






Article

Can nesting waterbirds influence the community structure of macroinvertebrates in southern Brazilian intermittent wetlands?

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ABSTRACT. The main goal of this study was to test the effect of the presence of nesting waterbirds on the taxonomic structure (richness, abundance and composition) of macroinvertebrate communities in southern Brazilian wetlands. Macroinvertebrate communities were seasonally sampled in eight intermittent wetlands differing according to the occurrence of nesting colonies of waterbirds (four with the presence of rookeries; four without). The influence of nutrients and water and sediment physicochemical variables on macroinvertebrate communities was also assessed. The community structure of aquatic macroinvertebrates was not affected by the presence of colonies of nesting waterbirds. Rather, macroinvertebrate communities varied seasonally and they were influenced by water-level environmental variables. Richness and composition changed among seasons and were influenced by nutrients and water physicochemical variables. Water turbidity and total dissolved solids influenced macroinvertebrate richness, while water nutrients affected macroinvertebrate abundance. Our results indicate that the lack of effect of nesting waterbirds on macroinvertebrates is possibly due to the variation in the composition of avian species and their reduced population sizes, and in such cases, any effects of birds on macroinvertebrates can be overridden by water chemistry and seasonal changes in intermittent wetlands.

KEYWORDS. Aquatic invertebrates, ponds, waterfowl, water chemistry.

RESUMO. Podem as colônias de nidificação de aves aquáticas influenciar a estrutura da comunidade de macroinvertebrados em áreas úmidas intermitentes do sul do Brasil? O principal objetivo deste estudo foi testar o efeito da presença de colônias de nidificação de aves aquáticas sobre a estrutura taxonômica (riqueza, abundância e composição) de comunidades de macroinvertebrados em áreas úmidas do sul do Brasil. As comunidades de macroinvertebrados foram amostradas sazonalmente em oito áreas úmidas intermitentes, diferindo de acordo com a ocorrência de colônias de nidificação de aves aquáticas (quatro áreas úmidas com e quatro áreas úmidas sem a presença de ninhais). A influência de nutrientes e das variáveis físico-químicas da água e do sedimento nas comunidades de macroinvertebrados também foi avaliada. A estrutura da comunidade de macroinvertebrados aquáticos não foi afetada pela ocorrência de colônias de nidificação de aves aquáticas. No entanto, as comunidades de macroinvertebrados variaram sazonalmente e foram influenciadas pelas variáveis ambientais da água. A riqueza e a composição variaram entre as estações e foram influenciadas pelas variáveis físico-químicas e pelos nutrientes da água. A turbidez e o total de sólidos dissolvidos da água influenciaram a riqueza, enquanto que os nutrientes afetaram a abundância de macroinvertebrados. Nossos resultados indicam que a falta de efeito da presença de colônias de nidificação de aves aquáticas na comunidade de macroinvertebrados é possivelmente devido à variação na composição de espécies de aves e ao tamanho reduzido de suas populações, onde em tais casos, quaisquer efeitos das aves sobre os macroinvertebrados podem ser superados pela química da água e pelas mudanças temporais em áreas úmidas intermitentes.

PALAVRAS-CHAVE. Invertebrados aquáticos, banhados, aves aquáticas, química da água.

The aquatic macroinvertebrate community is represented by different taxonomic groups that live all or part of their life cycles in freshwater habitats (METCALFE, 1989; BALDWIN *et al.*, 2018). The community structure of aquatic macroinvertebrates is sensitive to many local environmental factors (BATZER *et al.*, 2004; STENERT *et al.*, 2008; ROMERO *et al.*, 2017; BALDWIN *et al.*, 2018). Macroinvertebrate composition in subtropical intermittent wetlands is strongly affected by seasonal changes related either with climate or variation in water availability, as hydroperiod can either constrain the establishment of many taxa or affect water-level environmental conditions

(STENERT & MALTCHIK, 2007; BATZER, 2013; GLEASON & ROONEY, 2017). For instance, several studies showed that the richness and composition of aquatic macroinvertebrates is sensitive to changes in water physicochemical variables and nutrient enrichment (BATZER *et al.*, 2004; SIGNA *et al.*, 2015). Aquatic macroinvertebrates have therefore been usually used as indicators of the environmental integrity of freshwater ecosystems (CAIRNS & PRATT, 1993; USEPA, 2002; BONADA *et al.*, 2006; ESCRIBANO *et al.*, 2018).

Aquatic macroinvertebrates are key elements of the ecological dynamics of wetlands, linking producers and higher-level consumers such as waterbirds (METCALFE,

1989; BALDWIN *et al.*, 2018). Macroinvertebrates comprise a major part of the food items of waterbirds (MEYER *et al.*, 2015), supplying proteins and other essential nutrients for their survival (ANDERSON & SMITH, 2000; BALDASSARRE & BOLEN, 2006). It is thus recognized that the occurrence and distribution of macroinvertebrates can affect waterbird habitat selection (KRAPU & REINECKE, 1992; MEIRE *et al.*, 1994; SAFRAN *et al.*, 1997; DAVIS & SMITH, 1998; PALOMO *et al.*, 1999; BOLDOC & AFTON, 2004; ANDREI *et al.*, 2008; ZMUDCZYŃSKA-SKARBEB *et al.*, 2015). In turn, little is known on the effects of waterbirds on aquatic macroinvertebrates. Previous studies have detected effects of the occurrence of nesting waterbirds and the community structure of macroinvertebrates in ponds (MURKIN & KADLEC, 1986; WRUBLESKI, 1989; WISZ *et al.*, 2013), although these relationships are not consistent (ROONEY & BAYLEY, 2012).

