

Vertical distribution of epiphyton biomass and diversity in a shallow lake during contrasting ecosystem regimes



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ABSTRACT

We investigated seasonal and depth variations in biomass and composition of bulrush-associated epiphyton in a shallow seepage lake in Argentina and examined whether differences existed in the vertical profiles between sites, whether the zonation with respect to depth changed according to different regimes of the ecosystem, and what conditions most greatly affected the epiphyton vertical distribution. We performed sample collection every 4 weeks for one year at both the centre and the periphery of the bulrush stand, sectioned the bulrush stems into segments to give a fixed 7-level vertical profile, and recorded the water physicochemical characteristics over the same profile. The epiphyton vertical variations were similar at both sampling locations.

The epiphyton-biomass profiles underwent an abrupt change at a depth of 45–65 cm during the clear-water period, while comparable values were recorded along the profiles during the turbid phase. The temperature had a positive effect during late spring–early summer that coincided with the transitional period and beginning of the clear period.

The principal driver of the epiphyton-biomass vertical distribution is the light availability, followed by the exposure to water movements. The resident species with high contributions to the overall biovolume were related to the percentage of incident light, and particularly those community members that were predominant in the clear-water period.

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1. Introduction

Within macrophyte stands, the vertical physical structure created by the plants influences the light and substratum availability and thus the biomass and productivity of the corresponding periphytic communities (Vis et al., 2006). Several authors (e.g., Buczkó and Ács, 1997; Galanti and Romo, 1997; Håkanson and Boulion, 2004; Vis et al., 2006) have proposed that both the horizontal and the vertical distribution of benthic and epiphytic algae are strongly dependent on the distribution of substrates receiving light and therefore on the density and architecture of the plant canopy. For example, at low stem densities, the simple conical architecture of the shoots of bulrush or similar growth forms allows light to penetrate into the water column without interference, thus creating a gradient that depends mostly on the physical characteristics

of the water itself. Submerged macrophytes with more complex architecture, however, will affect the light attenuation more strongly (Vermaat et al., 2000).

Various authors have pointed out that older or senescent submerged stems and leaves frequently contain a different epiphytic community from that developed on the younger parts (Hutchinson, 1975; Goldsborough and Hickman, 1991). These differences may be caused by the shorter colonization time needed for the epiphytes of younger shoots and leaves (Hutchinson, 1975). For this reason, an understanding of the growth patterns of the plant species under study is necessary (Borum, 1987; Cebrian et al., 1994) when periphyton dynamics are of interest.

The lakes in the pampean region at the eastern part of the Buenos Aires Province, are subject to a humid, temperate climate, with regularly distributed precipitation (annual average: 1000 mm), mean temperature in summer of 19–23 °C and a winter temperature above 10 °C. The average monthly surface incident PAR radiation ($\mu\text{E m}^{-2} \text{d}^{-1}$) varied from 7.25 in winter to 30.78 in summer during 2001–2002 (calculated from NASA, 2013). Since the pampean lakes are eutrophic (Quirós, 1997) and usually have elevated concentrations of total phosphorus and nitrogen compounds, a substantial pool of nutrients is available to epiphytes and to phytoplankton from the water column.

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In Lacombe, a characteristic eutrophic pampean lake, we have registered successive periods of turbid water with high phytoplankton biomass and clear water mostly promoted by the presence of *Stuckenia striata* (Ruiz et Pavon) Holub. and *Myriophyllum quitense* Kunth., which we have interpreted (Cano et al., 2008, 2012; Casco et al., 2009) as alternative stable states sensu Scheffer (1998). These regimes have no seasonal pattern since the lake may stay in one or another state for long periods of time (i.e., more than an entire year) or somewhat shorter intervals (i.e., more than 5 months). Likewise, in several other pampean lakes, regimes (states) have proved to be not necessary linked to the change of seasons through the year but to external and internal agents that may force the system into one state or another (Allende et al., 2009).

