and the most frequent families of macroinvertebrate predators were Coenagrionidae and Libellulidae.

We identified 10 anuran species distributed in seven genera from five families: Bufonidae (two species), Cycloramphidae (one species), Hylidae (two species), Leiuperidae (three species) and Leptodactylidae (two species). Eight species were identified in larval stages. *Rhinella dorbignyi* was found only in the larval stage, *Odontophrynus maisuma* and *Pseudopaludicola falcipes* were observed only in the adult stage (Table 2).

Anuran species showed different patterns regarding wetland use. Adults and tadpoles of *Hypsiboas pulchellus* and *Pseudis minuta* were found in all hydroperiod classes. *Odontophrynus maisuma* occurred only in temporary wetlands. *Physalaemus gracilis* was more abundant in permanent wetlands. Reproduction of *Leptodactylus ocellatus* and *Rhinella arenarum* was observed only in long-term temporary wetlands, whereas *Rhinella dorbignyi* tadpoles were found only in permanent wetlands. Adults of *Leptodactylus gracilis* were more abundant in temporary wetlands, although tadpoles of this species were observed only in permanent wetlands. No anuran reproduced exclusively in short-term temporary wetlands.

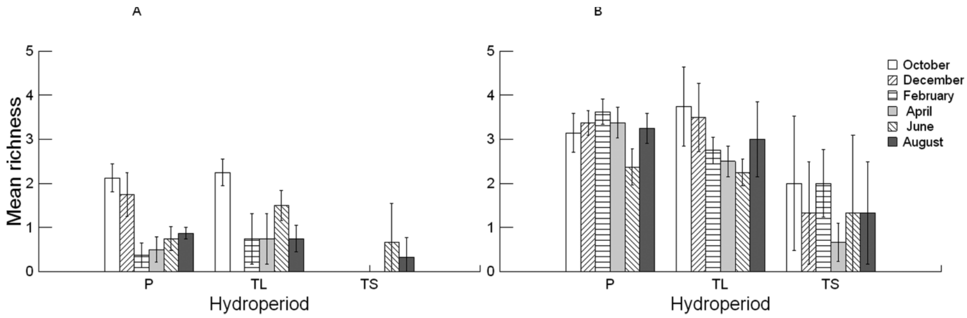

Figure 1. Mean anuran richness of coastal dune wetlands in southern Brazil, from October 2007 to August 2008, considering tadpoles (A) and adults (B): P, permanent; TL, long-term temporary; TS, short-term temporary.

Anuran species richness in adult and tadpole stages was influenced differently over time. Richness in the adult stage varied among the hydroperiod classes, but without changes over time [ANOVA repeated measures: Hydroperiod ($F_{2,12} = 11.885$; $p = 0.001$), Time ($F_{5,60} = 1.813$; $p = 0.124$), Hydroperiod × Time ($F_{10,60} = 0.540$; $p = 0.855$)]. Anuran richness in the adult stage was less in short-term temporary wetlands than other studied wetlands (Figure 1).

Anuran richness in the tadpole stage changed over time and was influenced by hydroperiod [ANOVA repeated measures: Hydroperiod ($F_{2,12} = 11.126$; $p = 0.002$), Time ($F_{5,60} = 3.768$; $p = 0.005$), Hydroperiod × Time ($F_{10,60} = 2.829$; $p = 0.006$)]. Whereas tadpole richness peaked in October and December in permanent wetlands, it peaked in October and June in short-term temporary wetlands (Figure 1).

Abundance of anuran adults and tadpoles was influenced differently through time. Abundance in the adult stage changed varied among hydroperiod classes, although did not change over time [ANOVA repeated measures: Hydroperiod ($F_{2,12} = 5.023$; $p = 0.026$), Time ($F_{5,60} = 1.985$; $p = 0.094$), Hydroperiod × Time ($F_{10,60} = 0.487$; $p = 0.888$)]. Adult abundance was smaller in short-term temporary wetlands than in other studied wetlands (Figure 2). While long-term temporary wetlands showed abundance peaks in October, short-term temporary wetlands showed abundance peaks in February (Figure 2). Permanent wetlands had peaks of abundance in October, February and August.