Waterbirds can affect macroinvertebrate distribution either through top-down (*e.g.*, via predation), as they have large foraging areas, or bottom-up control mechanisms (*e.g.*, nutrient enrichment) (HAIRSTON *et al.*, 1960; ODUM, 1969). The waterbirds deposit nutrients in the form of guano (phosphorus and nitrogen-rich feces) in wetlands, altering the nutrient flow in these ecosystems (ELLIS, 2005; SIGNA *et al.*, 2012). Studies in European lakes reported that the nutrient enrichment by waterbirds is comparable to the fertilization used in intensive farming (KOLB *et al.*, 2010; SEBASTIAN-GONZALEZ *et al.*, 2012; GWIAZDA *et al.*, 2014; TELESFORD-CHECKLEY *et al.*, 2016).

The high nutrient input (mainly of nitrogen and phosphorus) associated with nesting waterbird colonies (rookeries) (LINDEBOOM, 1984; BOSMAN & HOCKEY, 1986; KEATLEY *et al.*, 2009) affects both the water and sediment physicochemical characteristics of the wetlands (KEATLEY *et al.*, 2009; KOLB *et al.*, 2010; SEBASTIAN-GONZALEZ *et al.*, 2012; GWIAZDA *et al.*, 2014; SOMURA *et al.*, 2015; TELESFORD-CHECKLEY *et al.*, 2016; CHATTERJEE *et al.*, 2017). These changes in water quality directly influence the primary producers (VALIELA, 1984; ELSER *et al.*, 2007) and, consequently, should potentially impact the macroinvertebrate community, either by increasing or decreasing the abundance of zooplanktonic species (ZELICKMAN & GOLOVKIN, 1972), polychaetes (BOSMAN & HOCKEY, 1986), crustaceans (PALOMO *et al.*, 1999), chironomids (MICHELUTTI *et al.*, 2009), and fish (ONUF *et al.*, 1977). In fact, some authors showed that nitrogen enrichment by guano deposition was the driving force of the macroinvertebrate dynamics in coastal lagoons (SIGNA *et al.*, 2015). Despite the importance of the nutrient enrichment for wetland macroinvertebrates (MARTINEZ, 1993), few studies have assessed the relationships between waterbirds and the macroinvertebrate community through changes related to water nutrient and sediment regime (bottom-up effect) (VITOUSEK, 1986; BOSMAN & HOCKEY, 1986; POWELL *et al.*, 1989; MARTINEZ, 1993).

Beyond the northern hemisphere and particularly in Brazil, much of the current knowledge on the relationships between wetland macroinvertebrates and waterbirds is restricted to descriptions of the food items of waterbirds (SICK, 2001; BELTON, 2004). However, studies investigating

the effects of waterbird occurrence on the structure of wetland macroinvertebrate communities and limnological characteristics are missing. The main goal of this study was to assess the taxonomic structure of macroinvertebrate communities in wetlands with and without the presence of nesting waterbirds along two seasonal periods in southern Brazil. The specific objectives were to: 1) to test the effect of the presence of nesting waterbirds on macroinvertebrate richness, abundance and composition; 2) to analyze the relationship of water physicochemical variables, nutrients, sediment (organic matter) with the macroinvertebrate community structure (richness and abundance). Assuming that ponds with and without nesting waterbirds show differences in water and sediment physical and chemical features, and that the macroinvertebrate community varies among different seasonal periods (PRELLVITZ & ALBERTONI, 2004; BUENO *et al.*, 2003; STENERT *et al.*, 2008; KRAJENBRINK *et al.*, 2019), the following expectations were tested: 1) wetlands with nesting waterbirds have lower macroinvertebrate richness and diversity (ROONEY & BAYLEY, 2012; GUARESCHI *et al.*, 2015) than wetlands without nesting waterbirds; and 2) the macroinvertebrate composition differs between wetlands with and without nesting waterbirds.

MATERIAL AND METHODS

Study area. This study was conducted in the municipalities of Estância Velha, Ivoti, Lindolfo Collor, Novo Hamburgo, São Leopoldo and Portão, located in the Porto Alegre Metropolitan Region (PAMR) of the state of Rio Grande do Sul, southernmost Brazil (Fig. 1). The PAMR has an area of 10,300 km² and is characterized by elevated population density (389.7 inhab/km²) and urbanization rate (over 96%) (IBGE, 2016). The original vegetation in the study area ranges from Mixed Ombrophilous to Deciduous and Semi-deciduous Seasonal Forests, and the climate is subtropical humid, with temperate climate periods, and the rainfall is well distributed over the year (COMITESINOS, 2015).

Sampling design. Eight wetlands were selected for sampling in this study and classified according to the presence of waterbirds. In four wetlands it was recorded the occurrence of colonies of nesting waterbirds (hereafter 'rookery wetlands'). In the other four wetlands, there were no vestiges of nesting waterbirds (hereafter 'control' wetlands) (Fig. 1). The classification criteria and the bird counting data were retrieved from a simultaneous investigation in the study region that assessed the distribution and feces composition of waterbird species (A. S. Peter, unpubl. data). Over the study period, the following waterbird species were observed in the rookery wetlands: *Phimosus infuscatus* Poche, 1904, *Bubulcus ibis* Linnaeus, 1758, *Ardea alba* Linnaeus, 1758, *Egretta thula* Molina, 1782, and *Nycticorax nycticorax* Linnaeus, 1758. The estimated numbers of waterbird individuals in the rookery wetlands over the reproduction period was approximately 600. However, in one of the wetlands, this number reached ~1,600 individuals due the high abundance of *Phimosus infuscatus* dwelling in this pond all year round (A. S. Peter, unpubl. data).