Cano et al. (2012) demonstrated that the variation in biomass and composition of the bulrush epiphyton was related principally to changes in light availability and nutrient concentrations during turbid- and clear-water states. They found no differences in these parameters with respect to the spatial location within the stands—i.e., at the centre or the periphery—although differences in environmental conditions and bulrush density had been detected in preliminary field work (Cano, 2009). These conclusions were drawn from an analysis of the average depth profiles of epiphyton communities. Questions remained, however, as to whether the vertical distributions would also be similar between sites, and, how the epiphyton communities would be structured vertically during the two aforementioned ecosystem regimes. Explicitly, is the epiphyton equally responsive to the different regimes along the vertical profile, as may be reflected by a differential biomass or community composition?

The seasonal changes in environmental conditions (such as a longer photoperiod and a temperature increase) generally promote an increase in biomass and species richness within the periphyton communities (Wetzel, 1983; De Nicola, 1996; Hill, 1996). Also, other conditions, such as those given by a clear-water state benefit the periphyton development (e.g., better light conditions within the water column, an increase in water-column stability through the presence of submerged macrophytes) (Scheffer et al., 1993). We suggest that (a) If both positive conditions occur simultaneously, then the periphyton response should reflect the combination of these forces; (b) If a turbid state occurs during the spring, the periphyton growth will be disadvantaged independently of the length of the photoperiod or the increase in temperature; (c) Also, during a turbid phase, epiphytic algae would tend to be less abundant and would grow down to a depth (i.e., would have a shorter profile) where light became limiting; and (d) The influence on the epiphyton of mechanical abrasion from water turbulence should be more evident within the vertical profile at portions of the bulrush stems nearer the surface of the water—and especially so at sites more extensively exposed to wind and waves as well as during the turbid-water period, when submerged macrophytes are absent and consequently no longer can provide any stabilization of the water column.

Therefore, we analysed the relationship between the variation observed in epiphyton communities and the concurrent environmental variables, during an annual cycle where drastic regime changes occurred.

2. Materials and methods

2.1. Study site

Lacombe Lake is a small and shallow seepage lake, located in the Province of Buenos Aires (35°50' S, 57°53' W), Argentina. The details on Lacombe's morphology and the climate of the region are given in Cano et al. (2008) and Cano (2009).

Stands of *Schoenoplectus californicus* cover most of Lacombe's surface throughout the year, thus providing a relatively stable substrate for epiphyton. In preliminary studies we established that conditions at the centre and periphery of the stands were different (Cano, 2009). Those sites having a relatively central position were characterized by higher densities of bulrush stems than the more peripheral ones, and these latter sites were more exposed to wind, water turbulence and light penetrate depth (Cano, 2009).

During the present study period, Lacombe was influenced by three major rainfalls occurring in August 2001, October 2001, and March 2002 (Cano et al., 2008). In October, the lake water turned from turbid to clear (Secchi disc from 0.30 m to 1.20 m), and extensive stands of submerged macrophytes developed (Casco et al., 2009). Immediate increases in the water level (mean depth: 2.00 m with a maximum of 2.15 m in the turbid period and 2.33 m with a maximum of 2.54 m in the clear water period) and reduced conductivity were recorded as a result of the input of rainwater (Casco et al., 2009). Then, during the year, three periods or phases could be differentiated: a turbid-water period, from July through September, plus a clear-water phase from December through June. The transition occurred from October through November (Cano et al., 2008), when total-phosphorus concentrations reached maximum levels through inputs from runoff (452–664 $\mu\text{g L}^{-1}$), while phytoplankton chlorophyll *a* was low (1.3 $\mu\text{g L}^{-1}$).

2.2. Sampling methods

The sampling was carried out at two previously described sites (Cano et al., 2008), Station 1, placed in the central zone of the bulrush stands at 625 m from Station 2, which is located within the periphery at 250 m from the shore. Sample collection was performed every four weeks, from July 2001 through June 2002.

In order to make comparisons among the various epiphyton-vertical profiles, the chemical and physical characteristics of the water were recorded over a three-level depth interval—from level L1 at the surface (depth 5 cm), through L2 (depth 60 cm), to level L3 (depth 100 cm)—at each sampling station. The methods for measurement of the chemical and physical variables of the water in the field and in the laboratory are detailed in Cano et al. (2008) and Casco et al. (2009).

On the basis of the Secchi-disc readings we calculated for each sampling site and date the incident-light-extinction coefficients ($K_d = 1.7/Z_{SD}$) after Idso and Gilbert (1974).

