Small-scale structure of macrophytes and macrobenthos in coastal 'Laguna de Rocha'

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Abstract. We studied seasonally a community of submerged aquatic vegetation (SAV) present throughout the year and the associated macroinvertebrates in a bay of the southwest Atlantic coastal Laguna de Rocha in Uruguay. We found biomass and diversity of SAV were higher in summer than in winter, whereas benthos density was higher in winter. Three types of SAV were identified: A) those that were short and completely submerged, B) those that occupied half of the water column or reached its surface and C) those that emerged from the water's surface. Macrophytes in multispecific plots were dominated by *Eleocharis* sp. aff. *nana*, accompanied by Charophytes, *Myriophyllum quitense*, *Potamogeton pectinatus, P. pusillus*, *Ruppia maritima* and *Zanichelia palustris*. The 28 species assemblage of macroinvertebrates was dominated by *Heleobia australis, Erodona mactroides*, *Laeonereis culveri, Nephtys fluviatilis, Sinelobus stanfordi, Dies fluminensis* and *Hyalella curvispina.* The structure of the benthic community also differed seasonally. An RDA with the dominant benthos species as dependent variables retained *Eleocharis* sp., *R. maritima*, plant group B and total SAV biomass as the significant explanatory variables. We found a strong relationship between macrophyte biomass and macrofauna richness. Benthic species show a certain preference among SAV types and species.

Key words: benthos, coastal lagoons, submerged macrophytes, Uruguay

Resumen. Estructura a pequeña escala de las macrófitas y el macrobentos en la laguna costera de Rocha. Se estudió estacionalmente una comunidad de macrófitas sumersas (SAV), presente todo el año y sus macroinvertebrados asociados, en una bahía de la costera Laguna de Rocha (Atlántico SW) en Uruguay. La biomasa y diversidad de la SAV fueron mayores en verano que en invierno, mientras que la densidad del bentos fue mayor en invierno que en primavera. Se identificaron tres tipos de vegetación sumersa: A) una corta y completamente sumersa, B) una que ocupa media columna de agua o alcanza la superficie, y C) una que eventualmente emerge de la superficie. Las matas multiespecíficas fueron dominadas por *Eleocharis* sp. aff. *nana*, accompañada por carófitas, *Myriophyllum quitense*, *Potamogeton pectinatus, P. pusillus*, *Ruppia maritima* y *Zanichelia palustris*. Las 28 especies de invertebrados fueron dominados por *Heleobia australis, Erodona mactroides*, *Laeonereis culveri, Nephtys fluviatilis, Sinelobus stanfordi, Dies fluminensis* y *Hyalella curvispina*. La estructura de esta comunidad difirió estacionalmente. Un RDA con las especies dominantes del bentos como variables dependientes retuvieron a *Eleocharis* sp., *R. maritima*, grupo B de plantas y biomasa de la SAV como variables explicatorias. Hay una fuerte relación entre la biomasa de las macrófitas y la riqueza del bentos. Las especies bentónicas muestran preferencias por especies o tipo de SAV.

Palabras clave: bentos, lagunas costeras, macrófitas sumersas, Uruguay

Introduction

Coastal lagoons usually support important stands of aquatic macrophytes. Dense beds of submerged aquatic vegetation (SAV) reduces water turbulence and flow velocity (Peeters *et al*. 2004) promoting sediment deposition and stabilizing the sediment (Marklund *et al*. 2002). In shallow lakes, plants assume a greater role in ecosystem metabolism and structure, mainly through the cycling of nutrients both in the water and sediments (Menéndez & Forès 1998, Scheffer 1998). Moreover, they influence algal growth through reduction of light and turbulence as well as production of allelopathic exudates (Hilt *et al*. 2006), and they harbor high densities of grazing cladocerans (Lauridsen & Lodge 1996).

The presence of macrophyte stands is one of the main factors structuring animal communities, because of the refuge effect and the food supply (Jeppesen *et al*. 1998). Plant litter can be an important food source for benthos (Gonçalves *et al*. 2003). Aquatic invertebrates show minor preferences between different plant species (Duarte *et al*. 1994, Talbot & Ward 1987, Rooke 1984). Consequently, there is considerable concern about estuarine environmental change associated with macrophyte colonization (Hedge & Kriwoken 2000, Deng *et al*. 2004)

It is widely accepted that aquatic vegetation enhances the abundance and diversity of the benthic assemblage (Bergey *et al*. 1992, Mistri *et al* 2000, Tolonen 2004, Covazzi *et al*. 2006, Thomaz *et al*. 2008). However, both assemblages are usually composed of many different species whose correlations may vary greatly. Furthermore, SAV beds are not homogenous but include patches of very different plant composition, size and shape. Therefore, these general statements need to be examined at small-scales to analyze how SAV affect the associated macrobenthic fauna.