Anuran abundance in the tadpole stage varied with time and was influenced by hydroperiod [ANOVA repeated measures: Hydroperiod ($F_{2,12} = 5.626$; $p = 0.019$), Time ($F_{5,60} = 2.620$; $p = 0.033$), Hydroperiod × Time ($F_{10,60} = 2.094$; $p = 0.039$)]. The smallest abundance of tadpoles was observed between February and April in all studied wetlands (Figure 2).

Variables that remained in the model after the permutation tests were the following: wetland area, months of drought, richness of macroinvertebrate predators, occurrence of floating macrophytes, occurrence of emergent macrophytes and vegetation cover. The first two axes from the CCA explained 39% of the total variation in adult anuran composition (Table 3). According to the inter-set correlations between the explanatory variables and the CCA axes, the most important variables related to adult anuran composition were dry months and wetland area (Table 3, Figure 3).

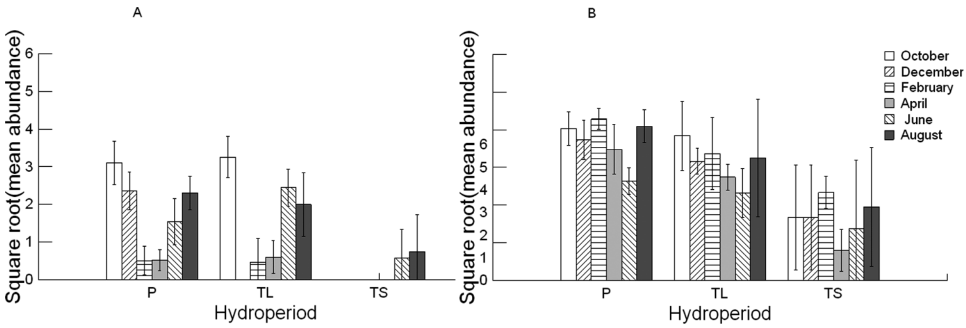

Figure 2. Mean anuran abundance of coastal dune wetlands in southern Brazil, from October 2007 to August 2008, considering tadpoles (A) and adults (B): P, permanent; TL, long-term temporary; TS, short-term temporary.

Table 3. Canonical correspondence analysis (CCA) results for adult anurans in the study wetlands of southern Brazil, from October 2007 to August 2008.

	CCA axes	
	1	2
Eigenvalue	0.255	0.100
Pearson correlation	0.854	0.684
Cumulative % variance	28.0	39.0
Inter-set correlation		
Emergent macrophytes	– 0.125	0.326
Months of drought	0.674	0.342
Area	0.502	–0.266
Macroinvertebrate richness	– 0.244	0.094
Monte Carlo test (*p*-value)	0.04	0.03

While *Leptodactylus gracilis*, *Odontophrynus maisuma* and *Physalaemus biligonigerus* were more abundant in wetlands with a longer dry period, *P. minuta* was more abundant in permanent wetlands with higher predator macroinvertebrate richness (Figure 3). *Leptodactylus ocellatus* and *Pseudopaludicola falcipes* were more abundant in wetlands without emergent macrophytes.

The first two axes from the CCA explained 46.6% of the total variation in the species composition in the larval stage (Table 4). Correlations between axes and environmental variables were significant only for the first axis (Table 4). The Monte Carlo simulation test indicated that the most important variables related to tadpole distribution were emergent and floating macrophytes, wetland area and vegetation cover (Table 4, Figure 4). *Physalaemus gracilis* and *Pseudis minuta* tadpoles were observed mainly in wetlands with floating macrophytes and higher vegetation cover (Figure 4). *Leptodactylus ocellatus* was closely associated with the wetland area, because this species was found in only one sampled wetland.

