Epiphytic Algal Biodiversity in Humic Shallow Lakes from the Lower Paraná River Basin (Argentina)

WETLANDS

Journal of the Society of Wetland Scientists

VOLUME 31 NUMBER 1 FEBRUARY 2011 (ISSN 0277-5212)
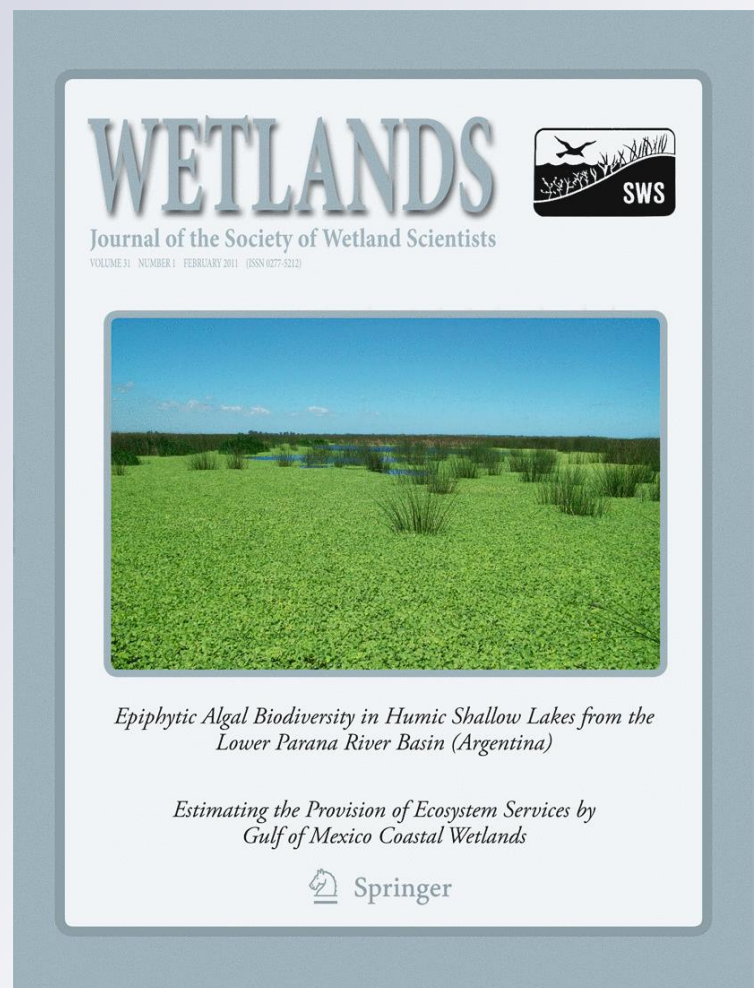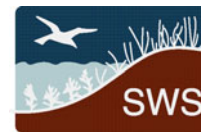
SWS

*Epiphytic Algal Biodiversity in Humic Shallow Lakes from the
Lower Parana River Basin (Argentina)*

*Estimating the Provision of Ecosystem Services by
Gulf of Mexico Coastal Wetlands*

Springer

Springer

ARTICLE

SWS

Epiphytic Algal Biodiversity in Humic Shallow Lakes from the Lower Paraná River Basin (Argentina)

Patricia Rodríguez · Guillermo Tell · Haydée Pizarro

Abstract We analyzed the algal composition (including Cyanobacteria) of epiphyton on macrophytes and the environmental data from five water bodies of a wetland from the Natural Reserve Otamendi (NRO) located in the Paraná River Basin, South America, during one year. Also, we described the diversity patterns (α, β, and γ diversity) of the epiphyton in the wetland. We selected two different macrophytes: the emergent rush *Schoenoplectus californicus* and the free-floating liverwort *Ricciocarpus natans*. We found 105 epiphytic taxa, of which 48% were represented by Bacillariophyceae, 22% were Cyanobacteria, 18% were Chlorophyta, and the rest (12%) belonged to Euglenophyta, Xanthophyceae, Synurophyceae and Cryptophyta. The structure of the epiphytic assemblage changed in relation to water level fluctuations, showing a major proportion of planktonic, metaphytic, and ticoplanktonic components during high water phases. The overall low algal richness may be related to the low light penetration in this humic wetland. The geographical pattern in taxa turnover was explained by the combination of metapopulation dynamics (dispersal distance) and continuum theories (infrequent connectivity followed by spatial differences associated in geographic habitat differences). Water level fluctuations affected the epiphytes on *S. californicus*, while temperature and light penetration influenced the epiphytes on *R. natans*.

Keywords Diversity patterns · Epiphyton · *Ricciocarpus natans* · *Schoenoplectus californicus* · Wetlands

P. Rodríguez (✉) · G. Tell · H. Pizarro
Laboratorio de Limnología, Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires—Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Intendente Güiraldes 2620. Pab. II, 4° piso. Lab. 44. C1428EHA, Ciudad de Buenos Aires, Argentina
e-mail: patriciar@ege.fcen.uba.ar

Introduction

In wetlands macrophytes provide much of the physical structure for microbial communities and are the major primary producers. In this kind of ecosystem algae also play a critical role in nutrient cycles and food web function because of their carbon fixation and sequestration of essential nutrients such as nitrogen and phosphorus (van der Valk 2007). Despite the fact that epiphytic algal communities are able to reach a high concentration in wetlands, they have received less attention in comparison to other microscopic phototrophic communities such as phytoplankton (Dodds et al. 1999; Vadeboncoeur and Steinman 2002).

Since the analysis of biodiversity is an early step for developing hypotheses about the functioning of water bodies, there are a large number of worldwide studies dealing with epiphytic algal biodiversity in lakes and its relationship with environmental factors. These surveys include the analysis of community composition in different kind of substrata, such as emergent and floating-leaved plants (Eminson and Moss 1980; Cattaneo et al. 1998). Examples of aquatic environments that have been examined for epiphytes include meromictic lakes (Laugaste and Reunanen 2005), shallow floodplain lakes (Rogers and

Breen 1981; Romo et al. 2007), north temperate lakes (Burkholder and Wetzel 1989), and freshwater marshes (Goldsborough and Robinson 1985). In South America, Rodrigues and Bicudo (2001) described the specific composition of periphytic communities on natural and artificial substrata in different environments (both lotic and lentic) from the Upper Paraná River basin. In Argentina, the relevance of environmental factors in modeling the structure of epiphytic communities in shallow lakes is largely undocumented (Pozzobon and Tell 1995; Tesolín and Tell 1996).

The objectives of our work were to analyze the influence of physical and chemical variables on the epiphytic algal community (including Cyanobacteria) of five shallow lakes with different optical characteristics from a wetland complex at the Natural Reserve Otamendi (Argentina) and to describe the diversity patterns (α, β, and γ diversity) of these microbial communities on two kind of macrophytes: the emergent rush *Schoenoplectus californicus* and the free floating liverwort *Ricciocarpus natans*.