The coastal, brackish Laguna de Rocha is included in the Biosphere Reserve "Bañados del Este" (MaB-UNESCO Program) and in the Uruguayan National System of Protected Areas. The importance of SAV in Laguna de Rocha has long been neglected, except by Santana & Fabiano (1999) who mapped the submerged macrophytes in this lagoon. Nevertheless, the ecology of phytoplankton, phytobenthos (Conde *et al*. 1999, Bonilla *et al*. 2005) and benthos (Pintos *et al*. 1991, Giménez et al. 2006) has been studied. Knowledge of the composition of communities associated to submerged aquatic vegetation in the lagoon is therefore needed in relation to environmental factors that control their survival and long term dynamics.

Recently, Arocena (2007) showed that beds of SAV hosts a zoobenthic assemblage that is richer and more abundant than unvegetated areas in this coastal lagoon.

Submerged macrophytes in Laguna de Rocha were previously thought to be restricted to small protected bays (Arocena 2007) because of the strong winds and resuspension of sediments that affect plant colonization. However, intensive sampling from 2003 to 2006 revealed that the vegetated area was more extensive (Rodríguez-Gallego 2011). An irregular pattern of local extinctions and recolonization has been observed several times, apparently related to salinity fluctuations. In two summer events (2001 and 2003) SAV colonized open water of northern areas of the lagoon. The causes of this are unknown, but it may be related to an increase of phosphorus in water (Aubriot *et al*. 2005) as well as to hydrologic and salinity changes (Rodríguez-Gallego *et al*. 2010).

The aim of this paper is to evaluate relationships between vegetation and fauna, in particular how the biomass of different plant species affects benthic community structure and species distribution, as well as modulating effect of environmental variables. The seasonal and small-scale spatial variations of both assemblages are also addressed.

Material and methods
Study area

Laguna de Rocha (34º 33'–41' S, 54º 02'–22' W) is a shallow (0.6 m mean depth) coastal lagoon of 72 km^2 surface area, located on the southeastern Atlantic coast of Uruguay. It corresponds to the choked lagoon type of Kjerfve (1986). A small channel often opens through the sand bar connecting the lagoon to the Atlantic Ocean at the South. Three rivers feed the lagoon with freshwater from the North (Fig. 1). A salinity gradient is developed few days after the bar opens, with increasing salinity from North (0.0-3.0 g L^{-1}) to South (5.8 – 27.7 g L^{-1}) (Sommaruga & Pintos 1991). The bottom sediment in the North is composed of sandy-silt with organic content of about 2.5% (Sommaruga & Conde 1990, Conde *et al*. 1999). A narrow belt of *Schoenoplectus californicus* (C. Meyer) Steudel and *Spartina densiflora* Brong surrounds the lagoon, mainly in the northern part. Several descriptions of the lagoon can be found elsewhere (Sommaruga & Conde 1990, Sommaruga & Pintos 1991,Conde *et al*. 1999, 2000, 2002, Bonilla *et al*. 2005, Arocena 2007).

The sampling site is a vegetated bay located at the North coast of the lagoon, between its two

main influents. Its size was 200 x 150 m during the survey, although dimensions are variable depending on water level, being partially subject to drought during low water periods.
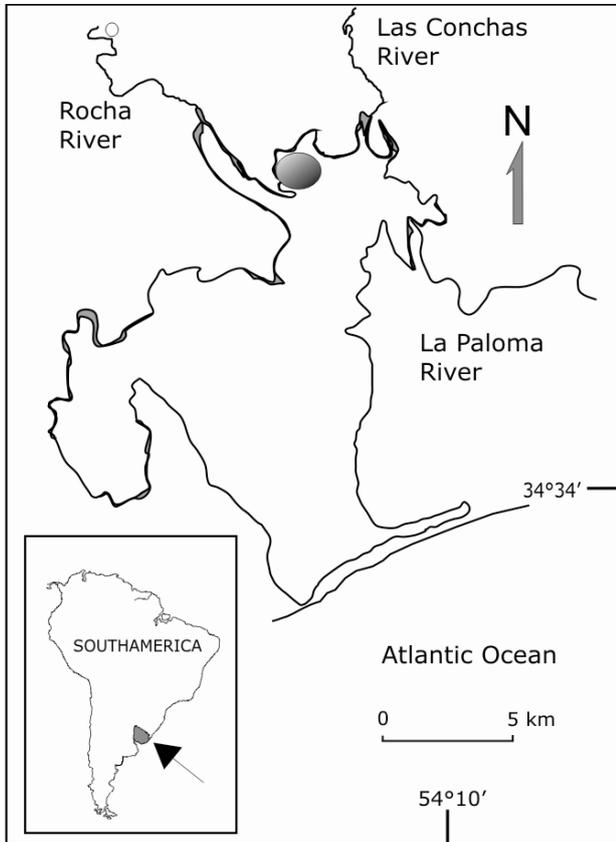

Figure 1. Map of Laguna de Rocha, indicating the sampling site (shadowed oval).

Sampling methods

Sampling was performed on February 23 (summer), June 13 (late fall) and November 18 (spring) 2001, representing the seasonal variation in Laguna de Rocha. To avoid the influence of diel variations, all samples were taken in the morning. Ten samples of vegetation and associated invertebrates were randomly taken from a grid of 10 x 10 sampling units of 20 x 15 m each (extension = 200 x 150 m) covering the whole vegetated bay. Samples were taken at the center of every sampling unit. Units already sorted in a previous sampling were not included for later samplings. Environmental water parameters were measured in the 10 plots at surface and bottom in February and November, but not in June due to logistic difficulties. We measured water depth, Secchi disk transparency, temperature, dissolved oxygen (Horiba D25), electrical conductivity (Horiba D24) and pH (Horiba D24).