With this coefficient and incident surface PAR irradiance data (NASA, 2013), we estimated light and the percentage of incident light for each level of the epiphyton vertical profile according to Wetzel (1983):

$$\text{Incident light} = e^{-(E)(\text{depth})}$$

2.3. Substrate selection, epiphyton sampling and processing

S. californicus is a highly common plant in pampean lakes. Tur and Rossi (1976) described the bulrush growth pattern as a rhizome having structural units consisting of four aerial stems on each of its ramifications. Each of these stems, plus the inflorescence and the fructifications at the top and the leaves at the base, constitute a shoot. Once the last of these four stems begins to grow, the first one becomes senescent; and growth in a lateral shoot becomes activated, with the latter then giving rise to another unit of four aerial stems. Those authors estimated that the aerial stems elongate with some 3 cm per day during the period of growth. These features allowed us to estimate, in an indirect way, the age of a bulrush

stem and thus the approximate age of the periphyton. In order to standardize the age of the substrate and consequently the age of the epiphytic community, we collected only green stems longer than 180 cm. These were taken without any signs of senescence, herbivory, or disease (e.g., fungal attack); and without reproductive structures. On the basis of these premises, we estimated that the epiphyton sampled had been developing for between 60 and 120 days.

At both sampling stations, we divided four bulrush stems into 7-cm sections, starting just below the first cm underwater. We designated each section on the basis of its position relative to the water surface, indicating S1 as the shallowest section and S16 as the deepest. Of the 16 sections, only 7 were included: S1, S2, S4, S7, S10, S13, and S16; each of these representing a corresponding depth range to a maximum depth of ca. 110 cm. Through this approach, we obtained four fixed 7-level discontinuous-section profiles per sampling site per occasion. Each section was placed in a flask with tap water, transported to the laboratory, and stored at 5–8 °C in the dark until analysis.

The stems were first removed from the water and then sectioned without disturbing the surface colonized by epiphytes. In this way, we obtained only the firmly attached epiphyton and deliberately excluded the plankton and other organisms less firmly adhered to the substrate. The vertical epiphyton sections S1–S16 corresponded to the water sample levels L1 to the L3. Thus, the physicochemical data of L1 corresponded to the depths of S1 and S2 sections, L2 to the depths of the S7 and S10 sections, and L3 to the depths of S13 and S16 sections.

In the laboratory, we used two of the four section profiles from each sampling station for epiphyte–photosynthetic-pigment determination following APHA (1995). We scraped each section of that pair of profiles into a Petri dish with a fine cover slip and calculated the chlorophyll-*a* concentration after extraction with 90% (v/v) aqueous acetone and spectrophotometric absorbance measurement, according to Lorenzen (1967), but including the modifications of Varela (1981).

The other two section profiles from each station were used for epiphyte quantification and biovolume determination. Two different methods had to be employed for single-layered and multilayered physiognomies of the communities. The details of the quantification in both circumstances are provided in Cano (2009) and Cano et al. (2012).

Measurements of the specimen sizes to be used for the estimation of biovolume were taken in the process of quantification. With large size variations in a species, size classification was employed (Rott, 1981). The biovolume of the total algae per unit area ($\mu\text{m}^3 \text{cm}^{-2}$) of each sample was divided by the corresponding total density (ind. cm^{-2}) to obtain the average biovolume per individual ($\mu\text{m}^3 \text{ind.}^{-1}$) in a given sample. In all instances, the area of each section of stem was determined by the truncated-cone formula.

2.4. Taxonomy

Algal identification was assessed with Bourrelly (1972, 1981, 1985), Ettl (1978), Kómarek and Anagnostidis (1989, 1998, 2005), Kómarek and Fott (1983), Kramer and Lange-Bertalot (1986, 1988, 1991), Printz (1964) and Tell and Conforti (1986).