Methods

Study Area

The studied water bodies are located in the Natural Reserve Otamendi (NRO) in Argentina (34° 10′ to 34° 17′ S and 58° 48′ to 58° 53′ W). The NRO is located between the Paraná de Las Palmas and Luján Rivers (Fig. 1). The hydrological

Fig. 1 Map of the study area showing the sampling sites at each water body
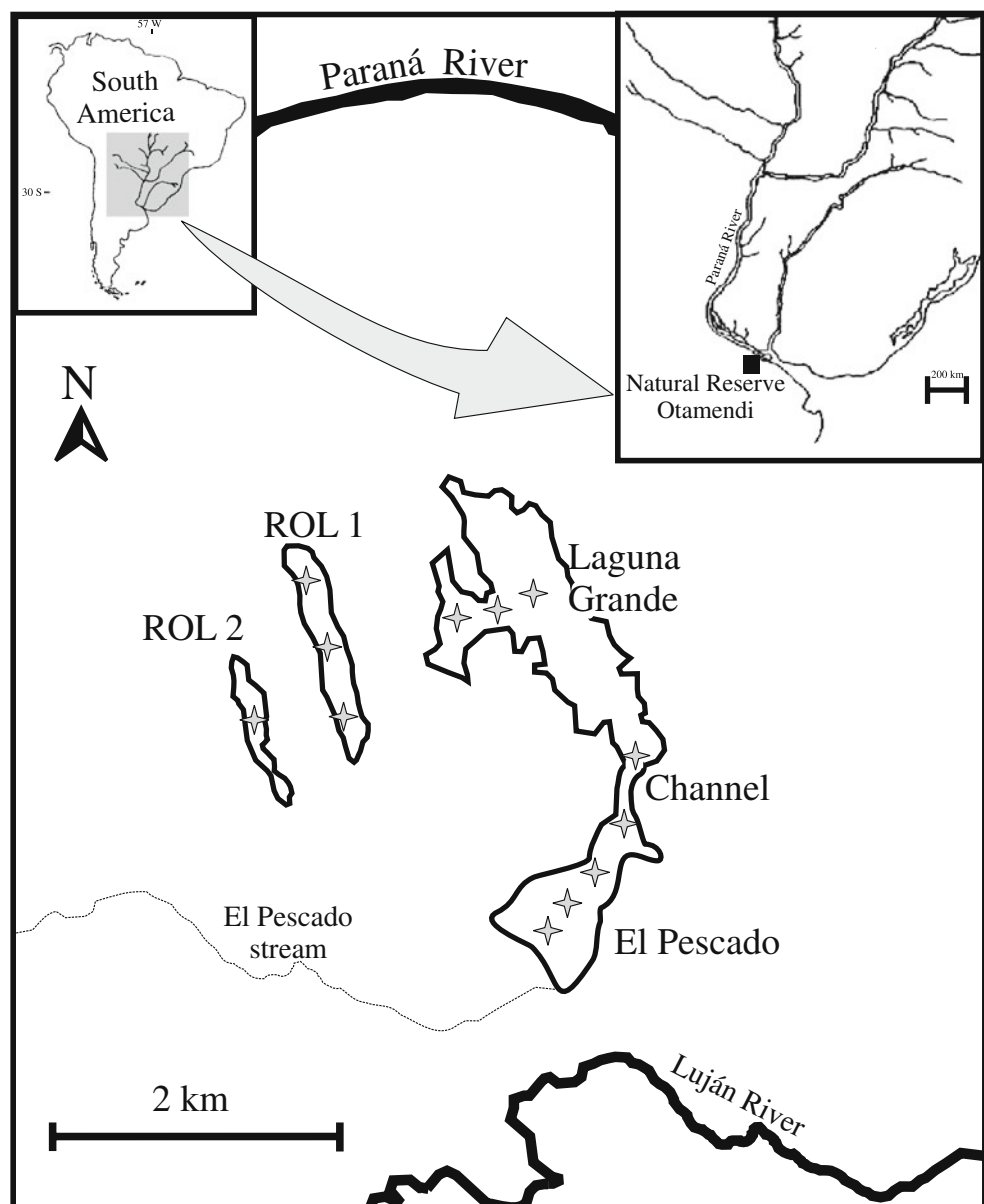
cycle of the region has an irregular pattern owing to the tidal influence of the Río de La Plata estuary and strong southeastern winds (sudestadas). The climate is temperate-sub-humid and the prevailing winds are from the southwest (Chichizola 1993). The average temperature during the study period (2004–2006) was 17.3°C, with January the hottest month (mean temperature: 29.3°C) and July the coldest (mean temperature: 6.5°C). The rainfall during the study period was around 1,200 mm per year.

Water bodies in the wetland include two large shallow lakes with depths generally <1 m: Laguna Grande (156 ha) and El Pescado (39 ha), which are connected through a channel (average depth=0.6 m). There are temporary swamps, ponds, and several relict oxbow lakes (ROL), the largest being about 17 ha (ROL 1) (Fig. 1). All water bodies in the wetland show different degrees of macrophyte development. The most abundant plant is *Schoenoplectus californicus* (rush), followed by *Typha latifolia* (cattail), and *Juncus acutus* (spiny rush). The relict oxbow lakes (ROLs) and the littoral zone of the large shallow lakes also have a variable coverage of free-floating plants, such as *Lemma minima* (duckweed) and other representatives of the family Lemnaceae, *Ricciocarpus natans* (liverwort), *Azolla filiculoides* (fern), and *Pistia stratiotes* (water lettuce). The smallest ROL (ROL 2) was covered with emergent vegetation during the sampling period while the ROL 1 and littoral zones of Laguna Grande and El Pescado lakes presented a variable cover of emergent and free-floating macrophytes.

Based on the broad classification for North American wetlands (Cowardin et al. 1979) the NRO would be classified as a permanently flooded wetland, as the standing surface water is present throughout the year. The main inflows of water are direct rainfall and surface and groundwater flows from the neighboring rivers and from uplands (van der Valk 2007). In the NRO, with the exception of the two major shallow lakes joined by a channel, water bodies are generally connected only during the periods of high rainfall.

The shallow lakes of the wetland always contain high concentrations of phosphorus and large amounts of organic matter, mainly owing to the decomposition of the plant tissue (Rodríguez and Pizarro 2007). The high concentrations of humic substances and total phosphorus make this wetland system mixotrophic (Williamsom et al. 1999).

Environmental Variables

Three sampling sites were established in each of Laguna Grande lake, El Pescado lake, and ROL1, two in the channel between the lakes, and one site at ROL 2 (N=12; Fig. 1). Samples and limnological data were taken seasonally: December 6, 2004 (spring); March 14, 2005 (summer); July 13, 2005 (winter); and January 24, 2006 (summer).

At each site and sampling date, depth was recorded with a meter stick in a fixed point of Laguna Grande lake. Rainfall is an important source of water level fluctuation in the wetland, and data on rainfall was provided by Estación Experimental Agropecuaria Delta del Paraná (INTA). We considered water level fluctuations in Laguna Grande as being representative of the whole wetland. We measured pH and conductivity with a HANNA HI 991301 portable meter and dissolved oxygen with a HANNA HI 9143 portable meter. Photosynthetic available radiation (PAR) was measured with a light meter Li-250A equipped with a spherical quantum sensor Li-192 SA. We recorded both incident and sub-surface irradiance in order to calculate the percentage of light transmission as a measure of light penetration in the water body.

Humic content was estimated with the 254 nm absorbance of water filtered through fiberglass filters of 0.7 μm nominal pore size (Kronberg 1999). Suspended solids were determined by filtering a known water volume through pre-dried (105°C) and weighed fiberglass filters of 1 μm of pore size. After filtration, filters were again dried and weighed (APHA 2005).

Dissolved nutrients were determined in water filtered through fiberglass filters of 0.7 μm nominal pore size using Hach® reagents and a DR 2800 spectrophotometer. Nitrate + nitrite were assayed with the cadmium reduction method, ammonia with the indophenol method, and phosphorus with the stannous chloride method (APHA 2005). Dissolved inorganic nitrogen (DIN) was obtained as the sum of concentrations of nitrate + nitrite + ammonia. Dissolved organic carbon (DOC) concentration was estimated through a hot oxidation with hot persulfate and then determined in an OI 1010 TOC analyzer.

