

# Spatial patterns of macrofaunal community structure in coastal lagoons of Uruguay

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**ABSTRACT:** The spatio-temporal variability of macrobenthic communities was investigated in the 5 main coastal lagoons of Uruguay, and faunal responses to environmental variables were evaluated. This is the first study that addresses spatial and temporal variability simultaneously for benthic subtidal communities of the coastal lagoons in Uruguay. Sampling was conducted in February, May, August, and November 2005, covering 3 spatial scales: lagoons, sites, and replicates. The lagoons were compared through environmental variables, using permutational multivariate analysis of variance and principal coordinates analysis. In addition, distance-based linear model analysis was performed to analyze which environmental variables best determined the macrobenthic community. The benthic community was characterized by a low number of species and high dominance. The most important difference in community structure occurred between Diario, a closed, eutrophic lagoon, and the other lagoons, which are intermittently connected with the ocean. Ocean–land gradients in community structure were observed within all lagoons. Greatest variability in community structure was observed at the largest spatial scale (among lagoons) and at the smallest scale (among replicates). Therefore, both large- and small-scale processes may shape the spatial patterns of these macrobenthic communities. The environmental variables that best explained the macrobenthic community structure were total suspended solids, conductivity, sediment organic matter, phytobenthic chlorophyll *a*, and macrophyte total biomass. Short-term temporal variability explained a small fraction of the total variation in comparison with spatial variation between lagoons.

**KEY WORDS:** Spatial patterns · Macrobenthos · Multiple scales of variability · Atlantic coastal lagoons

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## INTRODUCTION

The structure of macroinfaunal assemblages of marine and brackish water is patchy at several spatial scales (Thrush et al. 1989, Edgar & Barret 2002, Hewitt et al. 2002, Ysebaert & Herman 2002). Therefore, the identification of relevant distribution patterns at multiple spatial scales is necessary to

formulate possible explanations of the ecological processes or anthropogenic impacts structuring ecosystems (Underwood & Chapman 1996, Ysebaert et al. 2003).

Fraschetti et al. (2005) reviewed the scale variation of benthic marine assemblages and found that few studies had examined their spatial and temporal variations simultaneously. More recently, only a few

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studies have analyzed both dimensions of such communities simultaneously (França et al. 2009, Kraan et al. 2009). However, the dynamic nature of biological communities suggests that scale-dependent patterns may change through time in response to seasonal and other factors. This is particularly true for estuarine and coastal lagoon communities since they experience a highly dynamic environment owing to temporal variations in environmental factors, such as salinity, temperature, and water run-off, which may occur at scales of days, weeks, months, and seasons (Elliott & Whitfield 2011). When organisms migrate or die in response to these factors, temporal changes in the spatial patterns are expected (Coma et al. 2000).

Patterns of diversity and abundance in coastal lagoons respond to tidal level (e.g. intermittent estuaries from Australia, Currie & Small 2005), sediment characteristics (e.g. South African estuaries, Teske & Wooldridge 2003; intertidal macrofauna in Uruguayan lagoons, Giménez et al. 2006), distance to the ocean (South Africa, Teske & Wooldridge 2004; Australia, Dye 2006), and lagoon type (e.g. South Africa, Teske & Wooldridge 2003). These examples show that lagoon macrofauna may vary at large scales (among lagoons) as well as at intermediate scales (in response to factors varying among lagoonal sectors) and small scales (in response to tidal level and sediment characteristics).

In the eastern littoral zone of Uruguay, several coastal lagoons are connected to the Atlantic Ocean (Isla 2009). The Uruguayan coastal lagoons are priority sites for biodiversity conservation and sustain important inland fisheries which make up ecological (Brazeiro et al. 2008, Soutullo et al. 2010) and economical resources of significant importance (Fabiano & Santana 2006) in the region. However, we still do not have a clear picture of the distribution patterns of subtidal macrofauna at most of the relevant spatial and temporal scales of variation in these lagoons. Previous studies have focused on particular lagoons (e.g. Jorcín 1999, Giménez et al. 2006), and studies covering both large and small scales are restricted to the inundation flats (Giménez et al. 2005) or the subtidal brackish sector of one lagoon (Muniz et al. 2012). None of these studies examined spatial and temporal variation simultaneously at different scales.

In the present work, the spatial and short-term temporal variation of the macrobenthic communities of 5 coastal lagoons in Uruguay was evaluated at different scales: lagoon, sectors within each lagoon, and replicate samples within each sector. In addition, we evaluated whether the amount of variation found at

each spatial scale is consistent through time. Finally, we evaluated faunal responses to environmental variables.

## MATERIALS AND METHODS

### Study sites

The lagoons considered in this study are Castillos, Rocha, Garzón, José Ignacio, and Diario (Fig. 1). José Ignacio, Garzón, and Rocha coastal lagoons periodically connect to the ocean through a breach that is opened (naturally or artificially) in their sand bars (Table 1). In the case of Castillos, the connection with the ocean occurs by way of a stream that also periodically opens to the ocean through a breach in the sand bar (Wells & Daborn 1998, Rodríguez-Gallego et al. 2012). The lagoons are considered 'choked,' according to the geomorphologic classification of Kjerfve (1994), and are characterized by a single long narrow entrance channel. These lagoons are shallow water bodies (<3 m depth) with brackish waters (salinity range 0.5 to 12.5). In these systems, water fluxes converge; fresh water comes from the continent and salty water from the ocean. Due to this physical phenomenon, biotic communities of coastal lagoons show very dynamic changes both in time and space (Conde et al. 1999, Bonilla et al. 2005, Piccini et al. 2006); this is also true for physico-chemical properties, such as salinity (Wells & Daborn 1998). Diario lagoon was an intermittent coastal lagoon but since 1950 has been separated from the ocean due to the artificial closure of its sandbar during the building of a road (Table 1).