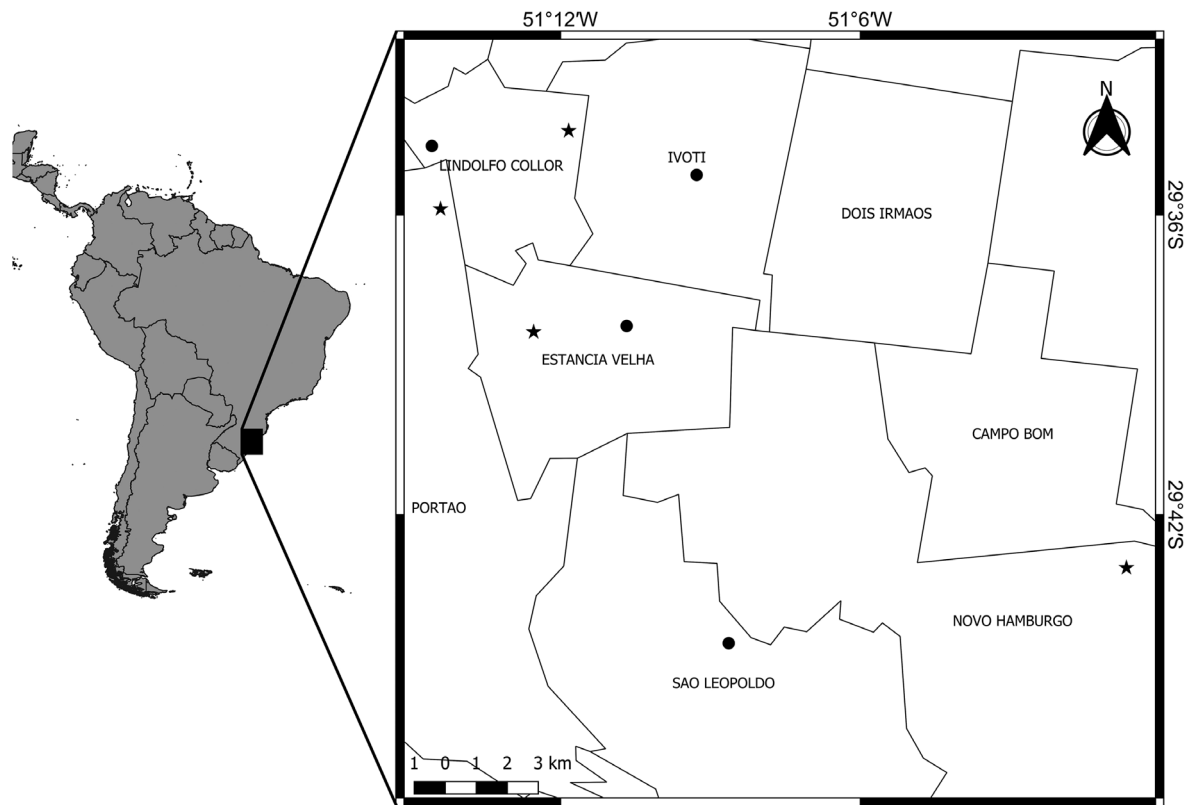


Fig. 1. Map of the study area with the location of the studied wetlands in southern Brazil. Filled circles indicate the control wetlands (wetlands without the presence of nesting bird colonies). Filled stars indicate the rookery wetlands.

All studied wetlands had similar surface flooding areas (~1 ha), maximum water depth of 50 cm, intermittent hydrological regime, and low anthropic impact. The composition of the surrounding vegetation in the studied wetlands was characterized by arboreal and/or shrubby plants, mainly represented by species such as *Mimosa bimucronata* (De. Candolle) Otto Kuntze, 1891, and *Cephalanthus glabratus* (Spreng) K. Schum, 1888.

Aquatic macroinvertebrate sampling. Macroinvertebrate sampling was carried out in two seasons: 1) September 2016 (austral spring), the period of the year that corresponds to the beginning of the reproductive period of waterbirds; and 2) May 2017 (austral autumn), corresponding to the waterbird post-reproductive period (PETRY & HOFFMANN, 2002; SCHERER *et al.*, 2006; ACCORDI & BARCELOS, 2006; SCHERER *et al.*, 2011).

On each sampling occasion (spring 2016 and autumn 2017), four subsamples were collected at each wetland with an aquatic frame dip-net (30-cm width; 250- μ m mesh size) (USEPA, 2002; BALDWIN *et al.*, 2005). Each subsample was represented by three 1-m sweeps, taken after kicking up the substrate and sweeping the disturbed area to capture dislodged or escaping individuals. Posteriorly, the four subsamples were pooled into a single sample and the collected material was fixed *in situ* with 10% formaldehyde. In the laboratory, the samples were sieved through a 250- μ m mesh and the aquatic macroinvertebrate individuals, collected under

stereomicroscope and identified to genus level whenever possible (FERNÁNDEZ & DOMINGUEZ, 2001; MERRITT *et al.*, 2008). All individuals were preserved in 80% ethanol and deposited in the aquatic macroinvertebrate collection of the Laboratory of Ecology and Conservation of Aquatic Ecosystems of UNISINOS. Data collection complied with current Brazilian environmental laws (SISBIO 53781-1).

Water and sediment variables. For nutrient content analysis, a 1-L water sample was collected at wetland in the first sampling occasion (September 2016), according to APHA (1998). In the two sampling occasions (autumn and spring seasons), the following water physicochemical variables were measured *in situ* with a multiparameter probe (HORIBA U-50): water temperature, pH, electrical conductivity, dissolved oxygen, oxygen saturation, total dissolved solids, turbidity and oxidation-reduction potential.

For the analysis of the percentage of organic matter, ~1-kg sediment sample was collected at each wetland in each sampling season for the analysis of the percentage of organic matter. The organic matter was determined after drying sediment at 60°C for 24h and burning it for 5h in an oven at 550°C (EMBRAPA, 2006).

Data analysis. Aquatic macroinvertebrate abundance and richness corresponded to the numbers of individuals and taxa collected at each pond, respectively. We used the Simpson's Diversity Index (Simpson's $D = 1-D$) to assess the dominance in aquatic macroinvertebrate communities.