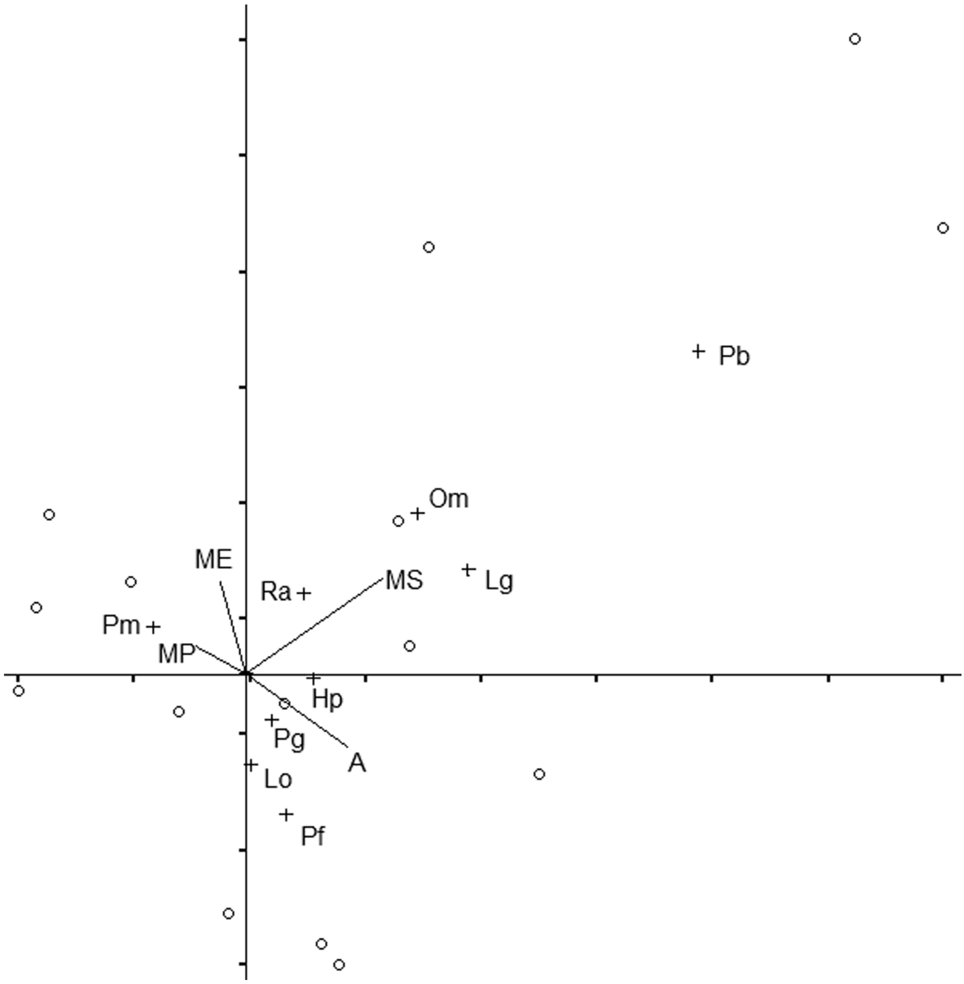

Figure 3. Canonical correspondence analysis ordination biplot (CCA) with adult anuran species composition related to the studied wetlands and structural complexity descriptors. First axis is horizontal, second axis vertical. ○, wetlands; Hp, *Hypsiboas pulchellus*; Lg, *Leptodactylus gracilis*; Lo, *L. ocellatus*, Om, *Odontophrynus maisuma*; Pb, *Physalaemus biligonigerus*; Pg, *Physalaemus gracilis*; Pm, *Pseudis minuta*; Pf, *Pseudopaludicola falcipes*; Ra, *Rhinella arenarum*. Variables: A, wetland area; ME, emergent macrophytes; MP, macroinvertebrate predators; MS, months of drought.

Discussion

Amphibian richness is strongly influenced by hydroperiod in wetland systems (Semlitsch et al. 1996); however, hydroperiod effects may be limited by seasonal rainfall in climates with marked seasonality. The effect of rainfall on anuran amphibian richness has been observed in several studies in Brazil (Eterovick and Sazima 2000; Prado et al. 2005; Moreira et al. 2007). Our results showed that hydroperiod influenced anuran richness and abundance of adult and tadpole stages in coastal dune wetlands under a non-seasonal rainfall regime. Santos et al. (2007) observed a positive relationship

Table 4. Canonical correspondence analysis (CCA) results for tadpoles in the study wetlands of southern Brazil, from October 2007 to August 2008.