### Sampling design

Sampling was conducted in February, May, August, and November 2005. Generally, we collected samples in seaward, middle, and inward sites; in inward sites, samples were taken near the outlet of the main tributaries and at sites where submerged aquatic vegetation is frequently found (except in José Ignacio lagoon, where such vegetation was absent during the study period). In José Ignacio, Garzón, and Rocha lagoons, we selected 4 sampling sites: 2 inward bays (NW and N), and the central (C) and seaward zones (S). In Diario, we only took samples in the seaward and inward zones (S and N), because a central zone was not definable due to the lack of a salinity gradient. In Castillos lagoon, a sea-

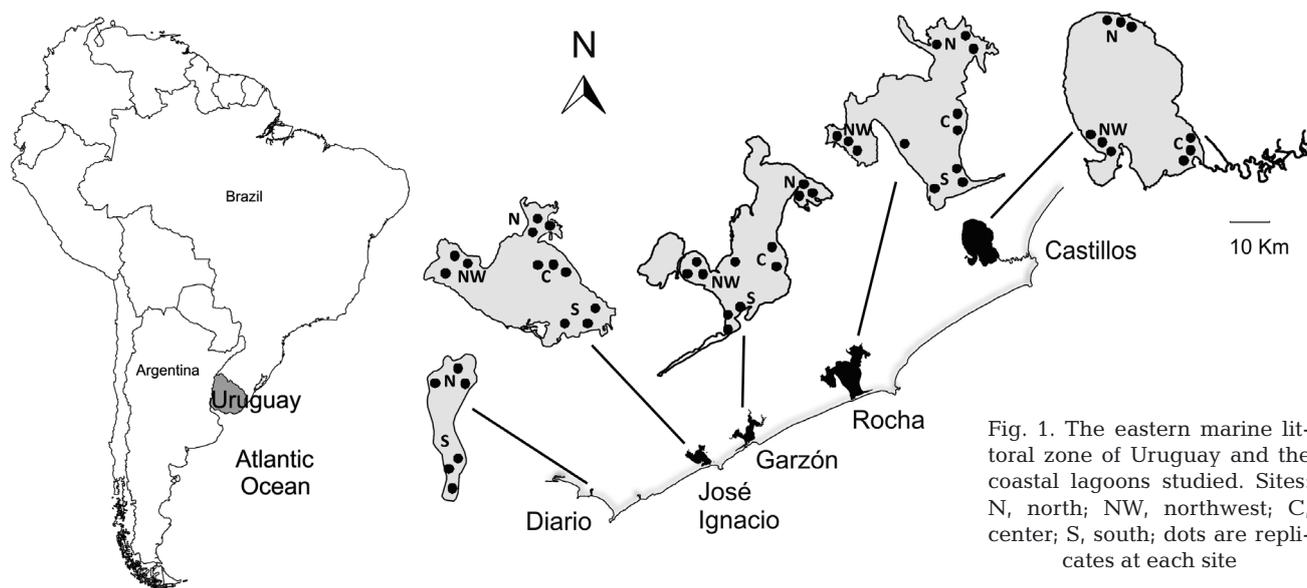


Fig. 1. The eastern marine littoral zone of Uruguay and the coastal lagoons studied. Sites: N, north; NW, northwest; C, center; S, south; dots are replicates at each site

ward zone was not sampled because according to the morphology of the system, this zone would theoretically be located in the Valizas stream, which has fluvial dynamics. We collected samples at 3 sites in Castillos lagoon (NW, N, C; Fig. 1). Three replicates were collected at each sampling site for all variables. Lagoons were separated by 10 to 40 km, sites were separated by 1 to 10 km, and replicates were taken at distances of 30 to 60 m.

Sampling sites were located with a GPS (Garmin 12) configured with the Geographic Military National Service coordinates (Gauss Projection, contact meridian 62G). At each sampling site, we designed a  $3 \times 3$  grid of squares of  $30 \times 30$  m each. At each sampling, 3 squares were sorted, and 1 replicate per square was obtained. Therefore, 3 replicates for all biotic and abiotic variables were obtained at each sampling site. Thus, 18 sites in total were visited during the 4 sampling occasions (Fig. 1).

At each site, we collected macrobenthos, hydrophytes, sediment, and water samples; in addition, abiotic *in situ* variables were measured (depth, conductivity, dissolved oxygen, water temperature). Benthos and hydrophytes were collected with an Ekman grab ( $0.05 \text{ m}^2$ ). The content of the grabs was separated from the sediment through a  $0.5 \text{ mm}$  mesh sieve with constant water flux. Macrophytes were separated into species and dried at  $70^\circ\text{C}$  for 48 h to determine dry weight. The remaining sediment was separated on a  $0.5 \text{ mm}$  mesh sieve. The fauna was preserved in formalin (10%), separated under a stereomicroscope, identified, and counted (Chu 1949, Lopretto & Tell 1995, Trivinho-Strixinio & Strixinio 1995). Sediment samples were manually col-

lected down to a depth of 2 cm using acrylic corers (5 cm in diameter). The organic content of the sediment was determined by ignition (APHA 1985), total nitrogen and total phosphorus were measured according to Valderrama (1981), and microphytobenthos abundance was estimated using chlorophyll *a* (chl *a*) extraction with 90% acetone (Lorenzen 1967). Abiotic *in situ* variables were measured with field equipment: depth (sounding line), conductivity (Horiba D-24), temperature, and dissolved oxygen (Horiba D-25). Salinity was derived from conductivity using a conversion factor of 0.6 (Margalef 1983). Water samples were manually taken below the surface with a Ruttner bottle to determine total suspended solids (according to APHA 1985) and chl *a* (90% acetone; Lorenzen 1967).

### Data analysis

Data were analyzed through the following steps: (1) determination of the variability in macrofauna among lagoons and sectors; (2) characterization of the variation in environmental parameters; and (3) determination of relationships between macrofauna and environmental parameters.