After the detection of non-normal distribution and heteroscedasticity in the diversity data (values of Simpson's D) across treatments, we compared the diversity of aquatic macroinvertebrate communities between rookery and control ponds with a Mann-Whitney test.

We tested the effect of the presence of nesting waterbirds on aquatic macroinvertebrate richness and abundance with generalized linear mixed-effect models (GLMMs). As both response variables were discrete, we fit GLMMs with negative binomial distributions using maximum likelihood estimation (Laplace approximation). The presence of nesting waterbirds was included as fixed factor. In view of the repeated-measurements design and the consequent non-independence of data originating from the same pond, we investigated for the possible effects of the sampling period by running a set of different models. We ran models including the effect of the seasonal period as a random factor and another as fixed additive factor. We also ran a model including the interaction between the presence of nesting waterbirds and of the seasonal period. We compared the performance of the aforementioned models against null models (intercept only), and we performed model-selection procedures using the Akaike information criterion conditioned for small sample sizes (AICc) (BURNHAM & ANDERSON, 2002). We retained only the models with $\Delta AIC < 2$ for further inference.

We used stepwise multiple linear regressions with forward selection to investigate the relationships of the environmental variables with the richness and abundance of aquatic macroinvertebrates. We separately investigated the effects of the water physicochemical variables and the effect of nutrients. The analysis of the influence of the environmental variables was undertaken with the full set of seasonal sampling (two sampling periods), and the influence of the nutrients, with the subset of the first sampling period only.

We tested for differences in composition of aquatic macroinvertebrates between rookery and control ponds with a nonparametric multivariate analysis of variance (PERMANOVA) followed by 9999 permutations. We assessed the variation in the composition of aquatic macroinvertebrate communities using nonmetric multidimensional scaling ordination diagram (NMDS). The NMDS and PERMANOVA analyses were based on a dissimilarity matrix (Bray-Curtis index) of the log-transformed abundance data. For the assessment of the influence of the environmental variables on the composition of aquatic macroinvertebrate communities, we fitted the full set of water physicochemical variables and nutrients to the previously generated NMDS ordination diagram of the fauna. All analyses were performed in the statistical environment R (version 3.5.1) (R DEVELOPMENT CORE TEAM, 2018). We fit the GLMMs using the *glmer.nb* function of the package *lme4* version 1.1–15 (BATES *et al.*, 2015). We respectively run the ordination diagram, the PERMANOVA and the adjustment of the environmental variables with the functions *metaMDS*, *adonis* and *envfit* from package *vegan* version 2.5-3 (OKSANEN *et al.*, 2018).

RESULTS

The values of the means and standard deviation of the water physicochemical variables, nutrient content and organic matter of the sediment are listed in Table SI (Supplementary Material). We collected 11,471 individuals from 70 taxa in the studied wetlands. Overall, 4,455 individuals from 50 taxa were collected in the rookery wetlands, and 7,016 individuals from 57 taxa, in the control wetlands. Insecta was the most representative group, corresponding to the majority of the taxa sampled (54 taxa). Coleoptera was the richest insect order, represented by 17 taxa. Chironomidae was the dominant taxon, representing 45% of all macroinvertebrates collected, followed by *Pisidium* (Mollusca) and Oligochaeta (15.2% and 13.3% of the total individuals, respectively). In the rookery wetlands, Chironomidae was the dominant taxon (58.7% of the individuals), followed by *Bezzia* sp. (10.4%) and Oligochaeta (10%). In the control wetlands, Chironomidae, *Pisidium* and Oligochaeta were the dominant taxa (36.5%, 25% and 15.3% of the total number of individuals, respectively). In the first sampling season, 9,001 individuals from 60 taxa were collected, while 2,470 individuals from 47 taxa in the second sampling season. The majority of the macroinvertebrate taxa were sampled in both sampling seasons (Tab. I).

Macroinvertebrate communities in rookery wetlands showed higher dominance than control wetlands ($U = 10.5$, $gI = 1$, $P = 0.001$) (Fig. 2). Model selection procedures showed that the presence of nesting waterbirds and sampling seasons did not increase the explanatory power compared to the null model (*i.e.*, models without explanatory variables) for explaining the patterns of macroinvertebrate richness (Tab. II). Macroinvertebrate abundance was not influenced by the presence of nesting waterbirds either, although it varied between sampling seasons. Abundance was higher in the first collection (spring) (Tab. II, Fig. 3).

The output of the stepwise regressions indicated that macroinvertebrate richness was negatively influenced by turbidity and total dissolved solids ($R^2 = 0.40$, $df = 2$, 12 , $P = 0.017$) (Fig. 4A,B, respectively). Water nutrients did not influence macroinvertebrate richness ($R^2 = 0.165$, $df = 4$, $P = 0.32$). Water physicochemical variables did not influence the macroinvertebrate abundance ($R^2 = 0.131$, $df = 8$, $P = 0.47$). A marginally significant relationship was observed between macroinvertebrate abundance and nitrate and organic phosphorus ($R^2 = 0.52$, $df = 5$, $P = 0.06$) (Fig. 4C,D, respectively).

The macroinvertebrate composition did not change between rookery and control wetlands (pseudo- $F = 1.24$, $df = 1$, $P = 0.28$) (Fig. 5A), but differed according to the sampling season (pseudo- $F = 2.60$, $df = 1$, $P = 0.02$) (Fig. 5B). This effect was clearly displayed by two axes of the NMDS ordination diagram, which showed that some taxa were more associated with the first sampling season (spring), such as *Mesovelgia* Mulsant & Rey, 1852, *Belostoma*, *Isotoma*, *Ilybius*, *Tramea*, while *Derallus*, *Lissorhoptus*, Oribatidae, *Oxyagrion*, *Dampfius* and *Erythemis* were more closely associated with the second sampling season (autumn) (Fig. 5B).

Tab. I. List and number of specimens of aquatic macroinvertebrate taxa recorded in the control and rookery wetlands in each sampling season, southern Brazil.