An Ekman grab (22.5 x 22.5 cm) was gently settled on the bottom and then totally closed by pushing both jaws by hand into the sediment. It was lifted keeping the jaws closed so as not to lose any part of the sample. Samples were carefully washed free of adhering clay and fine silt over a 1.0 mm mesh and then invertebrates were manually separated from plants in the laboratory with the aid of a magnifier. Macrophyte species were separated and their biomass was determined as dry weight after drying at 70 ºC to constant weight (more than 48 h, Mazzeo 1999). The sum of all species biomass per plot is named total SAV biomass. Invertebrates were identified to species whenever possible or otherwise to the lowest taxonomic level, counted, and frequencies were calculated. The sum of the density per plot of all species is named total benthos density.

Three additional Ekman grabs were randomly taken from the bay area for sediment analysis in February only, because major seasonal variations are not expected to occur in sediment composition. Grain size was determined by sieving the dry sample through a standard series of meshes from 2 mm to 64 μm every Φ unit. Water and organic matter contents were determined by weight differences between the humid, dry (110 ºC, > 24 h) and burned (450 ºC, 2 h) sediment samples (Arocena 1999). The grain size mean, median and standard deviation were computed after Folk & Ward (1957).

Statistical methods

The aggregation pattern of plant biomass and benthic density was determined with χ^2 tests (Elliott 1977). Total SAV biomass and total benthic density were compared between months with one-way ANOVA. Plant biomass and benthos density were compared between species and months with two-way ANOVA random factors (Underwood 2002). Only the species that represented more than 5% of the total biomass or density in at least one sampling were considered for both SAV and benthos analyses. The homoscedasticity of the variance was tested with the Bartlet and Cochran test and normality was tested with the Kolmogorov Smirnov test (Zar 1999). The only transformation needed was the square root of SAV biomass and benthos density in the two way ANOVAs, to fulfill the assumptions of this analysis. Post-hoc comparisons were done with the Tukey HSD test with a significance level of 0.05 in all cases. Correlations between SAV biomass and benthos were calculated with the Spearman coefficient (Zar 1999). Species number (richness), diversity and evenness (based on Shannon) were determined (Magurran 1988) for both biological

assemblages and compared between months with one-way ANOVA. Diversity was measured using the Shannon-Wiener Index (natural log). Distribution curves were also fitted to SAV species biomass and benthos species density (Magurran 1988).

To analyze the relationship between SAV and benthos density, a redundancy analysis (RDA) was used due to the short gradient length of the data obtained after a preliminary detrended correspondence analysis (ter Braak & Šmilauer 1998, Lepš & Šmilauer 2003). Biomass of plant species, plant richness and typology were used as explanatory variables and density of benthos species with occurrences exceeding 10% in each sampling, as dependent variables. Explanatory variables were chosen by a forward selection procedure with a Monte Carlo Permutation Test (Peeters *et al.* 2004). Variables with p < 0.1 and Variance Inflation Factors lower than 20 were retained. To complement the RDA, multiple regressions were done of the abundance of the seven main zoobenthic species (dependent variables) on the biomass of the vegetation variables retained by the RDA (independent variables).

Results
The Environment
The sampling area was deeper in February (35 - 65 cm) than in November (10 – 40 cm). Secchi disk transparency always reached the bottom. Surface mean temperature was 26.9 (2.6 Standard Deviation: SD) °C and 22.7 (1.0 SD) °C in February and November, respectively, with a maximum value of 29.2 °C in February. On average the oxygen saturation was around 100 (22 SD) % in February and 90 (3 SD) % in November with no difference between the surface and the bottom. The mean pH ranged from 7.4 (0.6 SD) in February to 7.9 (0.4 SD) in November. Mean conductivity was 9.7 (0.9 SD) mS cm^{-1} in February and 2.8 (0.9 SD) mS cm^{-1} in November. Water parameters were similar at the surface and the bottom most of the time. The three samples of sediment had similar grain size and water and organic content values. The sediment was composed by an average of 67.2 (10.2 SD) % sand and 32.8 (10.2 SD) % silt and clay, which were not separated. This corresponds to silty sand according to Sheppard's triangle. Median (125 μm) and mean (128 μm) values of grain size distribution correspond to fine sand following Wentworth nomenclature, while the standard deviation of 1.68 Φ corresponds to a "poorly selected" sediment. The

water content was 57.4 (3.2 SD) % and the organic content was 3.7 (0.4 SD) % of dry weight.