#### Scale-dependent variation in macrofauna

The multivariate structure of the community was evaluated with permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, McArdle & Anderson 2001) with square root transformed

Table 1. Main features of 5 Atlantic coastal lagoons in Uruguay. TSS: total suspended solids; DW: dry weight

Site	Lagoon area (km <sup>2</sup> ) <sup>a</sup>	Basin area (km <sup>2</sup> ) <sup>a</sup>	Main tributaries <sup>a</sup>	Distance to coast (km) <sup>a</sup>	Mean depth (m) <sup>a</sup>	Oceanic influence <sup>a</sup>	Connection to ocean <sup>a</sup>	Hydrological regime <sup>a</sup>	Salinity (mg l <sup>-1</sup> )	Dissolved oxygen (mg l <sup>-1</sup> )	TSS (mg l <sup>-1</sup> )	Sediment organic matter (mg g <sup>-1</sup> DW)
Diario	0.5	1.5	1	0.05	<1	Non-direct (drain)	Highly infrequent	Artificially isolated from the sea	0.95	8.5	19	132
José Ignacio	13	848	2	0.1	<0.5	Direct	High periodicity	Natural/artificial	11.75	9.6	16	19
Garzón	18	695	2	0.1	<0.5	Direct	Infrequent	sandbar opening Natural/artificial	7.3	9.2	45	36.5
Rocha	72	1.312	4	0.1	0.6	Direct	High periodicity	Natural/artificial sandbar opening	10.3	9.4	51	18.5
Castillos	90	925	2	12	1.5	Non-direct (stream)	High periodicity	Natural/artificial sandbar opening	2.3	9	43	15

<sup>a</sup>Modified from Conde & Rodríguez-Gallego (2002). Data without a superscript are mean values from the present work

density data and using the Bray-Curtis similarity index (Bray & Curtis 1957). In total, 9999 non-restricted permutations were used in all tests. A *posteriori* comparisons were also performed. In addition, a test of permutational multivariate dispersion (PERMDISP: Anderson 2006, Anderson et al. 2006) was used to determine whether there were differences in dispersion within the groups, based on the distance of samples to the group centroid. The design was based on 3 factors: (1) lagoon (5 levels, random factor), (2) site (nested in lagoon, random factor), and (3) time (sampling occasion, 4 levels, fixed factor), plus the appropriate interaction terms. The tests for differences in the locations between groups in the multivariate space (as PERMANOVA) are sensitive to differences in dispersion among groups. The rejection of the null hypothesis for PERMANOVA suggests that the groups can differ in their location, relative dispersion, or both. The PERMDISP analysis is used together with PERMANOVA to assist in identifying the possible reasons to reject the null hypothesis.

For PERMANOVA the relative importance of the factors and their interactions was quantified through the estimates of component of variation; these estimates are analogues of the estimators of variance components (Anderson & Gorley 2008). In addition, the different components of multivariate variance were compared using different transformations of the data, since data transformation determines the relative contribution of quantitative differences between samples in the final output of the multivariate analysis (Anderson et al. 2005). Multivariate patterns were visualized through principal coordinates analysis (PCO; Gower 1966), with the benthos density data of all replicates. This visualization was performed using the same transformations and matrix as the one for PERMANOVA.

#### Environmental variability

To analyze the multivariate structure of the environmental variables, we performed principal components analysis (PCA) for each sampling occasion, for the physico-chemical variables; we also included total biomass and richness of macrophytes, and phytobenthos chl *a*. Data were previously normalized (i.e. original value minus average and divided by the standard deviation).

Environmental variables and benthos total abundance were also compared between times (sampling occasions), lagoons, sites, and replicates. ANOVA

was used in cases where homoscedasticity and normality assumptions were satisfied (Bartlett and Cochran test). Differences were tested using a Tukey test *a posteriori* (Zar 1999). In cases where variables did not conform to the underlying assumptions, we used log transformation; transformed data were checked again and were normally distributed with homogeneous variance.

#### Relationships between macrofauna and environmental variables

To identify associations between macrofaunal patterns and environmental variables, distance-based linear models analysis (DistLM) was conducted based on data previously transformed to  $\log(x+1)$  and Bray-Curtis similarity (McArdle & Anderson 2001).

The ordination analyses and multivariate analyses of the community structure were done with the software PRIMER v6 (Clarke & Gorley 2006) that includes PERMANOVA+ in the package (Anderson & Gorley 2008). We also conducted multiple regressions (forward stepwise method, with data previously transformed to  $\log[x+1]$ ) to evaluate which variables were influential in determining the abundance of the main benthic species.

## RESULTS

### Macrofaunal patterns

The 4 intermittent coastal lagoons showed similar taxonomic composition (Table 2, Fig. 2) which was mainly represented by estuarine species. However, there were differences in the dominant species in each system (Fig. 2). The gastropod *Heleobia australis* was the dominant species in Rocha (49%) and Garzón (50%) lagoons; in Castillos, the dominant species was the bivalve *Erodona mactroides* (49%) while in José Ignacio, the dominant species was the polychaete *Nephtys fluviatilis* (47%). Diarío lagoon differed from the other lagoons in that the community was represented by freshwater taxa (Table 2, Figs. 2 & 3A). In this lagoon, the most abundant groups were Chironomidae (61%), Hirudinea (6.7%), Oligochaeta (7%), and the invasive bivalve *Corbicula fluminea* (6%). Given the differences in community composition, we conducted separated sets of analyses for (1) all 5 lagoons and (2) the 4 open/closed lagoons.

The community structure of the benthos varied significantly among lagoons, sites, and time (Table 3). The largest component of variation was the variability between lagoons, followed by the variation within sites (between replicates).

Table 2. Benthic species richness (no. of species; mean value for each lagoon on the 4 sampling occasions) and taxonomic composition of macrobenthos in the 5 lagoons. 'x' indicates presence at that site

Lagoon	Castillos	Rocha	Garzón	José Ignacio	Diarío
Species richness	6	9.75	8	7.75	11
Taxon					
Mollusca					
Gastropoda					
<i>Heleobia australis</i>	x	x	x		
Bivalvia					
<i>Erodona mactroides</i>	x	x	x	x	
<i>Tagelus plebeius</i>	x	x		x	
Annelida					
Polychaeta					
<i>Nephtys fluviatilis</i>	x	x	x	x	
<i>Heteromastus similis</i>	x	x	x	x	
<i>Laonereis acuta</i>	x	x	x	x	
Crustacea					
Isopoda					
<i>Dies fluminensis</i>	x	x	x	x	
Decapoda					
<i>Cyrtograpsus angulatus</i>		x	x	x	
Tanaidacea					
<i>Sinelobus stanfordii</i>	x	x			
Cirripedia					
<i>Balanus improvisus</i>		x	x	x	
Mollusca					
Bivalvia					
<i>Corbicula fluminea</i>					x
Insecta					
Chironomidae					x
Ephemeroptera					x
Himenoptera					x
Heteroptera					x
Odonata					x
Tricoptera					x
Coleoptera					x
Annelida					
Hirudinea					x
Oligochaeta					x
Crustacea					
Amphipoda					x