Taxa	Spring		Autumn		Total
	Control	Rookery	Control	Rookery	
BASOMMATOPHORA					
Planorbidae					
<i>Biomphalaria</i>	105	5	9	1	120
Physidae					
<i>Stenophysa</i>	1	3			4
SORBEOCONCHA					
Ampullaridae					
<i>Thiaridae</i>	1				1
<i>Pomacea</i>	5	9	7	5	26
Hydrobiidae					
<i>Heleobia</i>	2			1	3
<i>Potamopyrgus</i>	1		22		23
VENEROIDA					
Sphaeriidae					
<i>Pisidium</i>	1,083	83	667	73	1,906
OLIGOCHAETA	1,028	171	49	277	1,525
RHYNCHOBDSELLIDA					
Glossiphonidae					
<i>Haementeria</i>	75	275	31	60	441
<i>Helobdella</i>	17	17	10	53	97
DIPTERA					
Chironomidae	2,385	2,513	172	97	5,167
Ceratopogonidae					
<i>Bezzia</i> sp.	133	240	512	221	1,106
Tabanidae					
<i>Tabanus</i>	36	12	21	10	79
Culicidae					
<i>Culex</i>	20	22	3	3	48
Tipulidae					
<i>Tipula</i>	14	1	18		33
Ephydriidae					
<i>Hydrellia</i>	10		1		11
Stratiomyidae					
<i>Euparyphus</i>	29	137	26		192
<i>Beris</i>	6		8	1	15
Dolichopodidae					
<i>Dolichopus</i>	1			2	3
Syrphidae					
<i>Eristalis</i>			6		6
Sciomyzidae					
<i>Sepedon</i>	1	1			2
COLEOPTERA					
Dytiscidae					
<i>Celina</i>	2	1			3
<i>Laccophilus</i>	14	15	7	6	42
<i>Ilybius</i>				1	1

Tab. I. Cont.

Taxa	Spring		Autumn		Total
	Control	Rookery	Control	Rookery	
Hydrophilidae					
<i>Hidrophilus</i>	2				2
<i>Enochrus</i>	2		1		3
<i>Berosus</i>		1			1
<i>Laccobius</i>		7			7
<i>Hydrobius</i>	4		2		6
<i>Hydrobiomorpha</i>				1	1
Heteroceridae					
<i>Derallus</i>		7			7
<i>Dampfius</i>	1				1
Noteridae					
<i>Suphisellus</i>	1			1	2
<i>Hydrocanthus</i>	8	4	1		13
Notonectidae					
<i>Notonecta</i>	1				1
<i>Buenoa</i>		2			2
Amphizoidae					
<i>Amphizoa</i>			2		2
Curculionidae					
<i>Lissorhoptrus</i>	1				1
HEMIPTERA					
Veliidae					
<i>Microvelia</i>	4	1	2		7
Belostomatidae					
<i>Belostoma</i>	7	5			12
Corixidae					
<i>Sigara</i>		11	1		12
Naucoridae					
<i>Naucoris</i>			1		1
<i>Ambrysus</i>		1			1
Pleidae					
<i>Neoplea</i>		2			2
Mesoveliidae					
<i>Mesovelia</i>				1	1
Gerridae					
<i>Gerris</i>				2	2
Gelastocoridae					
<i>Gelastocoris</i>		1	1		2
Homoptera					
<i>Delphacidae</i>			6	3	9
ODONATA					
Aeshnidae					
<i>Aeshna</i>	2	2	1		5
Coenagrionidae					
<i>Acanthagrion</i>	1	8	4	1	14
<i>Ischnura</i>	2	1	1		4
<i>Oxyagrion</i>	1				1

Tab. I. Cont.

Taxa	Spring		Autumn		Total
	Control	Rookery	Control	Rookery	
Libellulidae					
<i>Erythrodiplax</i>	6	14	9	5	34
<i>Erythemis</i>	3				3
<i>Micrathyrta</i>	5	3	7		15
<i>Perithemis</i>		1			1
<i>Orthemis</i>	1	2	9	6	18
<i>Tramea</i>	2				2
EPHEMEROPTERA					
Baetidae					
<i>Callibaetis</i>	179	26	4		209
Caenidae					
<i>Caenis</i>	22		4		26
Leptophlebiidae					
<i>Leptophlebia</i>			1		1
TRICHOPTERA					
Hydroptilidae					
<i>Oxyethira</i>		2			2
<i>Ochrotrichia</i>	8				8
Rhyacophilidae					
<i>Rhyacophila</i>				1	1
COLLEMBOLA					
Isotomidae					
<i>Isotoma</i> sp.	8				8
<i>Isotomurus</i> sp.	2	4	3	1	10
Poduridae					
<i>Podura</i>	2		4	2	8
HYDRACARINA					
Oribatidae	1	9			10
DECAPODA					
Sesarmidae					
<i>Armases</i>	2		1		3
ISOPODA					
Aseliidae					
<i>Asellus</i>	135			1	136
Total	5,382	3,619	1,634	836	11,471

The water physicochemical variables significantly correlated with macroinvertebrate composition were water temperature ($R^2 = 0.79$, $P = 0.002$), oxidation-reduction potential ($R^2 = 0.35$, $P = 0.035$) and water turbidity ($R^2 = 0.48$, $P = 0.023$). The organic matter of sediment was also significantly correlated with macroinvertebrate composition ($R^2 = 0.49$, $P = 0.024$) (Fig. 5B). Water temperature and

sediment organic matter showed the highest values in the first sampling season (spring), while water turbidity and oxidation-reduction potential showed the highest values in the second sampling season (autumn) (Fig. 5B). In the first sampling season, orthophosphate was the water nutrient variable significantly correlated with macroinvertebrate composition ($R^2 = 0.8$, $P = 0.026$) (Fig. 5C).