Submerged aquatic vegetation
The bay was completely covered by submerged macrophytes during the sampling period. Submerged aquatic vegetation was classified by the way they occupied the water column. Three types of vegetation were identified: A) those short and completely submerged, such as *Eleocharis* sp. aff. *nana* Kunth, *Ruppia maritima* L., *Nitella* sp. and *Chara* sp., B) those that occupied half of the water column or that reached its surface, including *Zannichellia palustris* L., *Potamogeton pectinatus* L. and *P. pusillus* L. and C) those with highly dissected leaves that eventually emerged from water surface, such as *Myriophyllum quitense* HBK. All plots were multispecific, but were mainly composed by *Eleocharis* sp. aff. *nana*. The first group represented about 85% of the biomass in summer and winter, and about 50% in spring. *Nitella* sp. and *Chara* sp. were pooled due to time involved in their separation, and were classified as Charophytes.

Total richness was maximum in February (7 taxa), diminishing afterwards to 5 and 6 taxa in June and November respectively (Table I). However, mean richness of replicates was 5 species throughout the year and seasonal differences were not significant. Maximum richness was rapidly attained with around four samples.

Total SAV biomass was two times higher in February (up to 305.64 g DW m^{-2} in one plot) than in June (up to 134.72 g DW m^{-2}), achieving an intermediate value in November (Table I). Differences between months were significant ($F_{1,2}$= 5.01, p< 0.05) and the post hoc Tukey HSD test found differences between February, with the highest biomass, and June, but not with November (p< 0.05). Species biomass showed highly significant differences between taxa ($F_{2,5}$= 10.5, p□ 0.001), but differences between months were not significant, while the interaction between factors was significant ($F_{2,10}$= 3.8, p□ 0.001). The post hoc test identified *Eleocharis* sp. as the most abundant species while *P. pectinatus* and *Z. palustris* had the lowest biomass. The other species showed intermediate biomass values (p< 0.05). *Eleocharis* sp. was the dominant species throughout the year, while *M. quitense* and *R. maritima* were more abundant in November and the rest of the species were more abundant in February (Table I). There was a three to five-fold variation in biomass among plots, and only one plot in June was almost unvegetated.

Table I. Submerged aquatic vegetation mean biomass (standard deviation) of ten sampling plots in the North of Laguna de Rocha during the study period, expressed in g DW m^{-2}. Diversity indices are also indicated for the pooled 10 sampling plots.

	February	June	November
Eleocharis sp.	108.2 (88.4)	62.9 (37.9)	61.1 (43.6)
Myriophyllum quitense	11.7 (22.0)	9.6 (14.1)	44.2 (53.2)
Charophytes	44.8 (53.3)	6.8 (6.6)	1.3 (1.8)
Ruppia maritima	0.8 (1.7)	1.6 (2.1)	12.2 (23.3)
Zannichelia palustris	7.2 (12.2)	0.0	0.0
Potamogeton pectinatus	5.6 (4.5)	0.3 (0.8)	0.8 (1.6)
Potamogeton pusillus	2.0 (6.3)	0.0	0.5 (0.6)
TOTAL BIOMASS	180.4 (81.6)	81.3 (39.5)	120.1 (81.8)
Richness	7	5	6
Shannon Diversity	1.22	0.79	1.05
Evenness	0.55	0.44	0.58

In February, we found *Ruppia maritima* in only two of ten sampling plots, with reproductive structures softly coiled around *P. pectinatus* shoots and reaching the water surface. In June and November it was present in most of the sampling plots, but reproductive structures were not observed. Total and species biomass showed an aggregated spatial distribution (χ^2, p<0.05) every month, except *P. pectinatus* in June and *P. pusillus* in November when they were randomly distributed.

Shannon-Wiener species diversity was maximum in February (1.22) and minimum in June (0.79), when the evenness reached also its minimum (0.44). The distribution of biomass among species (Fig. 2) in every sampling fitted the log series ($\chi^2 < 2.06$, p>0.5) better than the broken stick ($\chi^2 < 4.66$) models.
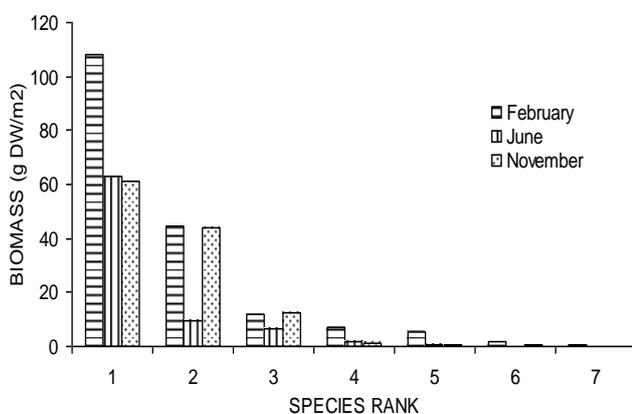

Figure 2. Distribution of SAV biomass among species for every sampling month.

Zoobenthos

The 28 species macroinvertebrate assemblage was dominated by only 7 species, which were present in all three sampling months and had the highest density and frequency. Benthos richness ranged from 5 to 11 species per plot and from 16 to 20 per month (Table II), without significant seasonal differences. The maximum richness was rapidly attained with around three samples in February and June, and six in November.