Phytoplankton chlorophyll *a* was estimated filtering a known volume of water through fiberglass filters of 0.7 μm pore size and then freezing the filters. Later, pigment was extracted with hot ethanol and absorbance at 665 and 750 nm was measured before and after the addition of HCl 0.1 N to correct for phaeopigments absorbance (Nusch 1980). Calculations were made according to Lorenzen (1967).

Periphyton on Natural Substrata

In this study we focused on the most widespread and abundant macrophytes in the wetland, the rush *Schoenoplectus californicus* and the liverwort *Ricciocarpus natans*. *Schoenoplectus californicus* is a rooted emergent hydrophyte of 150 cm or more in height growing in submersed or exposed soils; it is rhizomatous with aerial leaves and reproductive organs. *Ricciocarpus natans* is a small free-floating plant, with a lobed and dorsi-ventrally flattened thallus. It presents false roots or scales and may develop in

conspicuous floating carpets in riparian zones of shallow lakes (Sculthorpe 1967). We recorded the taxa with attachment mechanisms (e.g., basal cells, mucilaginous stems, etc.) and also epiphytic and motile benthic algae without them (we named all of them periphytic algae). We also recorded planktonic, ticoplanktonic, and metaphytic algae.

At each sampling site five pieces of similar size (ca. 10 cm long) and physiognomy of *S. californicus* and at least 10 individuals of *R. natans* were collected. We fractioned the samples for its live observation and fixed a sub-sample with formalin. The epiphytic community was scrapped from the submersed parts of the plants for its observation under a Zeiss microscope at a 1000× magnification. To identify algal genera and species and to determine habits of species, we used: Komárek and Anagnostidis (1999, 2005) for Cyanobacteria; Lange-Bertalot (2001) and Krammer and Lange-Bertalot (1986, 1988, 1991a, b) for Bacillariophyceae; Printz (1964) and Ettl (1983) for Chlorophyta; Tell and Conforti (1986) for Euglenophyta; and Ettl (1977) and Pizarro (1995) for Xanthophyceae. For higher classification we followed van den Hoek et al. (1995). Samples for diatom identification were acid treated and permanent slides were prepared (Battarbee 1986).

We registered the taxa found in at least 10 microscopy subsamples for each substratum and date and employed the minimum area method for benthos for quantification (Boudoresque 1971; Bicudo 1990). The method consists in the counting of taxa up to the number of new taxa is <10% of the number of taxa already registered in the sample.

Numerical and Statistical Analysis

For environmental data, we considered average values for all sites and sampling dates within each water body. For algal taxa we developed a presence-absence matrix of species for each water body. To analyze the relationship of algae with environmental variables, we performed canonical correspondence analyses (CCA) (ter Braak 1994) based on presence-absence data for epiphytic taxa and means of environmental variables. For this analysis we considered only those taxa that were recorded at least 10 times in the matrix of substrata and sampling sites. We performed separate analyses for the substrata *S. californicus* and *R. natans* substrata in order to compare the microhabitat provided by each plant for the algae.

Before running analyses we evaluated correlation coefficients among environmental variables, and employed forward selection to detect and remove from the analysis any environmental variables that were highly correlated. The final set of limnological variables considered were: conductivity, light transmission, DIN, dissolved P, and

phytoplanktonic chlorophyll *a*. We evaluated the significance of ordination axes through Monte Carlo permutation tests ($p<0.05$). Water depth was not included in the CCA because bottoms of the lakes were very irregular owing to high local deposition of organic matter of vegetal origin, resulting in a high heterogeneity of depth measurements. Instead we used conductivity as a surrogate for water depth because the two measures were related (Log_{10}conductivity $=-5.12 \ 10^{-3}$ Z $+3.6$; $R=0.36$, $p=0.013$, $N=46$; where Z is the water depth).

We followed the scheme proposed by Whittaker (1972) for describing diversity patterns. We determined the overall algal richness of the studied water bodies of the NRO as an estimate of γ diversity and the richness of each water body as a measure of the α diversity. The β diversity, the taxa change among water bodies, or taxa turnover was estimated employing the Whittaker index (β_W) (Magurran 2006):

$$\beta_W = S/\alpha$$

where S is the total number of recorded species (γ diversity) and α is the total number of species in the sample. Furthermore, another approach to assess taxa turnover was by means of the Jaccard index of community similarity (J) (Magurran 2006) which was calculated between all possible pairs of water bodies as:

$$J = a(a + b + c)^{-1}$$

where *a* represents the number of shared taxa in both samples, *b* is the number of taxa present in one sample, and *c* is the number of taxa in the second sample. The J index would equal one when all taxa are shared by samples, and zero when none are shared, and is considered an estimator of β diversity (Chase 2003).

Results

Physical and Chemical Variables

Table 1 shows the range, average and coefficient of variation for each environmental variable measured. Rainfall during the month prior to each sampling date was 66 mm in December 2004 (low water level), 45 mm in March 2005, 108 mm in July 2005, and 255 mm in January 2006 (high water level). The major difference in hydrometric height between high and low water levels in Laguna Grande was about 26 cm. Conductivity, and to a lesser degree suspended solids and abs 254 nm, reflected this change in water level (Fig. 2a and b). Incident irradiance fluctuated between 1408 μmol photons m^{-2} s^{-1} (channel in December 2004) and 18.4 μmol photons m^{-2} s^{-1} (ROL 2 in July 2005), showing the lowest values in winter. The

Table 1 Range (upper row), average ± 1 SD (middle row, bolded) and coefficient of variation (lower row, as percentage) of environmental variables during the sampling period. In all cases, $N=4$ with the exception of dissolved oxygen (which was not measured in July 2005) and DOC (data shown are average of DOC concentrations at sampling points of the studied water bodies)

	ROL 1	ROL 2	Laguna Grande	Channel	El Pescado
Depth (m)	0.25–0.39	0.24–0.25	0.35–0.52	0.53–0.62	0.28–0.34
	0.30±0.08	**0.25±0.01**	**0.42±0.09**	**0.58±0.05**	**0.32±0.03**
	24.9	2.9	21.2	7.9	10.2
pH	7.9–8.4	7–8.5	8.2–8.5	7.6–8.3	7.8–8.3
	8.16±0.23	**7.71±0.62**	**8.35±0.13**	**8.07±0.30**	**8.10±0.21**
	2.9	8.1	1.6	3.7	2.6
Conductivity (μS cm^{-1})	2010–6843	940–5660	890–3513	890–3340	880–3350
	4213±1989	**2693±2063**	**2318±1094**	**2341±1147**	**2385±1169**
	47.2	76.6	47.2	48.9	49.1
Suspended solids (mg L^{-1})	20–72	19–49	11–114	27–48	11–76
	51±23.0	**34±16.5**	**53±47.1**	**36±10.4**	**36±27.9**
	45.0	48.8	88.1	29.1	78.2
Dissolved O$_2$ (mg L^{-1})	2.37–10.8	1.1–6	4.4–6.5	5.5–7.5	4.7–7.4
	7.61±4.57	**3.37±2.40**	**5.41±1.06**	**6.65±0.99**	**5.80±1.42**
	60.5	71.3	19.6	14.8	24.4
Temperature (°C)	17–34	13–28	14–28	14–30	15–30
	28±7.6	**23±6.7**	**23±6.5**	**24±6.9**	**24±6.8**
	27.4	29.5	28.4	28.9	27.9
% transmited light	17–38	1.3–58	30–51	42–64	39–48
	27±9	**29±31**	**43±10**	**53±12**	**45±4**
	33.5	109	23.3	22.7	8.8
abs 254 nm	1.8–4.9	1.8–5.2	1.2–2.1	1.2–1.8	1.2–1.8
	3.28±1.27	**3.09±1.49**	**1.67±0.35**	**1.48±0.25**	**1.47±0.23**
	38.6	48.4	21. 1	17.3	15.8
DOC (mg L^{-1})	54.5 ±2.0	48.4	28.2±5.6	27.8±0.9	29.0±0.5
N-nitrate + nitrite (μg L^{-1})	37–298	28–282	20–70	16–207	17–193
	173±110	**178±109**	**57.5±25**	**92±82**	**85.4±75.4**
	64	61	43.5	89	88
N-ammonia (μg L^{-1})	15–136	30–79	8–145	1.7–547	14–277
	69±63	**57±23**	**84±58**	**177±250**	**123±120**
	92	40	69	142	98
Dissolved P (mg L^{-1})	0.2–2.5	1.2–8.9	0.3–1.6	0.5–1	0.4–1.5
	1.09±1.07	**3.44±3.71**	**1.09±0.60**	**0.78±0.22**	**0.90±0.49**
	97.9	107.9	54.4	27.8	54.4
Phytop. chl a (μg L^{-1})	60–243	12–174	23–102	4.9–76	2.7–66
	127.8±79.8	**76.8±74.7**	**77.7±36.7**	**46.2±35.4**	**40.6±27.4**
	62.4	97.3	47.2	76.7	67.5