Tab. II. Output of the model selection procedures for the effects of the presence of nesting birds and sampling season on the richness and abundance of aquatic macroinvertebrates in southern Brazil. Values in parentheses indicate standard errors. All results are given in the log-scale (df, degrees of freedom).

Response variable	Best model	Intercept	Fixed factors		AIC	df	Akaike weight
			Bird presence	Season (spring)			
Richness	~1	17.3	-	-	0	2	0.71
Abundance	~ Bird presence + Season	6.01 (0.32)	5.61 (0.37)	7.19 (0.75)	0	4	0.84

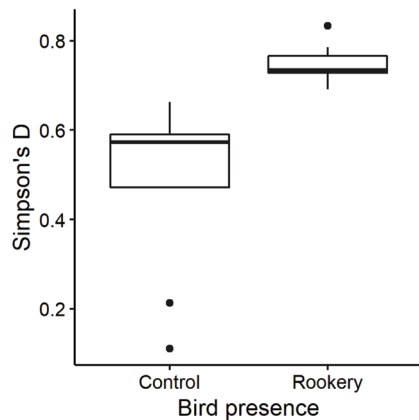


Fig. 2. Simpson's diversity index of the macroinvertebrate communities in control and rookery wetlands in southern Brazil.

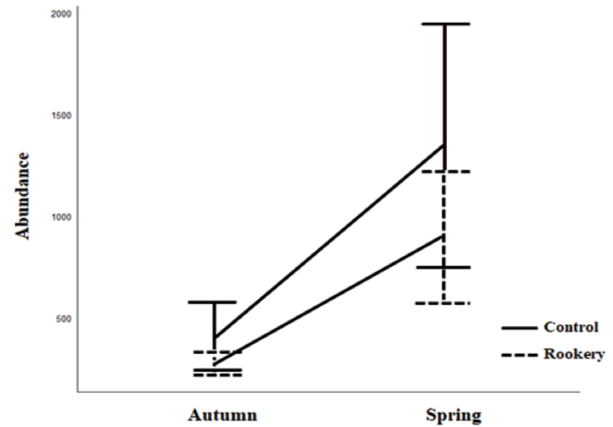


Fig. 3. Abundance of aquatic macroinvertebrates in control and rookery wetlands in each sampling season, southern Brazil. Whiskers indicate upper and lower 95% confidence intervals (\pm standard error).

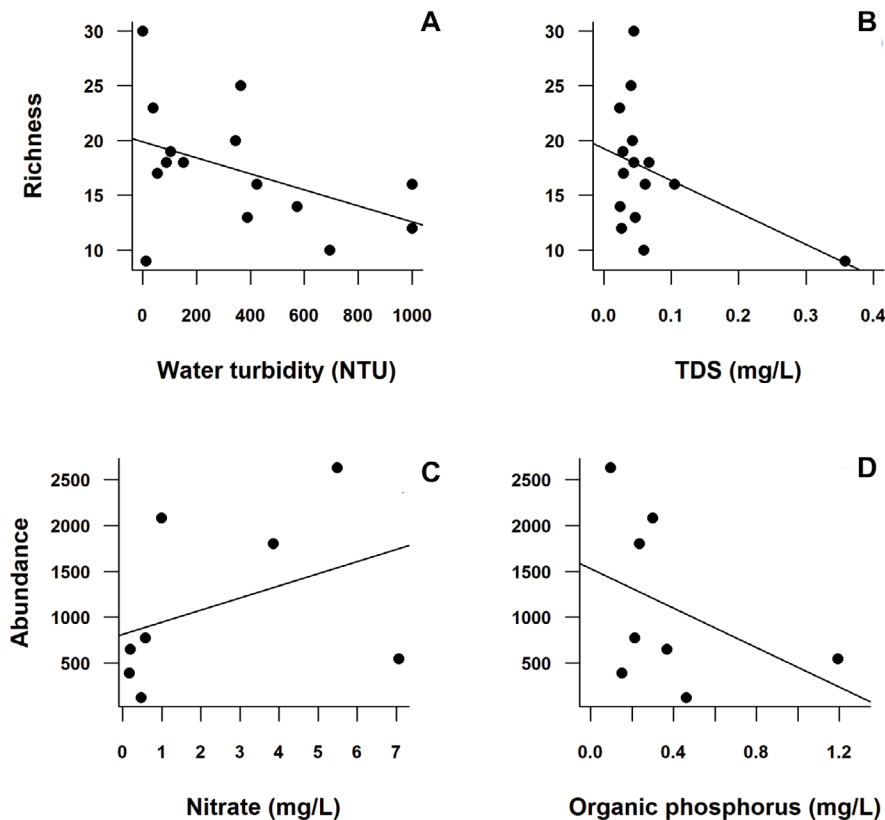


Fig. 4. Relationships between the richness of aquatic macroinvertebrate communities and water turbidity (A), total solids dissolved (B). Relationships between the abundance of aquatic macroinvertebrates and nitrate (C) and organic phosphorus (D)(TDS, total dissolved solids).