The total benthos density differed significantly between months ($F_{1,2} = 4.4$, p<0.05) and was higher in June than in November, but with no differences with February (Tukey HSD, p<0.05; Table II). The density of the six most abundant species differed significantly between taxa ($F_{2,5} = 19.6$, p<0.001). The post hoc test found *Heleobia* sp. (aff. *australis* D'Orbigny 1835) to have higher density than the other species, and *Dies fluminensis* Mañé Garzón 1944 to have a higher density than *Laeonereis culveri* Webster 1879 (p<0.05). *H. australis* largely dominated the density of the macroinvertebrate community in the three sampling months, achieving 75% of the total density (Fig. 3). The differences between the density of these species was not significant between months. The interaction between both factors was significant ($F_{2,10} = 7.2$, p<0.05).

The snail *H. australis* was present in all plots, followed by the clam *Erodona mactroides* Daudin 1802 (complete organisms in both cases) and the polychaete *Nephtys fluviatilis* Monro 1937 (present in 90% of plots but with low density), the isopod *D. fluminensis* (83%), amphipod *Hyalella*

Table II. Frequency (F), mean density (D, ind.m^{-2}) and standard deviation (SD) of benthos species in the North of Laguna de Rocha. Benthos mean density, total and mean richness and total and mean Shannon diversity per month with standard deviation are indicated at the bottom.

	February			June			November		
	F	D	SD	F	D	SD	F	D	SD
Heleobia sp. aff. *australis*	1.0	4257	1966	1.0	4808	932	1.0	2765	1209
Erodona mactroides	0.8	75	85	1.0	794	892	0.9	284	276
Glossiphoniidae indet.	0.1	2	6	0.0	0	0	0.0	0	0
Hirudinea indet.	0.0	0	0	0.0	0	0	0.1	2	6
Naididae indet.	0.1	2	6	0.0	0	0	0.0	0	0
Nephtys fluviatilis	0.8	103	77	1.0	132	62	0.9	142	74
Laeonereis culveri	0.9	342	418	0.8	32	23	0.3	14	31
Sinelobus stanfordi	0..8	757	1335	0.6	32	50	0.2	55	149
Dies fluminensis	0..6	40	56	1.0	302	261	0.9	198	260
Hyalella curvispina	0..5	26	38	0.8	99	127	1.0	397	558
Melita sp.	0..0	0	0	0,2	8	17	0,2	8	19
Brachura Megalopa indet.	0.0	0	0	0.0	0	0	0.2	4	8
Cyrtograpsus sp.	0.1	2	6	0.1	2	6	0.0	0	0
Hydracarids indet.	0.0	0	0	0.0	0	0	0.1	2	6
Coeniagrionidae indet.	0.1	2	6	0.2	10	25	0.5	32	46
Caenis sp.	0.0	0	0	0.0	0	0	0.5	34	47
Rheotanytarsus sp.	0.0	0	0	0.1	4	12	0.0	0	0
Chironomus sp.	0.3	10	17	0.3	8	14	0.2	6	13
Chironomini indet.	0.0	0	0	0.0	0	0	0.1	6	19
Dicrotendipes sp.	0.3	16	26	0.2	4	8	0.0	0	0
Tanypus sp.	0.0	0	0	0.0	0	0	0.1	2	6
Parachironomus sp. *B*	0.0	0	0	0.1	2	6	0.1	2	6
Parachironomus sp.	0.1	2	6	0.0	0	0	0.0	0	0
Hemiptera indet.	0.2	6	13	0.0	0	0	0.0	0	0
Berosus sp. (Coleptera)	0.4	8	10	0.1	4	12	0.1	2	6
Coleoptera indet.	0.0	0	0	0.0	0	0	0.1	2	6
Lepidoptera indet.	0.2	4	8	0.0	0	0	0.0	0	0
Nectopsyche sp. (Trichoptera)	0.0	0	0	0.1	2	6	0.6	14	13
	Total	Mean	SD	Total	Mean	SD	Total	Mean	SD
TOTAL DENSITY		5651	2250		6242	1334		3970	1638
RICHNESS	17	7	2	16	8	2	20	8	1
SHANNON DIVERSITY	0.905	0.741	0.458	0.863	0.738	0.271	1.179	0.991	0.359

curvispina Shoemaker 1942 (77%), polychaete *L. culveri* (67%) and tanaidacean *Sinelobus stanfordi* Richardson 1901 (53%). The remaining species (Table II) had low frequency and few organisms so they -together with *N. fluviatilis*- were not included in the two-way ANOVA.

The spatial pattern of the seven dominant species of benthos was aggregated, except for *L. culveri* in June and *N. fluviatilis* in June and November that was random. By consequence, the minimum number of replicates required to achieve 20% error in density should be 4, 1 and 5 in February, June and November respectively.

Benthos diversity and evenness were higher in November, although no significant differences among months were detected. The distribution of density among species (Fig. 4) fit the log series model in every sampling (χ^2 = 2.06, 5.74 and 1.37, p>0.5 for February, June and November). Most species had around ten or fewer individuals per sample and only one had more than 1000 (Fig. 4).