	CCA axes	
	1	2
Eigenvalue	0.622	0.139
Pearson correlation	0.967	0.663
Cumulative % variance	38.1	46.6
Inter-set correlation		
Emergent macrophytes	0.434	– 0.374
Area	0.690	0.046
Months of drought	0.068	0.411
Vegetation cover	– 0.609	– 0.119
Floating macrophytes	– 0.627	– 0.034
Monte Carlo test (*p*-value)	0.01	0.76

between anuran richness and rainfall and hydroperiod in a southeast Brazil area with a long dry period. In contrast, Vasconcelos and Rossa-Feres (2005) found anuran richness to be associated only with rainfall, and not with hydroperiod, in the seasonal climate of southeast Brazil.

Tadpole richness and abundance changed temporally, and hydroperiod was associated with these parameters. Permanent habitats provide reproductive conditions to many anuran species over the year (Afonso and Eterovick 2007). In temporary wetlands, anuran reproduction is more susceptible to climatic conditions than in permanent wetlands. However, month of occurrence has been the variable that best describes the seasonal trends in anuran activities (Kopp and Eterovick 2006; Canavero et al. 2008). Month of occurrence reflects changes in temporal variables such as photoperiod and temperature. Many studies in subtropical regions have shown that photoperiod is an important variable in explaining the richness and abundance of calling frogs (Kwet 2001; Both et al. 2008; Canavero et al. 2008; Canavero and Arim 2009). Photoperiod influences several physiological processes, such as rates of growth and larval development (Gotthard 2001). In regions without distinctive rainy and dry seasons, the evaporation rates are more associated with hydroperiod than rainfall. Hence, high evaporation rates and low water volume in wetland systems are a direct response to photoperiod increase.

Richness and abundance of adult anurans did not show seasonal variation over the study period. Preference for dry or wet periods for reproductive activities is related to life cycle, adaptations, and reproductive modes of anuran species (Duellman and Trueb 1994). Temporal segregation related to resource use is a common pattern in anuran communities (Prado et al. 2005; Kopp and Eterovick 2006), which may reduce interspecific interactions. Although anuran richness and abundance were lower in short-term temporary wetlands, many anuran species were observed in more than one hydroperiod class. The overlap among wetland use indicated that selective pressures may not be strong enough to lead to a complete differentiation in anuran composition over costal dune landscapes.