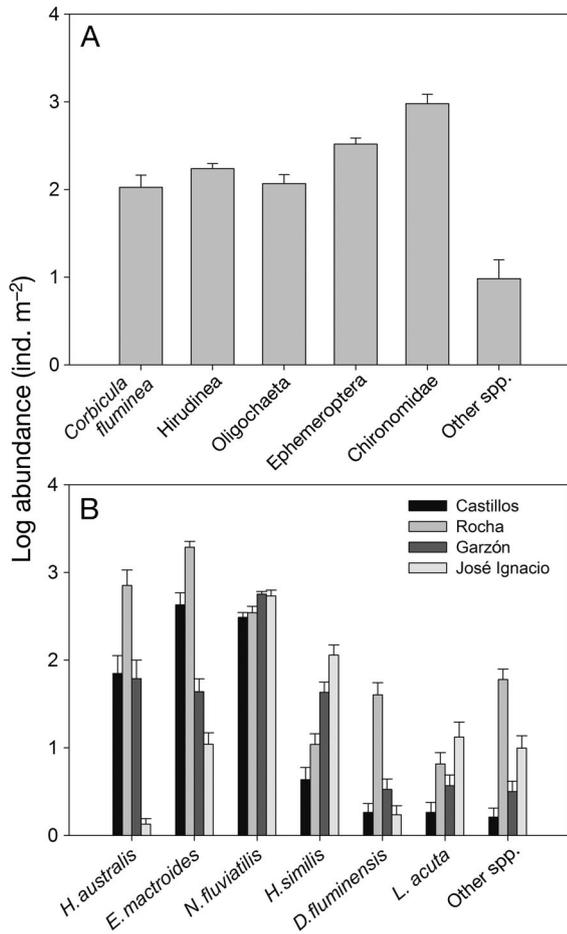


Fig. 2. Abundance (mean ± SE) of the main species/taxa of macrobenthos in 5 coastal lagoons of Uruguay: (A) Diario, (B) Castillos, Rocha, Jose Ignacio, and Garzón lagoons

The total macrofaunal abundance was significantly different among sampling occasions and lagoons with the magnitude of spatial variation depending on time (significant interaction of lagoon × sampling occasion: Fig. 4, Table 4). Multivariate analyses also showed variability among the 4 estuarine lagoons (Fig. 3B); no significant dispersion was observed among lagoons (Table 5). Within each lagoon, we also found significant variation among sites, with the seaward sites differing from inward sites (Fig. 5). The PERMDISP analysis did not show significant differences in the homogeneity of dispersion among lagoons or among sampling occasions (Table 5).

In terms of variance components, in the 4 intermittent coastal lagoons, the most important variation occurred among lagoons and among replicate samples within each site (Fig. 6), with the percentage depending on data transformation (lagoons: 36 to 37%; replicate sites: 20 to 30%). However, irrespective of transformation, variation in time or variation among sites was consistently low (8 to 12%).

**Environmental variability**

Multivariate analyses of environmental variables (Table 6, Fig. 7) showed that Diario lagoon differed consistently from the other lagoons. Diario was characterized by a high content of organic matter in the sediment, high depth of the water column, high biomass of macrophytes, and low water conductivity.

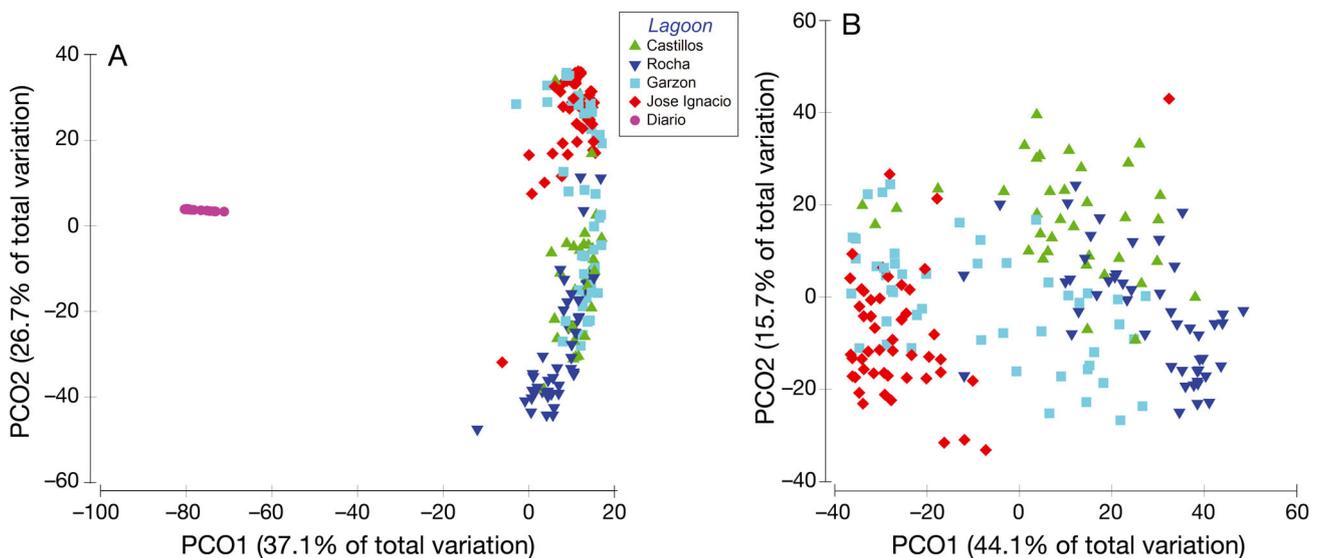


Fig. 3. Principal coordinates analysis for (A) all 5 studied coastal lagoons and (B) only the 4 intermittent lagoons (Castillos, Rocha, Garzón, and José Ignacio). Analysis was done from the species abundance matrix of all seasonal samplings; square root transformed data and Bray-Curtis distance were used

The intermittent lagoons were characterized by higher total suspended solids, conductivity, and phytoplankton chl *a* (Fig. 7).