Benthos community structuring factors

We conducted an RDA with the dominant benthos species as dependent variables and the SAV species as explanatory variables. The forward selection procedure retained *Eleocharis* sp., *R.*
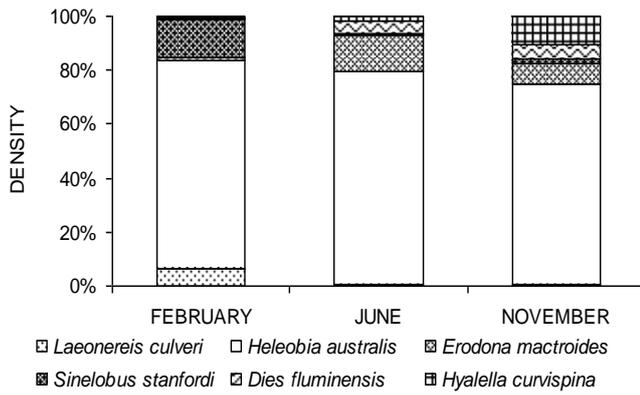
□ *Laeonereis culveri*   □ *Heleobia australis*   ⊠ *Erodona mactroides*
⊠ *Sinelobus stanfordi*   ⊡ *Dies fluminensis*   ⊞ *Hyalella curvispina*

Figure 3. Density of the six dominant species of zoobenthos in Laguna de Rocha during the study period.

Figure 4. Density distribution of zoobenthos species for data pooled from the three sampling months.

maritima, type B of plants and SAV total biomass as the significant explanatory variables. The permutation tests were both significant, and 36% of the total variance was explained by the analysis. The analysis identified three groups of samples: 1) *S. stanfordi* and *L. culveri* associated to the biomass of *Eleocharis* sp. and higher values of SAV total biomass which was composed of February samples, 2) *D. fluminensis* and *H. curvispina* mainly associated to *R. maritima* and type B of plants. *Erodona mactroides* and *N. fluviatilis* were also associated to this group, which was composed mainly of November samples, and 3) only *H. australis* which was the opposite of all SAV species and total biomass and was represented in all sampling months. When the benthos density and richness were plotted as supplementary variables they were associated with SAV species biomass and SAV total biomass, and opposed to *H. australis* (Fig. 5). No significant Spearman correlations were found between SAV total biomass and total or species benthos density of the seven most abundant species, either for total or for monthly data.

Multiple regressions with plant biomass were not significant for *N. fluviatilis* (p=0.35), *H. australis* (p=0.86) and *S. stanfordi* (p=0.62). Conversely, *L. culveri*, *D. fluminensis* and *H. curvispina* were dependent on *Ruppia maritima*, (p< 0.05), whereas *E. mactroides* was dependent on Type B species (p<0.01). Partial correlations gave the same results.

Discussion

In this study we analyzed the seasonal composition and abundance of the macrophyte and zoobenthos assemblages and limnological variables in a vegetated bay of the coastal Laguna de Rocha
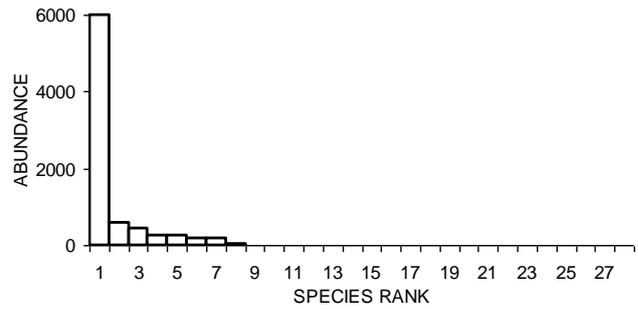
during 2001, as well as their relationships. We found seasonal patterns in macrophytes biomass and total benthos density. Furthermore, we found that the most abundant benthos species showed preferences for SAV types and plant species.

We found temporal variations in depth and salinity, which are common in Laguna de Rocha (Pintos *et al*. 1991). The water column was always mixed and well oxygenated throughout. Sediments were well illuminated allowing the growth of rooted SAV, as previously observed (Conde *et al*. 1999). During this study the conductivity, which is an estimator of salinity, ranged from oligohaline to slightly mesohaline conditions. Water and sediment parameters analyzed were within the range obtained for the freshwater –dominated northern coast of the lagoon (Sommaruga & Conde 1990, Pintos *et al*. 1991, Bonilla *et al*. 2005, Arocena 2007). Therefore, the environmental conditions and the sampling area were well representative of the northern coast of the lagoon.

The plant species found in Laguna de Rocha are typical of brackish and shallow estuaries (Kautsky 1988, Kantrud 1991) including coastal brackish lagoons of Uruguay, but with lower biomass (Bonilla *et al*. 2006). Submerged aquatic vegetation showed a clear seasonal pattern in this lagoon, with lower biomass in winter, as Arocena (2007) previously reported. This seasonal pattern is typical in temperate lakes (Wetzel 2001) and also freshwater lakes of Uruguay (Mazzeo *et al*. 2003). Shannon diversity, but not richness, followed the same seasonal pattern, indicating that temperature and/or light mainly affects species growth.