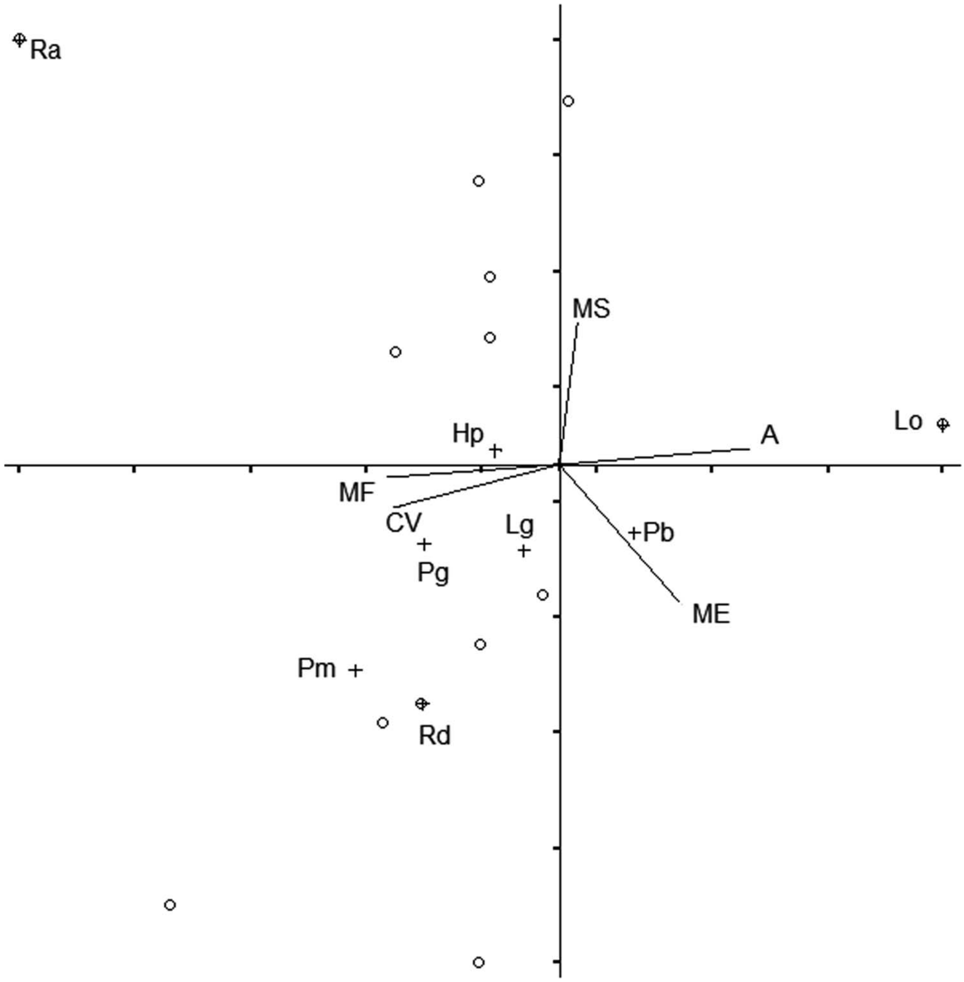

Figure 4. Canonical correspondence analysis ordination biplot (CCA) with tadpoles species composition related to the studied wetlands and structural complexity descriptors. First axis is horizontal, second axis vertical. ○ = wetlands, Hp, *Hypsiboas pulchellus*; Lg, *Leptodactylus gracilis*; Lo, *L. ocellatus*; Pb, *Physalaemus biligonigerus*; Pg, *Physalaemus gracilis*; Pm, *Pseudis minuta*; Ra, *Rhinella arenarum*; Rd, *R. dorbignyi*. Variables: A, wetland area; CV, vegetation cover; ME, emergent macrophytes; MF, floating macrophytes; MS, months of drought.

Our data showed that anuran composition was correlated with the number of dry months, area and vegetation cover. Habitat diversity is an important parameter associated with anuran richness; however, it has scarcely been tested in Brazil (Eterovick and Barata 2006; Kopp et al. 2006; Santos et al. 2007), including the coastal regions. Temporary wetlands are characterized by extremes of flooding and lack of surface water; such hydrological extremes can affect the biota in different ways (Maltchik 2003). Both et al. (2009) suggested that the variation of anuran occurrence in subtropical regions is related to hydroperiod. The number of dry months was the variable that best explained the abundance of adult anuran in our study. The anuran species associated with temporary wetlands showed adaptation to drought such as foam nests and burrowing behaviour. Foam nests protect eggs and tadpoles from desiccation (Heyer 1969) and provide some advantage in habitats with great water level fluctuations (Santos et al. 2007). Other non-analysed factors in the present study may also explain, partially, the coexistence of the anuran species in costal wetlands. The amphibians may have their reproduction site limited by the biotic and the abiotic factors, such as intra/interspecific competitions and physicochemical characteristics of surface water (Dayton and Fitzgerald 2001). Hence, preferences for reproduction sites by adults may limit the distribution of the tadpoles among the different wetlands.

Positive correlations between anuran richness and habitat complexity have been observed in lentic and lotic ecosystems with different vegetation types (Parris and McCarthy 1999; Vallan 2002; Krishnamurthy 2003; Eterovick and Barata 2006). Nevertheless, the studied area was located in an open area, with flat topography and typical vegetation of coastal dunes (see Loebmann and Vieira 2005). Despite the low height of the riparian vegetation, the occurrence of macrophytes (emergent or floating), and vegetation cover of the studied wetlands were important variables to explain anuran composition in coastal dune wetlands. Aquatic vegetation provides refuges against potential predators and calling sites (Kopp et al. 2006; Afonso and Eterovick 2007).