Spatial variability was observed for different environmental variables within each lagoon. In Castillos, water column depth at the NW and N sites (mean value 1.2 m) was higher than at C (0.8 m); spatial

variability was also observed in phytoplankton chl *a* (NW = 21.8, N = 6.5, C = 13.4  $\mu\text{g g}^{-1}$ , mean values). In Rocha lagoon, phytoplankton chl *a* also presented spatial variability (N-NW = 24.1, C-S mean = 9.6  $\mu\text{g g}^{-1}$ ). Phytoplankton chl *a* was also spatially heterogeneous in Garzón lagoon (N-NW = 53.8, C = 13.6, S = 23.6  $\mu\text{g g}^{-1}$ , mean values).

Table 3. Permutational multivariate analysis of variance based on the Bray-Curtis dissimilarity index for square root transformed data of the benthos abundances of 5 coastal lagoons in Uruguay. The analysis was done using 9999 permutations of the residuals under a reduced model. The estimation of multivariate variation at each scale was also included

Source	df	MS	F	p	Variance component (%)
Lagoon	4	63178	19.574	0.001	38
Season	3	3046.2	5.385	0.001	7
Site(lagoon)	12	3227.7	79.122	0.001	9
Lagoon × Season	12	1237.1	21.869	0.06	10
Site(lagoon) × Season	36	565.68	13.867	0.065	8
Residual	136	407.94			23
Total	203				

### Relationship between benthic community and environmental variables

The environmental variables that best explained the benthic community structure of the 5 coastal lagoons of Uruguay were: suspended solids, sediment organic matter, depth, phytoplankton chl *a*, and macrophyte total biomass (Table 7). The general response to environmental variables did not change when the analysis was restricted to the 4 intermittent

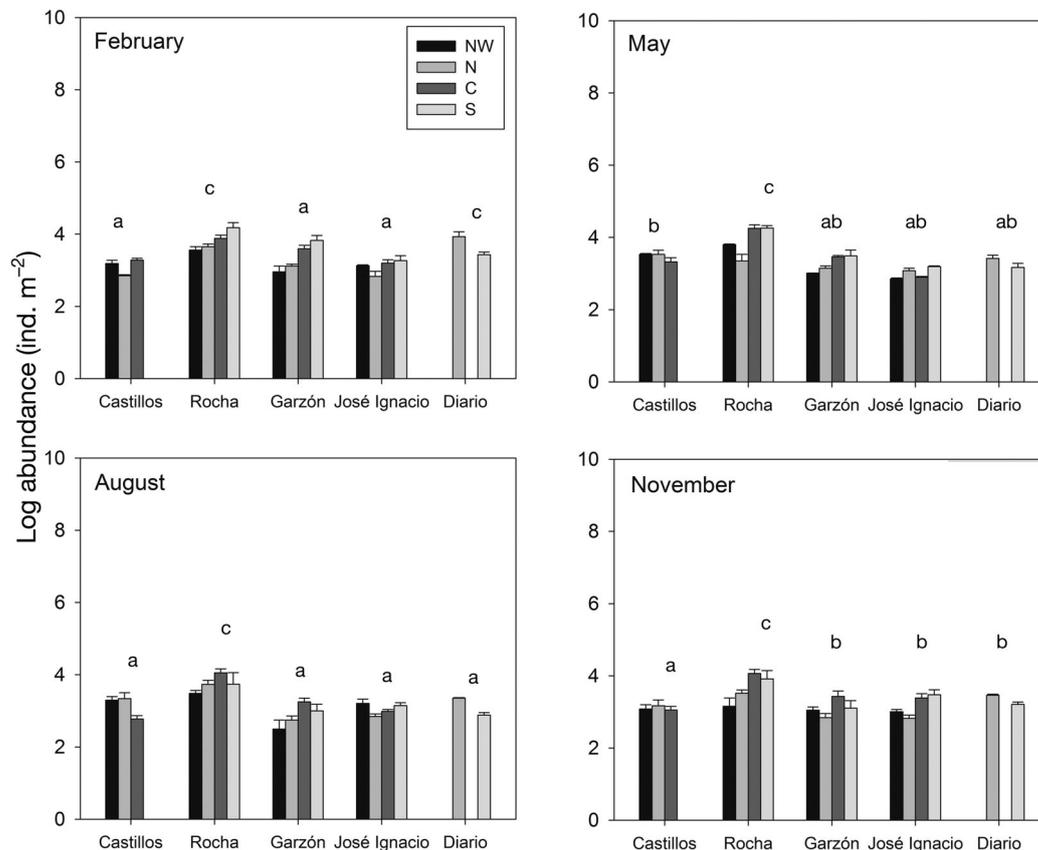


Fig. 4. Total abundance of benthos in the 5 studied coastal lagoons in Uruguay (lower case letters indicate significant differences in the *a posteriori* test [ $p < 0.005$ ]; 2 lagoons with the same letter were not significantly different). N: north, NW: north-west, C: center, S: south

Table 4. Three-way ANOVA results for evaluating time and spatial variation of macrobenthos total abundance and richness, and environmental variables (TSS: total suspended solids; data were transformed)

Variable	Factor	F	p
Benthos total abundance	Time	0.52	0.675
	Lagoon	4.65	<0.005
	Site	4.56	<0.005
TSS	Time	0.83	0.499
	Lagoon	6.04	<0.005
	Site	4.72	<0.005
Depth	Time	0.21	0.886
	Lagoon	46.07	<0.005
	Site	5.61	<0.005
Conductivity	Time	0.48	0.699
	Lagoon	23.32	<0.005
	Site	47.27	<0.005
Phytobenthos chl a	Time	0.04	0.988
	Lagoon	7.47	<0.005
	Site	1.96	0.001
Benthos richness	Time	0.85	0.486
	Lagoon	6.44	<0.005
	Site	2.32	<0.005
Sediment organic matter	Time	0.02	0.997
	Lagoon	5.02	<0.005
	Site	3.55	<0.005
Dissolved oxygen	Time	15.57	<0.005
	Lagoon	1.74	0.071
	Site	5.39	<0.005
Phytoplankton chl a	Time	0.27	0.848
	Lagoon	3.02	0.002
	Site	4.00	<0.005
Macrophyte biomass	Time	0.42	0.739
	Lagoon	31.43	<0.005
	Site	1.21	0.202

lagoons (Table 7). To determine which environmental variables were significant in explaining the dominant species, we performed multiple regression. Responses were species specific (Table 7), although some patterns emerged. The organic matter content of the sediment and phytobenthos chl a were important in explaining patterns of abundance in the epibenthic gastropod *Heleobia australis* and the infaunal bivalve *Erodona mactroides* (Table 7); phytobenthos chl a explained these species in an inverse way. The polychaetes *Nephtys fluviatilis* and *Laeonereis acuta* showed a strong response to phytobenthos chl a. Both freshwater groups, i.e. the bivalve *Corbicula fluminea* and the chironomids, responded to dissolved oxygen; however, the abundance of *C. fluminea* was directly explained by dissolved oxygen, whereas the abundance of chironomids was inversely explained by dissolved oxygen.