DISCUSSION

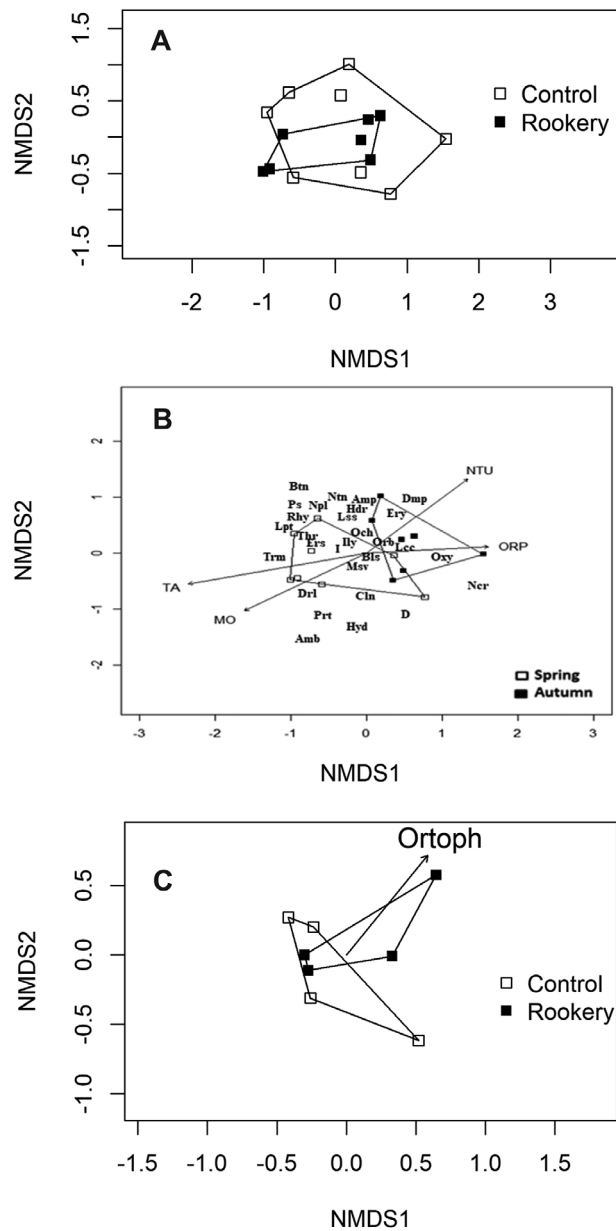


Fig. 5. NMDS ordination diagram of (A) the composition of aquatic macroinvertebrate communities in control and rookery wetlands in southern Brazil; (B) NMDS ordination diagram of the composition of aquatic macroinvertebrate communities and sampling seasons. Red arrows indicate the water physicochemical variables significantly correlated ($P < 0.05$) with the ordination, as detected by the *envfit* procedure. Abbreviation of water physicochemical variables: T (water temperature), MO (organic matter in the sediment), NTU (water turbidity); ORP (oxidation-reduction potential). Taxa abbreviation: *Physa/Stenophysa* (Ps), *Thiaridae* (Thr), *Sepedon* (Spd), *Celina* (Cln), *Hidrophilus* (Hdr), *Dampfius* (Dmp), *Notonecta* (Ntn), *Lissorhoptrus* (Lss), *Belostoma* (Bls), *Oxyagrion* (Oxy), *Tramea* (Trm), *Erythemis* (Ery), *Ochrotrichia* (Och), *Isotoma* sp. (I), *Oribatidae* (Orb), *Leptophlebia* (Lpt), *Eristalis* (Ers), *Amphizoia* (Amp), *Naucoris* (Ncr), *Delphacidae* (D), *Rhyacophila* (Rhy), *Mesovelgia* (Msv), *Gerris* (Grr), *Ilybius* (Ily), *Hydrobiomorpha* (Hyd), *Berosus* (Brs), *Laccobius* (Lcc), *Derallus* (Drl), *Buena* (Bun), *Ambrysus* (Amb), *Neoplea* (Npl), *Perithemis* (Prt). (C) projection of the water nutrients significantly correlated ($P < 0.05$) with the ordination of aquatic macroinvertebrate communities in the first sampling season (spring 2016), as detected by the *envfit* procedure (Ortoph, orthophosphate).

The richness of aquatic macroinvertebrates observed in the studied wetlands was similar to other studies developed in southern Brazilian intermittent wetlands (STENERT & MALTCHIK, 2007; STENERT *et al.*, 2008; MALTCHIK *et al.*, 2010; BOELTER *et al.*, 2018). Aquatic insects represented the majority of the wetland invertebrate fauna. The large dominance of insects is related to several life-history traits that allow their survival to temporary habitats (WILLIAMS, 2006). In particular, morphophysiological characteristics of insects such as egg resistance, the presence of wings which facilitate dispersal and the occurrence of terrestrial life stages in many insect species favor their adaptation to the wet-dry periods typical of intermittent wetlands (WILLIAMS, 2006; MERRITT *et al.*, 2008). Chironomidae was the most representative group (45% of the total number of individuals collected). Previous studies also observed the dominance of Chironomidae in southern Brazilian wetlands and across several regions of the world (ÁVILA *et al.*, 2011; SIGNA *et al.*, 2015; DAMANIK-AMBARITA *et al.*, 2016; PIRES *et al.*, 2016; BOELTER *et al.*, 2018; CHAWAKA *et al.*, 2018). The high dominance of Chironomidae in wetlands may be associated with their tolerance to adverse conditions, such as low oxygen levels and high organic load (DE HAAS *et al.*, 2006; SIGNA *et al.*, 2012).

The macroinvertebrate richness, abundance and composition in the studied wetlands did not change according to the presence of colonies of nesting waterbirds. Therefore, the two expectations of the study were not corroborated. This result contrasts with previous studies that detected relationships between the occurrence of nesting waterbirds and macroinvertebrate community structure in wetlands (MURKIN & KADLEC, 1986; WRUBLESKI, 1989; WISZ *et al.*, 2013; SIGNA *et al.*, 2015). For instance, GUARESCHI *et al.* (2015) showed that waterbird presence was negatively correlated to aquatic macroinvertebrate richness, while ROONEY & BAYLEY (2012) observed a weak correlation between waterbird and invertebrate communities in Canadian ponds. SIGNA *et al.* (2015) observed that the input of waterbird feces decreased the macroinvertebrate abundance and diversity in Italian pond systems.