This study identified the importance of hydroperiod in the spatial–temporal variation models and distribution of anuran amphibians in coastal dune wetlands in southern Brazil. Additionally, wetland use as a reproductive site was associated with habitat structural complexity, such as macrophyte occurrence and vegetation cover. The conservation of the wetland systems under a hydroperiod gradient was proposed as an important tool for amphibian conservation in the United States (Snodgrass et al. 2000). Our study indicates the need for promotion of the conservation of wetland systems in the coastal dunes of southern Brazil, regardless of their hydroperiod and habitat structural characteristics. These arguments should be considered as important to determine the environmental factors that shape and maintain the biodiversity in these ecosystems. Such information is essential to develop conservation and management programmes of wetlands in this region, where more than 90% of wetland systems have already been lost and those that remain are still at high risk because of the expansion of rice production, and exotic *Eucalyptus* and pine plantations in southern Brazil.

Acknowledgements

We are grateful to Arthur Ávila, who helped in field surveys; R. Bacca and Aline B. Moraes for collaboration in the identification of macroinvertebrates; and Drs Paula C. Eterovick and Demetrio L. Guadagnin, who revised an early version of the manuscript. We declare that the data collection complied with Brazilian current laws (IBAMA - 02001.001148/2007-61). This research was supported by funds from UNISINOS (02.00.023/00-0) and CNPq (52370695.2). Leonardo Maltchik holds a Brazilian Research Council–CNPq Research Productivity grant.

References

Afonso LG, Eterovick PC. 2007. Spatial and temporal distribution of breeding anurans in streams in southern Brazil. J Nat Hist. 41:13–16.

Babbitt, KJ, Baber MJ, Tarr TL. 2003. Patterns of larval amphibian distributions along a wetland hydroperiod gradient. Can J Zool. 81:1539–1552.

Babbitt KJ, Tanner GW. 1998. Effects of cover and predator size on survival and development of *Rana utricularia* tadpoles. Oecologia 114:258–262.

Both C, Kaefer IL, Santos TG, Cechin SZ. 2008. An austral anuran assemblage in neotropics: a seasonal occurrence pattern correlated with photoperiod. J Nat Hist. 42:205–222.

Both C, Solé M, Santos TG, Cechin SZ. 2009. The role of spatial and temporal descriptors for Neotropical tadpoles communities in southern Brazil. Hydrobiologia 624:125–138.

Brooks RT. 2000. Annual and seasonal variation and the effects of hydroperiod on benthic invertebrates of seasonal forest ("vernal") ponds in central Massachusetts, USA. Wetlands 20: 707–715.

Canavero A, Arim M. 2009. Clues supporting photoperiod as the main determinant of seasonal variation in amphibian activity. J Nat Hist. 43(47–48):2975–2984.

Canavero A, Arim M, Naya DE, Camargo A, Rosa I, Maneyro R. 2008. Calling activity patterns in an anuran assemblage: the role of seasonal trends and weather determinants. North-West J Zool. 4:29–41.

Carvalho-E-Silva SP, Izecksohn E, Carvalho-E-Silva AMPT. 2000. Diversidade e ecologia de anfíbios em restingas do sudeste brasileiro. In: Esteves FA, Lacerda LD, editors. Ecologia de Restingas e Lagoas Costeiras. Macaé: Nupem/Ufrj.; pp. 89–97.

Colombo P, Kindel A, Vinciprova G, Krause L. 2008. Composição e ameaças à conservação dos anfíbios anuros do Parque Estadual de Itapeva, município de Torres, Rio Grande do Sul, Brasil [Internet]. Biota Neotropica 8. Available from: http:// www.biotaneotropica.org.br/ v8n3/pt/abstract?inventory +bn01208032008.

Crump ML, Scott NJ. 1994. Standard techniques for inventory and monitoring: visual encounter surveys. In: Heyer WR, Donnelly MA, McDiarmid RW, Hayek LC, Foster MS, editors. Measuring and monitoring biological diversity. Standard methods for Amphibians. Washington: Smithsonian Institution Press. pp. 84–92.