Table 5. PERMANOVA results: p-values for the paired tests of significant variability among lagoons and seasons. Column 'U+D' shows p-values obtained with PERMANOVA and indicates the effect of 'location and/or dispersion'. 'D' are p-values obtained with PERMDISP, indicating effect of dispersion alone; D was always not significant (ns) so this column has been omitted. Analyses are based on benthos community data from all studied lagoons

Groups	U+D
Castillos, Rocha	ns
Castillos, Garzón	ns
Castillos, José Ignacio	ns
Castillos, Diario	0.001
Rocha, Garzón	ns
Rocha, José Ignacio	0.001
Rocha, Diario	0.001
Garzón, José Ignacio	ns
Garzón, Diario	0.001
José Ignacio, Diario	0.001

## DISCUSSION

### Main scales of benthos variability

We demonstrated that there are spatial and time variations in the structure of macrobenthic communities in 5 coastal lagoons of Uruguay. In addition, we found a low number of species and high dominance, in accordance to the general patterns observed by Giménez et al. (2006) for the estuarine communities along the Uruguayan coast, and other estuaries of the region (Ieno & Bastida 1998, Fonseca & Netto 2006).

Few studies have evaluated patterns of distribution in coastal lagoons and estuaries of different types (Teske & Wooldridge 2004, Dye 2006, Pillay & Perissinotto 2013). These have found important variations in structure among and within estuarine sites. Consistent with that work, coastal lagoons of Uruguay are characterized by important large- and small-scale spatial variability in the abundance of macrobenthos. This kind of pattern indicates that processes of small and large scales play important roles in shaping spatial patterns of macrobenthic communities (Tataranni et al. 2009).

Short-term temporal variation was low (variance between sampling occasion was 7% of the total variance), although our sampling occasions were spread over all seasons. Temporal variation explains a small fraction of the total variation in comparison with spatial variation between estuaries (Edgar & Barret 2002, Anderson et al. 2007) and within estuaries (Ysebaert & Herman 2002, Anderson et al. 2007, França et al. 2009).

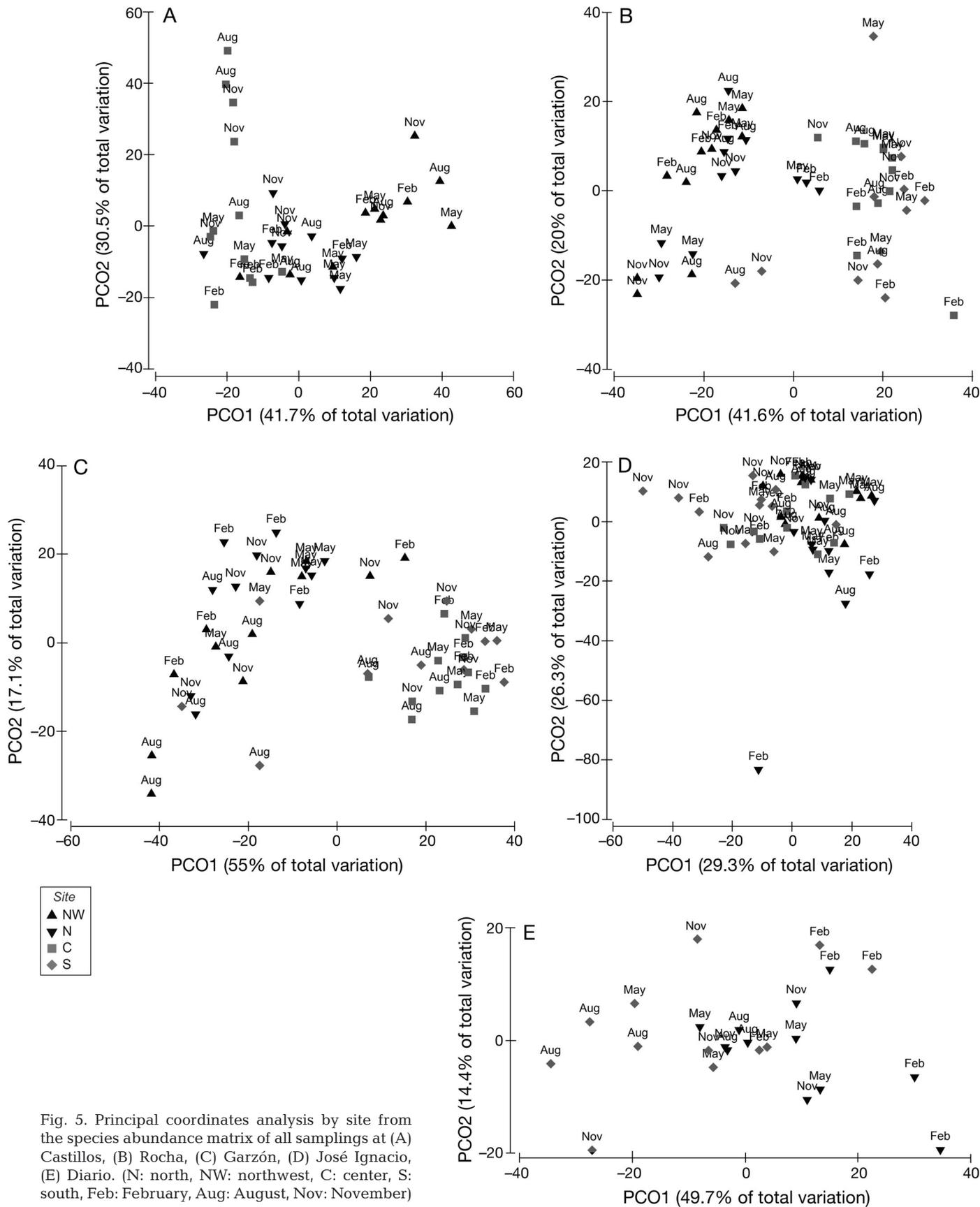


Fig. 5. Principal coordinates analysis by site from the species abundance matrix of all samplings at (A) Castillos, (B) Rocha, (C) Garzón, (D) José Ignacio, (E) Diario. (N: north, NW: northwest, C: center, S: south, Feb: February, Aug: August, Nov: November)