The community was composed of a mix of macrophyte species rather than of a mosaic of monospecific patches. Therefore, total species richness was reached with just four replicates. Nevertheless, total and specific biomass varied greatly among plots, showing an aggregated
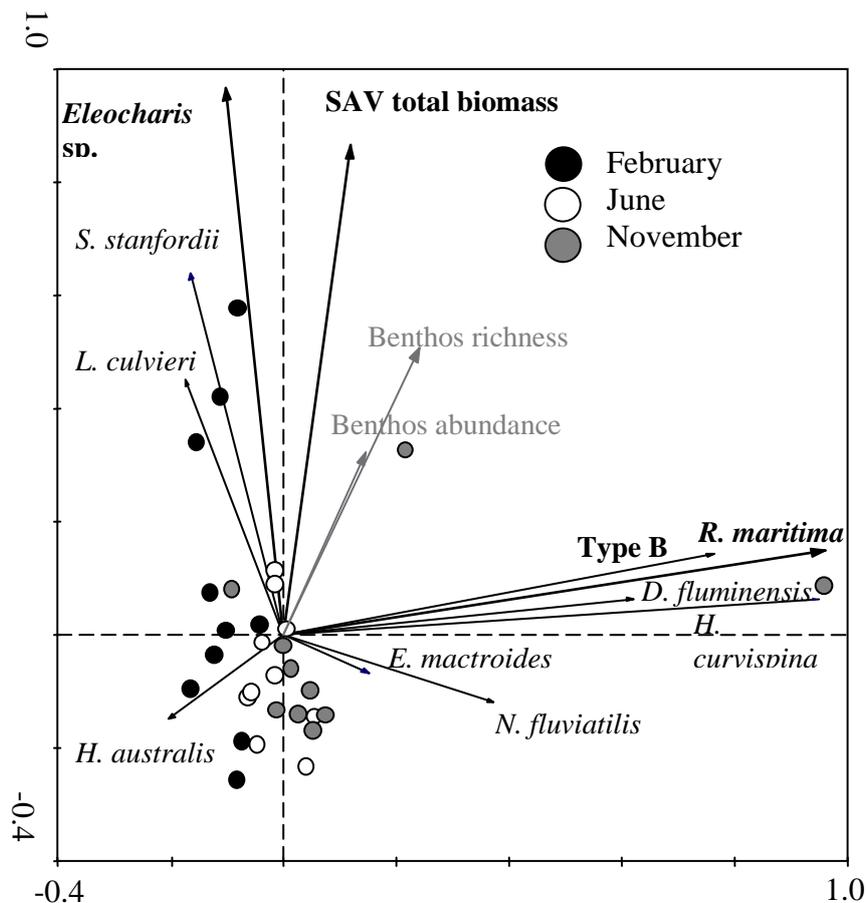
Figure 5. Redundancy Analysis (RDA) triplot representing the density of the most abundant benthos species (simple arrows: dependent variables) and the best explanatory variables (bold arrows: SAV species and total biomass and richness). Benthos richness and density were plotted as supplementary variables (grey arrows). Plant Group B includes *Zanichelia palustris* and the *Potamogeton* species. Black, grey and white circles represent samples from February, June and November respectively.

distribution of the biomass but not of the presence of the plants. Plant biomass varied significantly between species and months, but such differences were not independent between both factors, possibly due to the effects of seasonality and also different interactions among species such as competition. Salinity and wind-induced turbulence appear to be involved in the fluctuations of submerged aquatic vegetation (Rodríguez-Gallego *et al*. 2010), although eutrophication (Aubriot *et al*. 2005) and bird herbivory may also be important. The physical forces that dominate coastal lagoons (Day *et al*. 1989) maintain a relatively low biomass of SAV in Laguna de Rocha, and also a higher diversity with the co-occurrence of freshwater and salinity tolerant species (Estevez 2008). This may explain the higher species richness found in this lagoon in comparison

with other coastal lagoons of the region (Costa *et al.* 1997; Koch & Seeliger 1998; Bortolus *et al.*, 1998).

We found a high richness of benthos species in Laguna de Rocha (28 taxa), as in previous studies of vegetation (Arocena 2007). The species replacement was also high (only 15 taxa were shared between both studies with a comparable sampling effort). Laguna de Rocha showed higher benthos richness than Patos Lagoon (Rosa & Bemvenuti 2006) and Laguna System (Fonseca & Netto 2006), due to the presence of many insects in the former. However, sampling strategies especially designed to determine species richness are needed to confirm this observation. Total density was well within the observed range in previous studies (around 5000 ind. m^{-2} in Arocena 2007). Seasonal patterns of benthos richness and total density were not consistent and

statistical differences were not significant. However, the significant interaction between species and months indicate that seasons have certain influence on the benthic community. Density was higher in winter, which is opposite to previous studies in this lagoon (Arocena 2007; Rodríguez-Gallego *et al.* 2010) and coastal lagoons of Southern Brazil (Rosa and Bemvenuti 2006, Fonseca & Netto 2006) characterized by summer maxima. Nevertheless, inter-annual variations are very common in coastal lagoons (Nicolaidou *et al.* 2006).