The lack of influence of nesting waterbirds on the community structure of aquatic macroinvertebrates could be related to the low number of individuals in the rookery wetlands studied. In the studies that found relationship between macroinvertebrate community structure and waterbird occurrence (MURKIN & KADLEC, 1986; WRUBLESKI, 1989; WISZ *et al.*, 2013) the abundance of nesting waterbirds ranged between 4,000 and 45,000 individuals, *i.e.*, much higher than the bird populations observed in this study.

Another possible reason for the absence of effect of nesting waterbirds on macroinvertebrate communities is the variation in the reliance on macroinvertebrates for consumption along waterbird life cycles and among species. Specifically, the rate of consumption by waterbirds differs according the phases (*i.e.*, among reproduction, development,

feather substitution phases, etc.) (ANDREI *et al.*, 2008; ZMUDCZYŃSKA-SKARBK *et al.*, 2015). In addition, there is large interspecific variation in the diet types and foraging modes among waterbird species (STAFFORD *et al.*, 2016). That is, such differences could lead to varying effects of waterbirds on macroinvertebrates either among species or seasons. In this study, the composition of waterbirds varied among wetlands and could be related to the lack of systematic effect.

Although the community structure of aquatic macroinvertebrates did not change between rookery and control wetlands, the richness and composition were influenced by the water nutrients and physicochemical variables. Richness was negatively influenced by water turbidity and total dissolved solids, and the composition was influenced by water temperature, oxidation-reduction potential, turbidity, sediment organic matter, and orthophosphate. Many studies detected relationships between water physicochemical variables and macroinvertebrate communities in wetlands (ZIMMER *et al.*, 2000; BATZER *et al.*, 2004; STENERT & MALTCHIK, 2007; STENERT *et al.*, 2008; TOKESHI & ARAKAKI, 2012; BISCHOF *et al.*, 2013; STRACHAN *et al.*, 2015; BARROS *et al.*, 2016; GLEASON & ROONEY, 2017; ROMERO *et al.*, 2017; BALDWIN *et al.*, 2018). Some authors detected reductions in macroinvertebrate richness with increasing turbidity (BATZER, 2013; JOHNSON *et al.*, 2013; SUNDBERG *et al.*, 2016; BALDWIN *et al.*, 2018). Elevated turbidity is associated with a higher number of suspended organic and inorganic matter in the water, usually due to the allochthonous material input and the sediment stirring (GONÇALVES *et al.*, 2012; DAVIES-COLLEY & SMITH, 2001; KARNA *et al.*, 2015), which can significantly impact the aquatic biota (BILOTTA & BRAZIER, 2008), including the macroinvertebrate community (JONES *et al.*, 2012). Organic matter (detritus particles and other kinds of food, such as phytoplankton, periphytic algae, and bacteria) is one of the main food item of wetland macroinvertebrates (BRÖNMARK & HANSSON, 1998). PIEDRAS *et al.* (2006) observed a positive relationship between densities of Oligochaeta and Chironomidae with sediment organic matter in lentic habitats. In our study, the macroinvertebrate community was dominated by collectors and scrapers, such as Oligochaeta, dipterans, mollusks, and gastropods, *i.e.* taxa that feed on suspended particles in the water column (MERRITT *et al.*, 2008). This result may explain the effect of sediment organic matter on the macroinvertebrate composition.

Macroinvertebrate abundance and composition varied over the seasons in this study. Seasonal changes in the community structure of aquatic macroinvertebrates in temporary wetlands are described in the literature. STENERT *et al.* (2008) and KRAJENBRINK *et al.* (2019) observed seasonal changes in macroinvertebrate richness over the time in ponds. Temporal variations in macroinvertebrate abundance, richness, and composition may be due to the alterations of

the water physical and chemical variables observed over the time in lentic habitats (TUNDISI & MATSUMURA-TUNDISI, 2008; GLEASON & ROONEY, 2017; ROMERO *et al.*, 2017; BALDWIN *et al.*, 2018; CHAWAKA *et al.*, 2018). Intermittent wetlands alternate wet and dry cycles over time, and the duration of the drought period is considered the major force driving the composition of macroinvertebrates (WELLBORN *et al.*, 1996; WILLIAMS, 1998, 2006). In addition, seasonal changes in climate can also affect macroinvertebrate composition, as several taxa have their life cycles attached to temperature in subtropical regions (DALLAS & ROSS-GILLESPIE, 2015).

In summary, our results showed that the nutrients and physicochemical variables in the water and sediment along with seasons influenced the aquatic macroinvertebrate communities in the studied wetlands rather than the occurrence of nesting colonies of waterbirds. Although our study did not detect significant relationships of aquatic macroinvertebrate community structure with the presence of nesting waterbirds (in contrast with the original expectations), this study is, to our knowledge, the first attempt to relate patterns in wetland macroinvertebrate communities and waterbirds in subtropical regions from Brazil. These results are loosely in accordance with the reviews describing unpredictable relationships of wetland macroinvertebrate and their potential predators (BATZER, 2013) and with other findings that suggest that relationships between the waterbirds and their invertebrate prey vary among study regions and are dependent on several contingencies (SANDERS, 2000; MA *et al.*, 2010; STAFFORD *et al.*, 2016). Nevertheless, the relationships between nutrient enrichment and macroinvertebrate communities detected in the wetlands could have been associated with waterbird presence, suggesting the need for future studies. A deeper understanding of the ecological interactions between these groups is of fundamental importance for wetland ecology and waterbird conservation in southern Brazil, since wetlands in southern South America are important habitats for many resident and migratory waterbird species (CBRO, 2016). Finally, we highlight the need to take into account different sampling periods for the assessment of the effects of nesting colonies on macroinvertebrate communities in southern Brazil (PETRY & HOFFMANN, 2002; PETRY & FONSECA, 2005; SCHERER *et al.*, 2006, 2011, 2014; PETRY & SCHERER, 2008).

Supplementary material. The following online material is available for this article: Mean and standard deviation (\pm) of the physical and chemical variables of water, nutrients and organic matter of the sediment in the control and rookery wetlands.

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