Dayton GH, Fitzgerald LA. 2001. Competition, predation, and distribution of four desert-anurans. Oecologia 129:430–435.

Duellman WE, Trueb L. 1994. Biology of Amphibians. Baltimore: The Johns Hopkins University Press.

Eterovick PC, Barata IM. 2006. Distribution of tadpoles within and among Brazilian streams: the influence of predators, habitat size and heterogeneity. Herpetologica 62:365–377.

Eterovick PC, Sazima I. 2000. Structure of an anuran community in a montane meadow in southeastern Brazil: effects of seasonality, habitat, and predation. Amphibia-Reptilia 21:439–461.

Gotthard K. 2001. Growth strategies of ectothermic animals in temperate environments. In: Atkinson D, Thorndyke M, editors. Environment and animal development. Oxford: BIOS Scientific Publishers. pp. 287–304.

Guerry AD, Hunter ML. 2002. Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. Conserv Biol. 16:745–754.

Hecnar SJ, Closkey RTM. 1996. Amphibian species richness and distribution in relation to pond water chemistry in south western Ontario, Canada. Freshwater Biol. 36:7–15.

Heyer WR. 1969. The adaptive ecology of the species groups of the genus *Leptodactylus* (Amphibia, Leptodactylidae). Evolution 23:1–28.

Irgang BE, Gastal CVS. 1996. Plantas aquáticas da planície costeira do Rio Grande do Sul. Porto Alegre: Edição dos autores.

Kopp K, Eterovick PC. 2006. Factors influencing spatial and temporal structure of frog assemblages at ponds in southeastern Brazil. J Nat Hist. 40:1813–1830.

Kopp K, Wachlevski M, Eterovick PC. 2006. Environmental complexity reduces tadpole predation by water bugs. Can J Zool. 84:136–140.

Krishnamurthy SV. 2003. Amphibian assemblages in undisturbed and disturbed areas of Kudremukh National Park, Central Western Ghats, India. Environ Conserv. 30:272–282.