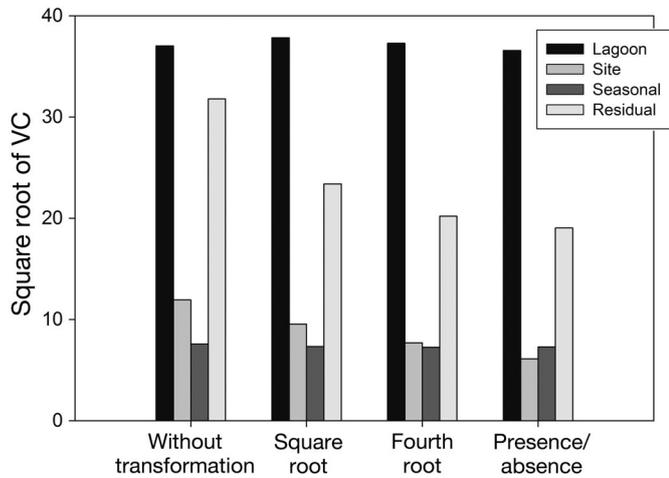


Fig. 6. Multivariate variance components at different spatial and temporal scales for all taxa, obtained using mean squares of PERMANOVA made with different transformations (without transformation, square root, fourth root, and presence/absence transformation). Values in the graph are the square root of the variance components, to put the values at a scale of Bray-Curtis dissimilarities (expressed as the difference in percentages between ensembles; the contribution of the interaction to the overall variation in the benthic assemblage is not significant, independent of the transformation)

**Spatial variability**

One main difference between the lagoons that affects the community structure is their connection to the ocean. The kind of connection promotes the dominance of estuarine species in Castillos, Rocha, Garzón, and José Ignacio lagoons, in accordance

Table 6. Correlations between factors and environmental variables in the PCA for all sampling occasions (biomass: macrophyte total biomass, K: conductivity, DO: dissolved oxygen at the surface, OM: sediment organic matter, phytoplankton: phytoplankton chl a, phytobenthos: phytobenthos chl a, richness: macrophyte richness, T: water temperature, TSS: total suspended solids)

Variable	PC1	PC2
TSS	0.05	0.35
OM	-0.52	0.20
Depth	-0.50	0.00
DO	0.05	0.41
K	0.46	0.25
T	0.12	0.56
Phytoplankton	0.01	0.41
Phytobenthos	-0.20	0.28
Richness	-0.08	0.21
Biomass	-0.46	0.11

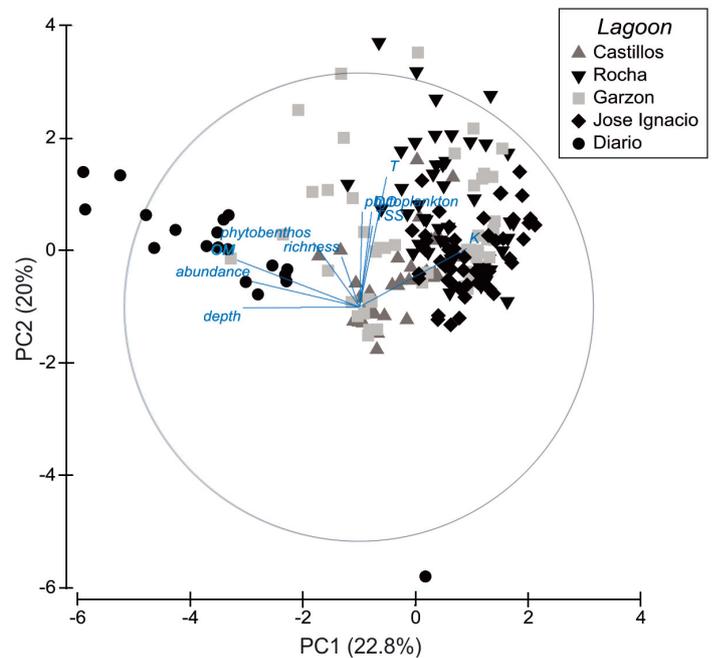


Fig. 7. Principal components analysis of the environmental variables from 5 coastal lagoons in Uruguay (data from all sampling occasions are included). Biomass: total macrophyte biomass, K: conductivity, richness: macrophyte richness, OD: dissolved oxygen at the surface, OM: sediment organic matter, phytoplankton: phytoplankton chl a, phytobenthos: phytobenthos chl a, T: water temperature, TSS: total suspended solids

with previous studies (Corbellini 1983, Cardezo 1989, Jorcín 1999, Conde et al. 2004, Giménez et al. 2005, 2006, Rodríguez-Gallego et al. 2010). The structure of the macrobenthic communities in the lagoons with intermittent connection to the ocean was qualitatively similar to other Atlantic estuaries in South America (Olivier et al. 1972, Capitoli et al. 1978, Ieno & Elias 1995).

The highest source of variability occurred among lagoons. ANOVA components showed that at this scale, the variability was almost entirely due to variation in the presence/absence of species. Further analyses showed that there were 2 important types of variation. First, due to permanent isolation, a freshwater community was developed in Diario lagoon that contrasts with the estuarine community present in all other lagoons. Diario lagoon was characterized by low salinity and high nutrient concentrations, caused by the artificial closure of its sandbar during the building of a road. We consistently found various genera of Chironomidae that are typical of eutrophic systems (Clemente 2008). Results are thus consistent with Wooldridge (1999) in that the isolation of the ocean influences the recruitment of individuals and therefore

Table 7. Environmental variables that explained the benthic community structure of all 5 studied coastal lagoons in Uruguay and of only the 4 intermittent lagoons (results from DistLM analysis;  $F^*$  is the pseudo- $F$  statistic, the direct multivariate analogue of Fisher's  $F$  ratio) as well as the dominant species ( $\beta$  is the regression coefficient, in all cases  $p < 0.005$ , SOM: sediment organic matter, DO: dissolved oxygen, TSS: total suspended solids, T: temperature)