percentage of transmittance of incident light was highly variable at ROL 2 (coefficient of variation of 109%) and was similar at both lakes and the channel (Fig. 2c). Humic content (abs 254 nm) and DOC concentration were higher at both ROLs (Table 1). DIN concentrations at Laguna Grande, the channel, and El Pescado were highest in winter, while in the ROLs the highest values were detected in December 2004 (Fig. 2d). Dissolved P values were high at all sites and peaked at ROL 2 in December 2004 (Fig. 2e). Phytoplankton chlorophyll a concentrations fluctuated between 243.0 and 2.7 μg L^{-1} (ROL 1 in March 2005 and El Pescado in July 2005, respectively). Although no spatial or temporal trend was observed for phytoplankton chlorophyll a, a correlation with water temperature was found (Spearman correlation coefficient=0.64; $p=0.002$).

Epiphytic Algae

A total of 105 epiphytic algal taxa from both *S. californicus* and *R. natans* substrata were recorded, of which 48% were Bacillariophyceae, 22% were Cyanobacteria, 18% were Chlorophyta, and the rest (12%) belonged to Euglenophyta,
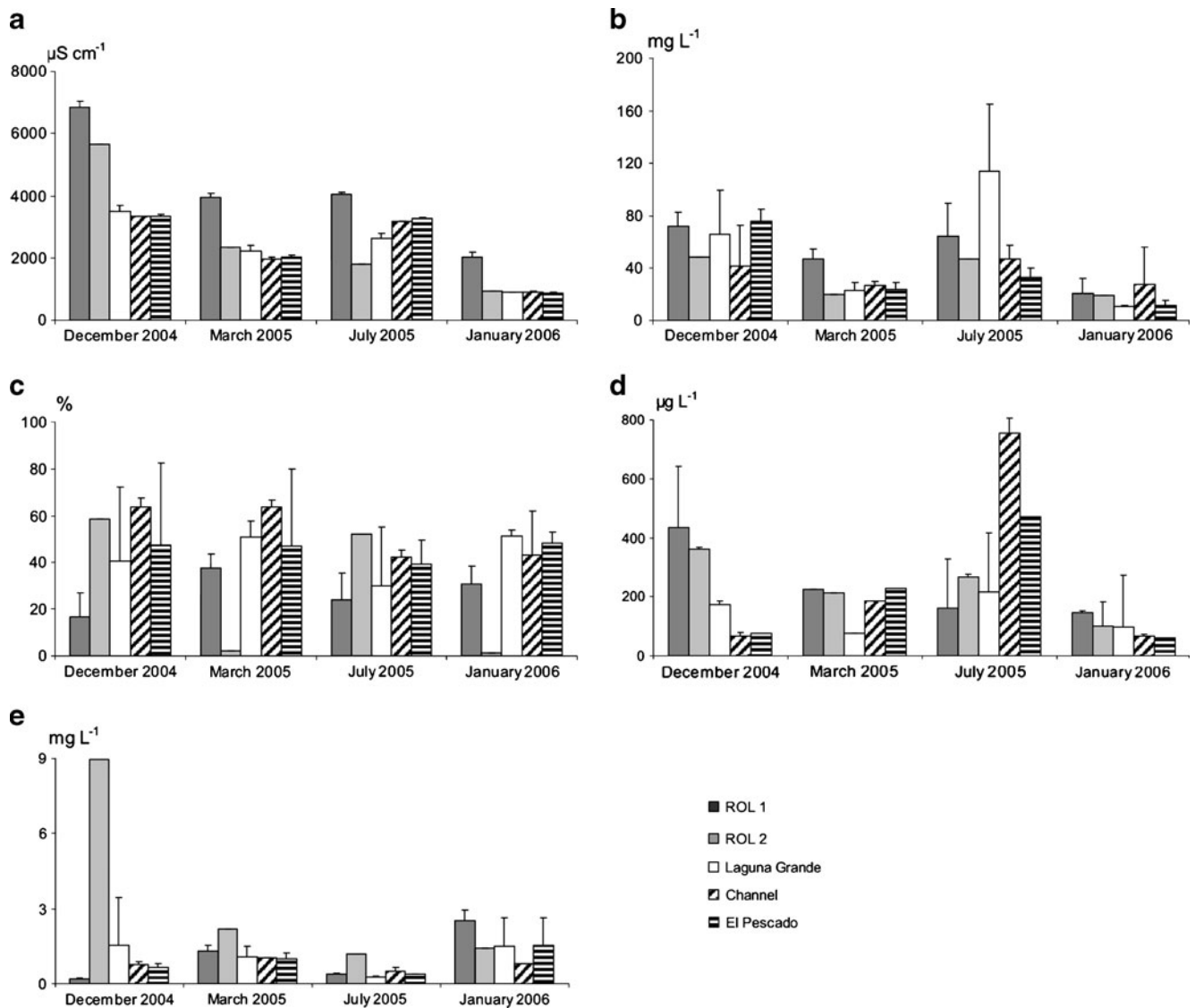
Fig. 2 Temporal fluctuations of **a**) conductivity, **b**) suspended solids, **c**) percentage of penetration of incident light, **d**) dissolved inorganic nitrogen (DIN), and **e**) dissolved P during the study period at each water body. Error bars represent + 1 SD

Xanthophyceae, Synurophyceae, and Cryptophyta (Table A, electronic supplementary material). Periphytic algae dominated in the period of low water level, comprising the 92% of the algae recorded; while in January 2006 (high water level) planktonic, ticoplanktonic, and metaphytic taxa accounted for 36% of the community (Fig. 3). The *S. californicus* substrate was present in all sampling dates in all sites with the exception of ROL 2 in January 2006; *R. natans* was absent at all sites in January 2006, and was never encountered at ROL 2.