The increase of total benthos density observed in winter was driven by *H. australis* which was the dominant taxa. This species preferred lower SAV biomass in this study and Arocena (2007) also found it in higher densities in non-vegetated zones than in vegetated ones. Therefore, this species possibly benefited from the SAV biomass reduction that occurred in winter, explaining the season pattern of the total benthos density. Although Canepuccia *et al.* (2007) found *H. australis* associated with *Spartina alterniflora* and Albertoni *et al.* (2001) with *Chara,* it is known as a common species of unvegetated estuarine bottoms of south Brazil (Netto & Lana. 1997).

We also found differences in benthic composition related to the differet types of vegetation and plant species. *Sinelobus stanfordi* and *L. culveri* preferred the short and completely submerged *Eleocharis* sp., while *D. fluminensis*, *H. curvispina* and also *E. mactroides* and *N. fluviatilis* preferred *R. maritima,* as well as type B, composed of plants that occupied more than half of the water column (*Potamogeton* spp. and *Z. palustris*). By contrast, type C plants such as *M. quitense*, with highly dissected leaves that eventually emerged from water surface, seem not to be preferred by the most abundant benthos species. We found *E. mactroides* associated to SAV species, but with lower plant biomass. Indeed, Arocena (2007) found these species in unvegetated sediments. This clam is a typical inhabitant of unvegetated sediments of Laguna de Rocha (Jorcin 1996).

As in the RDA, in Multiple Regressions, *Heleobia australis* was unrelated to vegetation, *D. fluminensis* and *Hyalella curvispina* were dependent on *R..maritima*, and *E. mactroides* was dependent on Type B. Conversely, *N. fluviatilis* was not related to *R. maritima* or other vegetation, although this is partially coincident with RDA results that showed only a weak association. Nevertheless, unlike the RDA, *S. stanfordi* and *L. culveri* were not related to *Eleocharis* sp. or to any other plant variable. Since partial correlations gave the same results as complete ones, this implies that the effect of every plant type or species on invertebrates is not affected by other types or species. Significant correlations of the intercept for *N. fluviatilis* and *Heleobia australis* indicate that the abundances of these species are greater than zero, no matter how much plant biomass is present.

Our results support the idea that the plant architecture is a small-scale structuring factor for benthos assemblages. Plant morphology has been postulated as a structuring factor for benthos either in natural vegetation stands (Thomaz *et al.* 2008) or in artificial plants mimicking submerged beds (Jeffries 1993). Hanson (1990) showed that benthos species had different preferences between *Chara* sp. and rooted submerged plants species due to differences in the refuge and food quality. Furthermore, Marklund *et al.* (2001) found that benthos species have different spatial and diel use patterns of the SAV mats to avoid predation and obtain food of better quality as periphyton. To better understand the specific association among benthos and macrophytes species in Laguna de Rocha *in situ* or laboratory experiments should be conducted, where plant species could by analyzed in isolation or in monospecific stands instead of in plots with a mix of species.

Although we found preferences of some benthos taxa with plant species, as did other authors (Strayer *et al.* 2003), we did not find significant correlations between total or specific benthic density with total SAV biomass. This result may be explained by the specific preference of some benthos taxa for plant species with low to intermediate biomass such as *R. maritima* and Type B, and mainly due to the fact that *H. australis*, which was the most abundant benthos taxa, preferred lower plant biomass.

The total variance of benthos explained by the RDA analysis was low, which means that other variables not considered in the study, besides SAV biomass, could be determining the structure of this assemblage. Rodríguez-Gallego *et al.* (2010) found that even though SAV is an important structuring factor for the benthos assemblage, other variables that are strongly associated to hydrology may be important as well. Factors such as organic matter of the sediments and salinity were important, but predation pressure by macroinvertebrates, fish and aquatic birds should also be explored (Rodríguez-Graña 2008).

The log-series model fit the abundance distribution of plant species as well as zoobenthic species. Although this is a typical distribution for non-stressed systems (Koutsoubas *et al.* 2000), it was found in the highly fluctuating Laguna de

Rocha. The salinity fluctuation in this lagoon may promote the co-occurrence of freshwater and salinity SAV tolerant species (Estevez 2008), avoiding the dominance of one or few species and promoting the development of a more equal community. This may also be the case for benthos species, which may be further enhanced by the presence of a rich SAV community and the benthos species preferences of certain plant species or types. Macrophytes are not directly used as a food source, as was shown by a stable isotope reconstruction in Laguna de Rocha (Rodríguez-Graña *et al*. 2008). However, effects of submerged aquatic vegetation could scale up through their structuring effects on benthos, which is one of the main trophic pathways (Rodríguez-Graña *et al*. 2008).

In this paper we determined the species composition of SAV and associated invertebrates and compared it with other nearby lagoons. We found that the northern freshwater-dominated edge of Laguna de Rocha was colonized by SAV the whole year. Nevertheless, SAV biomass and diversity were higher in summer than in winter, whereas benthos density was higher in winter than in spring. This may be due to the dominance of *Heleobia australis*, which prefers low SAV biomass. Several taxa of benthic fauna seem to show plant species or architecture preferences. Submerged aquatic vegetation is therefore postulated as structuring factor for benthos in coastal lagoons, although surely it is not the only one.

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