	$R^2$	$F$	SOM	Conductivity	Phyto-benthos chl $a$	DO	Phyto plankton chl $a$	Depth	Biomass	TSS	T
Benthos (all lagoons)	0.455		$F^* = 98.5$				$F^* = 3.1$	$F^* = 42.2$	$F^* = 50.8$	$F^* = 4.4$	
Benthos (intermittent lagoons)	0.237		$F^* = 9.8$		$F^* = 11.5$			$F^* = 10.3$	$F^* = 14.4$		$F^* = 4.9$
<i>Heleobia australis</i>	0.2	7.02			$\beta = -0.24$			$\beta = 0.205$	$\beta = 0.23$		
<i>Erodona mactroides</i>	0.28	13.2	$\beta = -0.19$		$\beta = -0.16$		$\beta = -0.15$		$\beta = 0.4$		
<i>Nephtys fluviatilis</i>	0.1	6.4			$\beta = 0.17$			$\beta = -0.21$			
<i>Laonereis acuta</i>	0.18	10.2			$\beta = 0.28$						
<i>Corbicula fluminea</i>	0.83	6.4		$\beta = 0.53$		$\beta = 0.35$		$\beta = -0.66$			
Chironomids	0.66	5.7				$\beta = -0.5$		$\beta = -0.04$	$\beta = 0.5$		

the persistence of species that require a marine dispersive phase. In artificially closed lagoons, we would expect that estuarine macrobenthos would be impoverished, but total richness should not necessarily decrease because insects augment richness. In this sense, the high richness and the taxa found in Diario lagoon are similar to those found by Dye (2006) in coastal lakes of New South Wales, Australia.

A second source of variation occurred among estuarine lagoons, with Rocha and José Ignacio lagoons situated at the extremes of a community gradient (Fig. 3). Rocha lagoon was dominated by the gastropod *Heleobia australis* and the bivalve *Erodona mactroides*, whereas in José Ignacio polychaetes were dominant.

Within lagoons, we found ocean–land gradients in community structure in association with their connection to the ocean in the case of estuarine lagoons. In particular, in Rocha lagoon, the spatial pattern of the benthic community reflected the variations in the abundance of the dominant *Heleobia australis*, but none of the environmental factors considered here can completely explain the gradient. Most likely, the gradient reflects dependence of *H. australis* on connectivity with the marine environment. In addition to that, *H. australis* is an opportunistic species (Lana 1986, Bemvenuti et al. 1992, Netto & Lana 1994) and could be favored in the south of the lagoon by the disturbance caused by the sandbar openings. Opportunistic species are the first to respond to disturbance and dominate the initial stages of succession. Their ability to respond quickly to disturbance and attain high densities has been primarily attributed to their life-history features (e.g. wide dispersal ability, tolerance to disturbed conditions, high reproductive rates; Whitlatch & Zajac 1985, Gray & Elliott 2009).

### Small-scale spatial patterns

Small-scale spatial variability was high and consistent with other studies of benthic communities (Fraschetti et al. 2005); this emerges as a general property of benthic ensembles in marine coastal habitats being determined mainly by biological interactions and/or physical local factors (Ekman 1979, Underwood & Chapman 1996, Benedetti-Cecchi 2001). Variance components using several data transformations showed that small-scale variability was mainly affected by changes in presence–absence that contributed to 20 out of the ca. 30% of variability explained by variation in untransformed abundance data. This suggests the presence of small-scale patches produced by strong variations in abundance of organisms of different species; this result is in accordance with Anderson et al. (2005b).

### Relationship between environmental variables and benthic macrofauna

Relationships between macrobenthic abundance and environmental factors are not easy to explain because macrofauna, sediment characteristics, and phytobenthos are part of a complex web of trophic and non-trophic interactions (Thrush et al. 2012). Rocha lagoon was characterized by low levels of sediment organic matter, suspended solids, and phytobenthos chl  $a$ ; by contrast, the other lagoons were more heterogeneous with regard to these environmental variables. These factors cannot explain the observed responses. However, spatial heterogeneity through its effects on availability of optimal habitats may be a factor that perhaps explains why *Erodona mactroides*

and *Heleobia australis* peak at Rocha lagoon (spatially homogeneous optimal habitat) but not at José Ignacio (more heterogeneous with areas characterized by high levels of organic matter content in the sediment). A second contributing factor may be the presence of macrophytes in all but José Ignacio lagoon.

Macrophyte biomass has already been established as a determinant variable in benthic communities (Thomaz et al. 2008, Rodríguez-Gallego et al. 2010, Arocena & Rodríguez 2011). Empirical studies have demonstrated that total abundance of epiphytic and benthic invertebrates is correlated with submerged macrophyte biomass and the characteristics of the hydrophyte community (Cyr & Downing 1988, Rasmussen 1988, Hedge & Kriwoken 2000, Arocena 2007, Rodríguez-Gallego et al. 2010). Silver et al. (2004) suggested that the qualitative composition of insects is higher when the resources are dispersed through many small patches than when they are aggregated in homogeneous patches.

In summary, the benthic communities of coastal lagoons of Uruguay are characterized by strong large- and small-scale variation in community structure and species abundances. Some of the large-scale variation reflects different levels of isolation from the sea that determine the nature of the community and the patterns of species richness. In the case of open/closed lagoons there are also important variations in abundance of the most important species that may respond to variations in availability of optimal habitat. Small-scale variation again appeared as a property of benthic communities in these lagoons. Our results confirm that the use of a single scale for investigating macrobenthic communities of coastal lagoons is inappropriate, highlighting the importance of multi-scale approach in the analysis of spatial patterns. The foodweb of Rocha lagoon is dominated by the benthic domain, showing a strong trophic coupling between benthic primary producers and pelagic subsystems (Milessi et al. 2010). Moreover, most of the focal conservation species of these lagoons, including migratory and resident aquatic birds, are dependent on benthic resources (Meerhoff et al. 2013). Factors that can cause multi-scale perturbation to the benthic community can cascade up the trophic web, affecting local and regional fisheries. Therefore, management of these lagoons must accommodate the consequences of pressures emanating from outside the system (e.g. exportation of agricultural nutrients from the catchment area) and the causes and consequences of pressures from within the system (such as the artificial opening of the lagoon sand bars).

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