The CCA biplot of sites and environmental variables for *S. californicus* is represented in Fig. 4a. Conductivity, as an estimation of water level was most associated with Axis 1 (correlation coefficient=−0.56) followed by light transmittance (cc=−0.35). Phytoplankton chlorophyll *a* (cc=0.73) and DIN (cc=−0.43) were associated with Axis 2, while
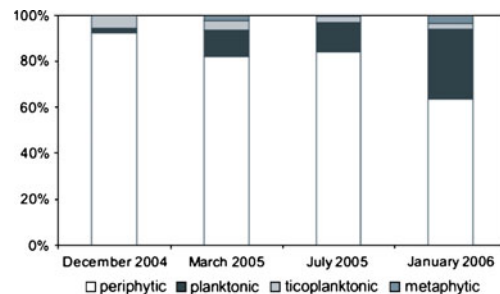

Fig. 3 Temporal fluctuation of the percentage of each algal (including Cyanobacteria) habit considering all water bodies together. Pseudo-periphytic = planktonic, ticoplanktonic, and metaphytic algae
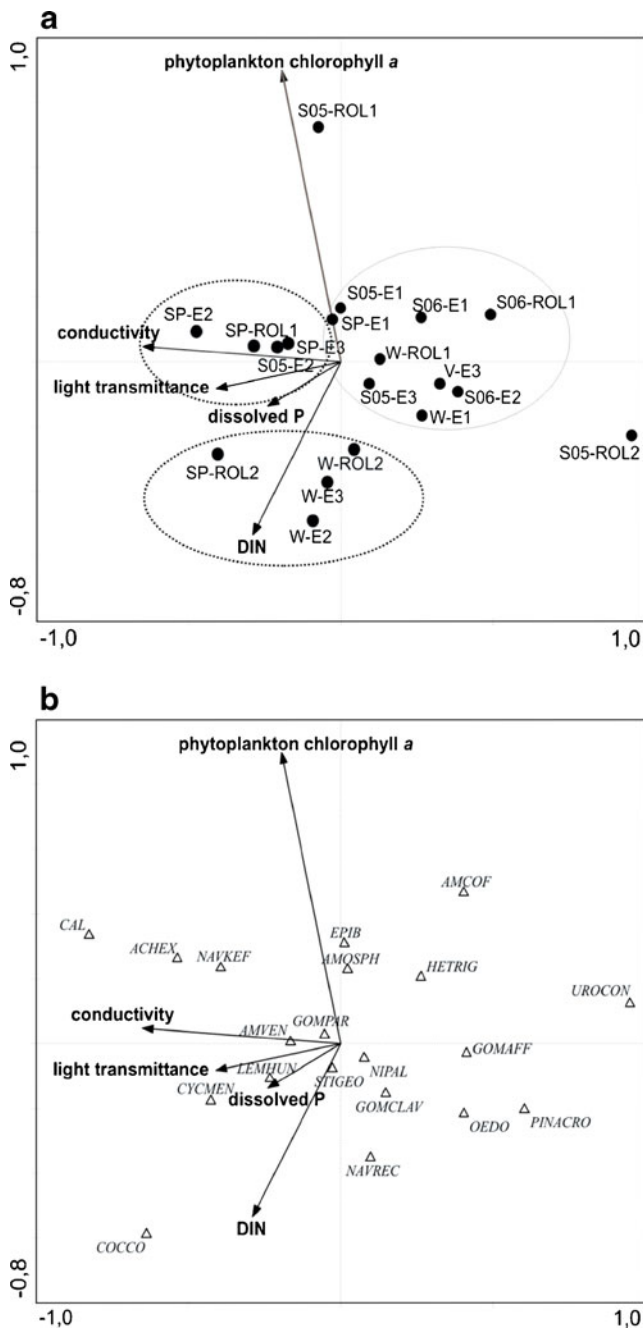
Fig. 4 CCA biplots of environmental variables and a) sites and b) species performed for the substrate *Schoenoplectus californicus*. SP = spring (December 2004); S05 = summer 2005 (March 2005); W = winter (July 2005); S06 = summer 2006 (January 2006). E1 = Laguna Grande, E2 = Channel and E3 = El Pescado. ACHEX = *Achnanthidium exiguum*, AMCOF = *Amphora* aff. *coffeaeformis*, AMVEN = *Amphora veneta*, AMOSPH = *Anomoeoneis sphaerophora*, CAL = *Caloneis* sp. 1, COCCO = *Cocconeis placentula*, CYCMEN = *Cyclotella meneghiniana*, GOMAFF = *Gomphonema affine*, GOMCLAV = *Gomphonema clavatum*, GOMPAR = *Gomphonema parvulum*, LEMHUN = *Lemnicola hungarica*, NAVKEF = *Navicula kefvingensis*, NAVREC = *Navicula recens*, NIPAL = *Nitzschia palea*, PINACRO = *Pinnularia acrosphaeria*, HETRIG = *Heteroleiblenia rigidula*, EPIB = *Epibolium* sp. 1, OEDO = *Oedogonium* sp. 1, STIGEO = *Stigeoclonium* sp. 1, UROCON = *Uronema confervicolum*

dissolved P was associated with both canonical axes. The Monte Carlo permutation test for the first canonical axis was significant ($p=0.024$), and eigenvalues were 0.140 and 0.052 for the first and the second canonical axes, respectively. The percentage of variance explained by the relationship species-environment was 72.5% (first plus second axis). In summer 2005, ROLs separated from the rest of the sites mainly because of high phytoplankton chlorophyll *a* concentrations at ROL 1, and low light penetration at ROL 2. The other sites could be divided into three groups, one of them was mainly composed of spring samples and was characterized by high conductivity, light transmittance, and dissolved P. A second group was characterized by high DIN values and was represented by three winter samples and one at the ROL 2 in spring. The third and most heterogeneous group of sites was characterized by low conductivity, dissolved P, and light transmittance values. Finally, a vertical axis divided sites by conductivity (i.e., water level), with low water level samples on the left and high water level ones on the right side of the biplot. Figure 4b shows the biplot of species and environmental variables associated with *S. californicus*. We distinguished one continuum of species distributed along the environmental gradient and one outlier species (*Cocconeis placentula*) characterized by high DIN and dissolved P and low chlorophyll *a* concentrations. The majority of species were found in the central part of the biplot.

The CCA biplot for sites and environmental variables for *R. natans* is presented in Fig. 5a. The variables associated with Axis 1 were phytoplankton chlorophyll *a* (cc=0.37) and conductivity (cc=−0.36); variables associated with Axis 2 were light transmittance (cc=0.61) and DIN concentration (cc=−0.61). Again, dissolved P reached intermediate values between both axes. The Monte Carlo permutation test for the first canonical axis was significant ($p=0.004$), and eigenvalues were 0.197 and 0.111 for axes 1 and 2, respectively. The percentage of variance explained by the species-environment relationship was 69.1% (axes 1 +2). Water temperature, as a measure of seasonality, allowed us to distinguish three groups of sites in the CCA corresponding to *R. natans*, with the ROL 1 sample in spring (high chlorophyll *a* concentration and light transmittance) being an outlier. The group of winter samplings was characterized by high DIN and low light transmittance, P, and phytoplankton chlorophyll *a*. The summer and spring groups possessed low DIN and high light transmittance, P, and phytoplankton chlorophyll *a* and differed in conductivity, with the summer samplings being characterized by low conductivity and spring samplings by high conductivity (i.e., high and low water level, respectively). The species and environmental variable diagram for *R. natans* is shown in Fig. 5b. The majority of species tended to be at the central part of the biplot, with a reduced number of
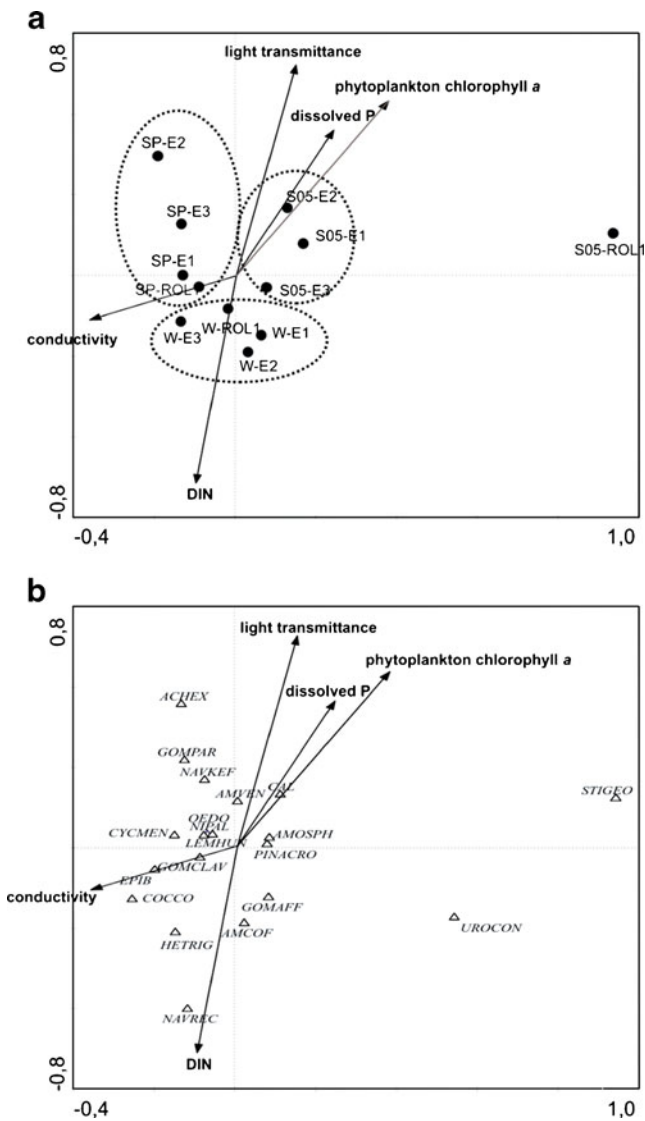
Fig. 5 CCA biplots of environmental variables and **a**) sites and **b**) species performed for the substrate *Ricciocarpus natans*. SP = spring (December 2004); S05 = summer 2005 (March 2005); W = winter (July 2005); S06 = summer 2006 (January 2006). E1 = Laguna Grande, E2 = Channel and E3 = El Pescado. Species codes as in Fig. 4