Kupferberg SJ. 1997. Bullfrog (*Rana catesbeiana*) invasion of California river: the role of larval competition. Ecology 75:1736–1751.
Kwet A. 2001. Frösche im brasilianischen Araukarienwald – Anurengemeinschaft des Araukarienwaldes von Rio Grande do Sul: Diversität, Reproduktion und Ressorcenaufteilung. Münster: Natur und Tier-Verlag.
Loebmann D. 2005. Guia Ilustrado: Os Anfíbios da Região Costeira do Extremo Sul do Brasil. Pelotas: Useb.
Loebmann D, Vieira JP. 2005. Relação dos anfíbios do Parque Nacional da Lagoa do Peixe, RS, Brasil. Rev Brasil Zool. 22:339–341.
Machado IF, Maltchik L. 2007. Check-list da diversidade de anuros no Rio Grande do Sul (Brasil) e proposta de classificação para as formas larvais. Neotrop Biol Conserv. 2:101–116.
Maltchik L. 2003. Three new wetlands inventories in Brazil. Interciência 28:421–423.
Maltchik L, Costa ES, Becker CG, Oliveira AE. 2003. Inventory of wetlands of Rio Grande do Sul (Brazil). Pesquisas Bot. 53:89–100.
McCune B, Mefford MJ. 1999. PC-ORD – multivariate analysis of ecological data, version 4.2. Gleneden Beach (OR): MjM Software Design.
Moreira LFB, Machado IBF, Lace ARGM, Maltchik L. 2007. Calling period and reproductive modes in an anuran community of a temporary pond in southern Brazil. S Am J Herpetol. 2:129–135.
Palmer MW. 1993. Putting things in even better order – the advantages of canonical correspondence analysis. Ecology 74:2215–2230.
Parris KM, McCarthy MA. 1999. What influences the structure of frogs assemblages at forest streams? Aust J Ecol 24:495–502.
Peltzer P, Lajmanovich RC. 2004. Anuran tadpole assemblages in riparian areas of the Middle Paraná River, Argentina. Biodivers Conserv. 13:1833–1842.
Prado CPA, Uetanabaro M, Haddad CFB. 2005. Breeding activity patterns, reproductive modes, and habitat use by anurans (Amphibia) in a seasonal environment in the Pantanal, Brazil. Amphibia-Reptilia 26:211–221.
Rambo B. 2000. A Fisionomia do Rio Grande do Sul: Ensaio de Monografia Natural. São Leopoldo: Universidade do Vale do Rio dos Sinos (UNISINOS).
Rocha CFD, Hatano FH, Vrcibradic D, Van Sluys M. 2008. Frog species richness, composition and β-diversity in coastal Brazilian restinga habitats. Brazil J Biol. 68:101–107.
Rozas LP, Odum WE. 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. Oecologia 7:101–106.
Santos TG, Rossa-Feres DC, Casatti L. 2007. Diversidade e distribuição espaço-temporal de anuros em região com pronunciada estação seca no sudeste do Brasil. Iheringia 97:37–49.
Schneider JAP, Teixeira, RL. 2001. Relacionamento entre anfíbios anuros e bromélias da restinga de Regência, Linhares, Espírito Santo, Brasil. Iheringia 91:41–48.
Semlitsch RD, Scott DE, Pechmann JHK, Gibbons JW. 1996. Structure and dynamics of a community: evidence from 16-year study of a natural pond. In: Cody ML, Smallwood JA, editors. Long-term studies of vertebrate communities. San Diego: Academic Press. pp. 217–248.
Shaffer HB, Alford RA, Woodward BD, Richards SJ, Altig RG, Gascon C. 1994. Standard techniques for inventory and monitoring: quantitative sampling of amphibian larvae. In: Heyer WR, Donnelly MA, McDiarmid RW, Hayek LC, Foster MS, editors. Measuring and monitoring biological diversity. Standard methods for Amphibians. Washington: Smithsonian Institution Press. pp. 130–141.
Skelly DK, Werner EE, Coutwright S. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology 80:2326–2337.
Snodgrass JW, Komoroski MJ, Bryan AL, Burger J. 2000. Relationships among isolated wetlands size, hydroperiod, and amphibian species richness: implication for wetlands regulations. Conserv Biol. 14:414–419.

Systat 2007. 'Systat Software.' Richmond (CA): Systat.
Tagliani PRA. 1995. Estratégia de planificação ambiental para o sistema ecológico da restinga da Lagoa dos Patos - planície costeira do Rio Grande do Sul [Doctoral thesis]. Universidade Federal de São Carlos.
Ter Braak CJF, Smilauer P. 1998. Canoco reference manual and user's guide to Canoco for Windows: software for canonical community ordination, Version 4. Ithaca (NY): Microcomputer Power.
Vallan D. 2002. Effects of anthropogenic environmental changes in amphibian diversity in the rain forests of eastern Madagascar. J Trop Ecol. 18:725–742.
Vasconcelos TS, Rossa-Feres DC. 2005. Diversidade, distribuição espacial e temporal de anfíbios anuros (amphibia, anura) na região noroeste do estado de São Paulo, Brasil [Internet]. Biota Neotropica 5: http:// www.biotaneotropica.org.br/ vfn2/pt/abstract?article+bn01705022005.
Wellborn GA, Skelly DK, Werner EE. 1996. Mechanism creating community structure across a freshwater habitat gradient. Annu Rev Ecol Syst. 27:337–363.
Zimmerman BL, Simberloff D. 1996. An historical interpretation of habitats use by frogs in a Central Amazonian Forest. J Biogeog. 23:27–46.
Zina J, Ennser J, Pinheiro SCP, Haddad CFB, Toledo LF. 2007. Taxocenose de anuros de uma mata semidecídua do interior do Estado de São Paulo e comparações com outras taxocenoses do Estado, sudeste do Brasil [Internet]. Biota Neotropica 7: http:// www.biotaneotropica.org.br/vfn2/pt/abstract?article+BN00607022007