them located at high DIN (*Navicula recens*), low conductivity (*Stigeoclonium* sp. 1, and *Uronema confervicolum*), and high light transmittance, P, and phytoplankton chlorophyll *a* (*Achnanthidium exiguum*).

Diversity Patterns

For the 105 total species, the site with highest α diversity was El Pescado lake in March 2005. ROL 2 was the least diverse site, also in March 2005 (Fig. 6a). Based on the Whittaker index, ROL 2 was the most unique site (Fig. 6b). When considering all sampling together, ROL 2 possessed the highest β diversity index (β_W=4), while Laguna Grande had the lowest β_W value (Table 2). Jaccard indices
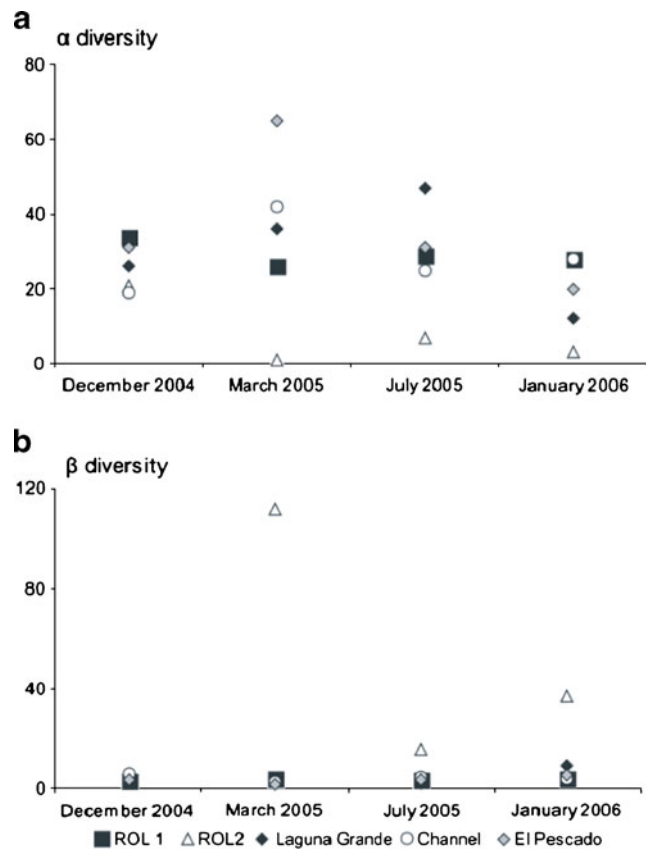

Fig. 6 Values of **a**) α and **b**) β diversity index for both substrata analyzed over the study period

indicated that El Pescado, Laguna Grande, and ROL 1 were most similar, and ROL 2 was dissimilar to the other locations (Table 2).

Discussion

We detected a strong influence of environmental variables in the composition of the epiphytic algae in the studied water bodies of the Natural Reserve Otamendi. Most of the epiphytic algae recorded from both *S. californicus* and *R. natans* are common in wetlands (Goldsborough et al. 2005). A large proportion of the taxa recorded here have been found on macrophytes in other kinds of environments (Tell 1977; Ács and Buczó 1994; Pozzobon and Tell 1995; Tesolín and Tell 1996; Gómez et al. 2003; Bauer et al. 2007) where the Bacillariophyceae is also the most conspicuous algal class. Following van Dam et al. (1994) most of the diatoms recorded in this study share similar ranges of tolerance to environmental variables, thus enabling them to thrive in a variety of habitats. Most of species are adapted to live in alkaline to neutral waters, tolerating intermediate to high salinities, and are, in general, autotrophic for nitrogen metabolism. Also, they tolerate

Table 2 Rows 1 and 2: Values of species richness (α diversity) and β diversity (β_W index) for sampling sites, based on pooled substratum and sampling date data. Rows 3 to 7: Values of Jaccard index between pairs of sites after pooling all sampling dates and both analysed substrata data

	ROL 1	ROL 2	Laguna Grande	Channel	El Pescado
α diversity	60	28	69	64	78
β diversity	1.9	4.0	1.6	1.8	1.4
ROL 1					
ROL 2	0.33				
Laguna Grande	0.56	0.35			
Channel	0.53	0.37	0.56		
El Pescado	0.52	0.33	0.53	0.58	

from intermediate to low oxygen concentrations, occur in sites with elevated nutrients, and in general tolerate desiccation. Because of this tolerance, most species were shared between macrophytes and among water bodies: conductivities were high in all sampling sites; the trophic conditions were similar in the water bodies, and the dissolved P concentrations were, in general, high. In this sense, Cattaneo and Kalff (1979) observed that environmental characteristics of water bodies are more important than the type of substrata in determining the characteristics of the periphyton. Thus, it is likely that the periphyton assemblages from two different substrata of the same water body are more similar than communities living on the same substratum but from different water bodies.

The highest proportion of phytoplanktonic, ticoplanktonic, and metaphytic species was recorded during high water level and may be related to the strong interactions between the limnetic and epiphytic habitats in shallow lakes. In this kind of system these habitats often overlap (Goldsborough and Robinson 1996) and it is common to find high amounts of true planktonic algae in the epiphyton (pseudoperiphyton) owing to mixing processes and resuspension of sediments (Schallenberg and Burns 2004). Moreover, during high water periods, phytoplankton usually constitutes the dominant community in wetlands (Goldsborough and Robinson 1996), accounting for the relatively high proportion of non-periphytic taxa encountered in the epiphyton during the high water level periods.

In floodplains of large rivers, the flood pulse is usually the main modulator of both the physicochemical characteristics and the biota (Junk et al. 1989). In the Natural Reserve Otamendi, variations in water level are the result of a combination of factors (rainfall, surface and groundwater flows) (Chichizola 1993). The homogenization in the values of some variables (conductivity, DIN, suspended solids, humic content) in the different sites during January 2006 (high water level) would be the result of connectivity processes that occur in this system. Laguna Grande and El Pescado lakes, which are always connected to each other through the channel, were similar in some limnological and biotic characteristics. Both relict oxbow lakes (ROLs), which are not always connected together nor with the lakes

from which are isolated, were in general richer in inorganic N and P than the lake sites. The higher inorganic nutrient level in the ROLs did not favor a higher algal diversity. Conversely, Laguna Grande, the channel, and El Pescado exhibited a large number of epiphytic algal species, probably owing to the better light conditions at these sites, a result of their lesser humic content and lower vegetation cover. Moreover, El Pescado lake possesses a stream, and incoming water carries algae into the lake, perhaps explaining the high alpha diversity in this lake in summer (March 2005).

Cattaneo et al. (1998) observed that plant architecture (floating and submersed) was an important factor affecting the quantitative variables of epiphyton, while the effect of macrophyte life form was not so evident on epiphyton, composition, as we observed in our study. Although there was a high similarity in the taxonomic composition of the epiphyton from *S. californicus* and *R. natans*, some differences may be distinguished related to the characteristics of each substratum. According to the CCA results, even when DIN and phytoplankton chlorophyll *a* were important variables for both substrata, light penetration was more important for periphyton of *R. natans* and water level (actually conductivity) was more important for periphyton of *S. californicus*. While epiphyton on rush probably receives light coming from almost all directions, the attached community on *R. natans* is subject to the shadowing of its own thallus and of the surrounding floating carpet. In this sense, light transmittance is more important as a resource for organisms attached to *R. natans* than to *S. californicus*. In contrast, water level influenced the community attached to *S. californicus* more than that attached to *R. natans*, probably because of the fixed characteristic of the rushes. Furthermore, temperature fluctuations affected the ordination of species in the CCA for *R. natans*, showing that the development of these floating plants was more influenced by seasonality than was *S. californicus*.

The analysis of γ diversity led us to contextualize the NRO in terms of "geographic-scale species diversity" (Hunter 2002). The algal richness registered by us was low when compared with the findings of Jacobs and Noten

(1980) for epiphyton on eelgrass, Tesolín and Tell (1996) for a lake from a floodplain of the Paraná River, and Putz and Junk (1997) and Rodrigues and Bicudo (2001) for different wetlands from Brazil. The extreme environmental conditions of the shallow lakes at NRO may be the reason for the low diversity in epiphytic algae. First, the high humic content in the water bodies restrict light penetration and second, the extensive development of phytoplankton (as reflected in the chlorophyll *a* concentrations) and macrophytes (in particular at the ROLs), that compete with periphyton for nutrients and light, restrict its growth (Borchardt 1996; Hill 1996).

The values of Whittaker (β_W) and Jaccard (J) indices showed a clear taxa turnover among the water bodies at NRO that was influenced by the combination of spatial isolation and environmental heterogeneity. Considering similarity as an index of β diversity (higher similarity yields lower β diversity), a clear positive trend was observed between taxa turnover, the distance among water bodies, and habitat heterogeneity. Taking into account all the water bodies analyzed, the epiphytic algal community from ROL 2 was the most different. ROL 2 was the smallest water body and possessed a profuse development of emergent macrophytes that restricted light penetration. Moreover, connectivity with ROL 2 was minimal because of this site's distant location. These characteristics suggest that taxa turnover agrees with the predictions of both metapopulation dynamics and continuum ecological models. Metapopulation dynamics (Hanski 1999) predicts that increased distance between discrete habitats suitable for population establishment will reduce the probability of a population becoming established because of limited dispersal at a metacommunity level. In the context of β diversity, increased compositional difference is predicted when the distance between habitats increases. Thus, ROL 2 as the most distant site should have the most distinct community. The continuum concept model assumes that species are regularly interchanged along ecological gradients (Oksanen and Minchin 2002) and that the spatial distribution of species mainly follows changes in environmental conditions. The continuum concept predicts a positive relationship between environmental variation and β diversity. In this sense, ROL 2 had the greatest fluctuations in light conditions and the highest β diversity values, suggesting that assemblages respond to light gradients.

The study of the ecology of epiphytic communities on natural substrata in shallow lakes has special relevance in the context of global climate change. Macrophyte distribution, specially floating plants, may be affected by local warming (Meerhoff and Mazzeo 2004), which in turn will affect the ecology of algal communities associated to them. Because of this, it is important to learn about the structure and functionality of epiphytic communities, and analyze the forces that modulate them in order to predict future changes in a warming scenario.

References

Ács E, Buczkó K (1994) Daily changes of reed periphyton composition in a shallow Hungarian lake (Lake Velence). In: Marino D, Montresor M (eds), Proceedings of the 13th International Diatom Symposium. Biopress Limited, Bristol:1–10

American Public Health Association (2005) Standard Methods for the Examination of Water and Wastewaters, 21st Edition. Centennial Edition. APHA, American Water Works Association, Water Environmental Federation, Washington, DC

Battarbee EW (1986) Diatom analysis. In: Berglund BE (ed) Handbook of holocene paleoecology and paleohydrology. Wiley, New York, pp 527–570

Bauer DE, Gómez N, Hualde PR (2007) Biofilms coating *Schoenoplectus californicus* as indicators of water quality in the Río de la Plata Estuary (Argentina). Environmental Monitoring and Assessment 133:309–320

Bicudo DC (1990) Consideraçoes sobre metodologias de contagem de algas do perifiton. Acta Limnologica Brasiliensia 1:459–475

Borchardt MA (1996) Nutrients. In: Stevenson RJ, Bothwell ML, Lowe RL (eds) Algal ecology: freshwater benthic ecosystems. Academic, London, pp 183–227

Boudoresque CF (1971) Méthodes d'étude qualitative et quantitative du benthos. (em particular du phytobenthos). Tethys 3:79–104

Burkholder JM, Wetzel RG (1989) Epiphytic microalgae on natural substrata in a hardwater lake: seasonal dynamics of community structure, biomass and ATP content. Archiv für Hydrobiologie 83:1–56

Cattaneo A, Kalff J (1979) Primary production of algae growing on natural and artificial aquatic plants: a study of interactions between epiphytes and their substrate. Limnology and Oceanography 24:1031–1037

Cattaneo A, Galanti G, Gentinetta S, Romo S (1998) Epiphytic algae and macroinvertebrates on submerged and floating-leaved macrophytes in an Italian lake. Freshwater Biology 39:725–740

Chase JM (2003) Community assembly: when should history matter? Oecologia 136:489–498

Chichizola S (1993) Las comunidades vegetales de la Reserva Natural Estricta Otamendi y sus relaciones con el ambiente. Parodiana 8:227–263

Cowardin LM, Carter V, Golet EC, LaRoe ET (1979) Classification of wetlands and deepwater habitats of the United States. US Fish and Wildlife Service FWS/OBS 79/31

Dodds WK, Biggs BJ, Lowe RL (1999) Photosynthesis-Irradiances patterns in benthic microalgae: variations as a function of

assemblage thickness and community structure. Journal of Phycology 35:42–53

Eminson D, Moss B (1980) The composition and ecology of periphyton communities in freshwaters. 1. The influence of host type and external environment on community composition. British Phycological Journal 15:429–446

Ettl H (1977) Xanthophyceae. In: Pascher A (ed) Süßwasserflora von Mitteleuropa, 3. Gustav Fischer Verlag, Suttgart

Ettl H (1983) Chlorophyta I. Phytomonadina. In: Pascher A (ed) Süßwasserflora von Mitteleuropa, 9. Gustav Fischer Verlag, Jena

Goldsborough LG, Robinson GC (1985) Seasonal succession of diatom epiphyton on dense mats of *Lemna minor*. Canadian Journal of Botany 63:2332–2339

Goldsborough LG, Robinson GC (1996) Patterns in wetlands. In: Stevenson RJ, Bothwell ML, Lowe RL (eds) Algal ecology: freshwater benthic ecosystems. Academic, London, pp 78–117

Goldsborough LG, McDougal RL, North AK (2005) Periphyton in freshwater lakes and wetlands. In: Azim ME, Verdegem MC, van Dam AA, Beveridge MCM (eds) Periphyton: ecology, exploitation and management. CABI Publishing, United States, pp 71–89

Gómez N, Licursi M, Hualde RR (2003) Epiphytic algae on the bulrush (Scirpus californicus (Mey) Steud) in the Río de la Plata (Argentina): structure and architecture. Archiv für Hydrobiologie 147:231–247

Hanski I (1999) Metapopulation ecology. University Press, Oxford

Hill W (1996) Effects of light. In: Stevenson RJ, Bothwell ML, Lowe RL (eds) Algal ecology: freshwater benthic ecosystems. Academic, London, pp 121–148

Hunter M Jr (2002) Fundamentals of conservation biology, 2nd edn. Blackwell Science, Massachusetts

Jacobs RPWM, Noten TMPA (1980) The annual pattern of the diatoms in the epiphyton of eelgrass (Zostera marina L.) at Roscoff, France. Aquatic Botany 8:335–370

Junk WJ, Bayley PB, Sparks R (1989) The flood pulse concept in river-floodplain systems. In: Podge JP (ed) Proceedings of the International Large River Sympsoium. Canadians Special Publication of Fisheries and Aquatic Sciences, Ohawa, pp 110–127

Komárek J, Anagnostidis K (1999) Cyanoprokariota. 1. Teil: Chroococcales. In: Ettl H, Gärtner G, Heynig H, Mollenhauer D (eds) Süßwasserflora von Mitteleuropa. Gustav Fisher, Stuttgart

Komárek J, Anagnostidis K (2005) Cyanoprokariota. 2. Teil: Oscillatoriales. In: Büdel B, Gärtner G, Krienitz L, Schagerl M (eds) Süßwasserflora von Mitteleuropa. Elsevier, Heidelberg

Krammer K, Lange-Bertalot H (1986) Bacillariophyceae. 1. Naviculaceae. In: Ettl H, Gerloff J, Heying H, Mollenhauer D (eds) Süßwasserflora von Mitteleuropa 2/1. Gustav Ficher Verlag, Jena

Krammer K, Lange-Bertalot H (1988) Bacillariophyceae. 2. Bacillariaceae, Epithemiaceae, Surirellaceae. In: Ettl H, Gerloff J, Heying H, Mollenhauer D (eds) Süßwasserflora von Mitteleuropa 2/2. Gustav Ficher Verlag, Jena

Krammer K, Lange-Bertalot H (1991a) Bacillariophyceae. 3. Centrales, Fragilariaceae, Eunotiaceae. In: Ettl H, Gerloff J, Heying H, Mollenhauer D (eds), Süßwasserflora von Mitteleuropa 2/3. Gustav Ficher Verlag

Krammer K, Lange-Bertalot H (1991b) Bacillariophyceae. 4. Achnanthaceae, Kritischie Ergänzungen zu Navicula (Lineolate) und Gomphonema. In: Ettl H, Gerloff J, Heying H, Mollenhauer D (eds) Süßwasserflora von Mitteleuropa 2/4. Gustav Ficher Verlag, Jena

Kronberg L (1999) Content of humic substances in freshwater. In: Keskitalo J, Eloranta P (eds) Limnology of humic waters. J. Backyus Publishers, Leiden, pp 9–10

Lange-Bertalot H (2001) Navicula sensu stricto. 10 Genera separated from Navicula sensu lato. Frustulia. In: Lange Bertalot H (ed), Diatoms of Europe. Volume 2

Laugaste R, Reunanen M (2005) The composition and density of epiphyton on some macrophyte species in the partly meromictic Lake Verevi. Hydrobiologia 547:137–150

Lorenzen CJ (1967) Determination of chlorophyll and pheopigments: spectrophotometric equations. Limnology and Oceanography 12:343–346

Magurran AE (2006) Measuring biological diversity. Blackwell Science Ltd., United States

Meerhoff M, Mazzeo N (2004) Importancia de las plantas flotantes libres de gran porte en la conservación y rehabilitación de lagos someros de Sudamérica. Ecosistemas 13:12–22

Nusch EA (1980) Comparison of different methods for chlorophyll and phaeopigment determination. Ergebnisse der Limnologie 14:14–36

Oksanen J, Minchin PR (2002) Continuum theory revisited: what shape are species responses along ecological gradients? Ecological Modelling 157:119–129

Pizarro H (1995) The genus *Characiopsis* Borzi (Mischococcales, Tribophyceae). Taxonomy, biogeography and ecology. J. Cramer, Stuttgart

Pozzobon MV, Tell G (1995) Estructura y dinámica de la comunidad perifítica sobre *Ricciocarpus natans* (Hepaticae) de la Laguna de Los Padres (Buenos Aires, Argentina). Boletín de la Sociedad Argentina de Botánica 30:199–208

Printz H (1964) Die Chaetophoralen der Binnengewasser (eine systematische Ubersicht). Hydrobiologia 24:1–376

Putz R, Junk WJ (1997) Phytoplankton and periphyton. In: Junk WJ (ed) The Central Amazon floodplain: ecology of a pulsing system. Ecological Studies, 126. Berlin, Springer-Verlag, pp 207–222

Rodrigues L, Bicudo D (2001) Similarity among periphyton algal communities in a lentic-lotic gradient of the upper Paraná river floodplain, Brazil. Revista Brasileira de Botânica 24:235–248

Rodríguez P, Pizarro H (2007) Phytoplankton productivity in a highly colored shallow lake of a South American floodplain. Wetlands 24:1153–1160

Rogers KH, Breen CM (1981) Effects of epiphyton on *Potamogeton crispus* L. leaves. Microbial Ecology 7:351–363

Romo S, Villena MJ, García-Murcia A (2007) Epiphyton, phytoplankton and macrophyte ecology in a shallow lake under in situ experimental conditions. Archiv für Hydrobiologie 170:197–209

Schallenberg M, Burns C (2004) Effects of sediment resuspension on phytoplankton production: teasing apart the influences of light, nutrients and algal entrainment. Freshwater Biology 49:143–159

Sculthorpe CD (1967) The biology of aquatic vascular plants. Arnold, London

Tell G (1977) Estudios ecológicos sobre algas epífitas de *Ricciocarpus natans*. Ecosur 4:117–135

Tell G, Conforti V (1986) Euglenophyta pigmentadas de la Argentina, Biblioteca Phycologica 75. J. Cramer, Berlin

ter Braak CJF (1994) Canonical community ordination. Part I: Basic theory and linear methods. Ecoscience 1:127–140

Tesolín G, Tell G (1996) The epiphytic algae on floating macrophytes of a Paraná river floodplain lake. Hydrobiologia 333:111–120

Vadeboncoeur Y, Steinman A (2002) Periphyton function in lake ecosystems. Scientific World 2:1449–1468

van Dam H, Merters A, Sinkeldam J (1994) A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. Netherlands Journal of Aquatic Ecology 28:117–133

van den Hoek C, Mann DG, Jahns HM (1995) Algae. An introduction to phycology. Cambridge University Press

van der Valk AG (2007) The biology of freshwater wetlands. Oxford University Press

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21:213–251

Williamsom C, Morris DP, Pace ML, Olson OG (1999) Dissolved organic carbon and nutrients as regulators of lake ecosystems: Resurrection of a more integrated paradigm. Limnology and Oceanography 44:795–803