2.5. Statistical analysis of the data

Analysis of similarities (ANOSIM) was done to detect: (1) differences between depth levels with respect to environmental variables, (2) differences between samples at the two sites with respect to epiphyton-descriptive variables, (3) differences between the samples associated with the turbid- and the clear-water periods

through the use of the same community variables and (4) differences in species density and biovolume with respect to depth and between sites. In the first three analyses, the data were log-transformed to comply with the assumption of normal distribution and the similarity matrices were constructed with normalized Euclidian distances. The ANOSIM-test results with respect the environmental variables were then supported by an analysis of multidimensional-scaling (MDS) ordination. In test (4), the data were fourth-root transformed and then standardized. A similarity matrix was constructed with the Bray–Curtis similarity index. In all ANOSIM analyses, *R* greater than 0.75 and *p* < 10% pointed out strongly significant differences (Clarke and Gorley, 2001). The ANOSIM and MDS analyses were performed with PRIMER 5.2.9 (2001).

Covariance analyses were performed to test the relation between the community-descriptive variables (total density, total biovolume, Shannon–Wiener diversity index and chlorophyll *a* concentration) and the environmental variables (named in Table 1). Pearson correlation analyses were used to confirm the relationships between the same community-descriptive variables and the PAR incident light. Data were log- or square-root transformed. Non-parametric Spearman correlations were employed to test the relationships between species biovolume and the PAR incident light.

3. Results

3.1. Environmental variables

Differences between the sites and along the vertical profiles at each of the sites for the three levels were not evident for most of the physicochemical variables of the water (Table 1).

An ANOSIM analysis addressing differences between sites—performed with the following environmental variables: temperature, conductivity, turbidity as NTU, total suspended solids, dissolved oxygen, total phosphorus, nitrate-plus-nitrite concentrations, and phytoplanktonic chlorophyll *a*—was not significant (*R* global: 0; *p* = 99%), as was also true for the ANOSIM analysis and the associated pairwise tests accounting for depth-level differences (*R* global: 0; *p* = 100%; *R* statistics for pairwise tests 0.03–0.04 at significance levels between 96 and 99%). In contrast, the ANOSIM analyses that examined the differences between turbid-water, transitional, and clear-water periods were highly significant (*R* global: 0.83; *p* = 0.001%). The pairwise tests comparably the turbid- and the clear-water periods were all significant (*R* global: 0.95; *p* = 0.001%), with smaller differences being indicated between the turbid-water and transitional periods (*R* global: 0.6; *p* = 0.001%).

An MDS analysis supported the ANOSIM results, pointing to negligible differences in the vertical and horizontal spatial dimensions but marked differences among the turbid-, transitional, and clear-water periods (stress, 0.11; Fig. 1): the samples became distributed principally as a function of the sampling date rather than their site of origin or section level.

Since no differences in the physicochemical water variables were observed along the vertical profile, light intensity was the only parameter remaining that varied with depth. The average percentage of incident light declined from 71 to 79% at the surface level L1 to 5–6% at the deepest level L3 and differences between regimes were also detected (Table 1). During the turbid period, the PAR incident light was scarcely higher at the different depth levels at St. 2 (Table 2). After the start of the submerged macrophytes development in October (transitional period) the water became clearer and the more intense spring PAR radiation could penetrate deeply in the water column. This effect was even more evident during the clear water period (Table 2).

Table 1

Average and standard deviation (in brackets) of physical and chemical parameters in both sampling stations of Lacombe Lake taking in account the annual estimation for each level of the vertical profile and the estimations of the three regimes recorded.

	Depth levels			Regime		
	L1 (n = 12)	L2 (n = 12)	L3 (n = 12)	Turbid (n = 15)	Transitional (n = 12)	Clear (n = 35)
Temperature (°C)						
St. 1	18.2 (5.6)	18.0 (5.6)	17.7 (5.5)	11.7 (1.4)	22.4 (1.0)	19.4 (5.0)
St. 2	17.8 (5.9)	17.6 (5.6)	17.5 (5.5)	11.4 (1.3)	22.1 (0.9)	19.0 (5.1)
Turbidity (NTU)						
St. 1	44 (36)	42 (36)	39 (34)	98.4 (14.3)	27.8 (4.3)	21.0 (5.8)
St. 2	43 (37)	44 (40)	42 (41)	107.2 (9.1)	27.2 (4.2)	20.4 (7.8)
pH						
St. 1	9.9 (0.5)	9.9 (0.5)	9.8 (0.4)	10 (0.1)	9.8 (0.3)	9.9 (0.6)
St. 2	9.8 (0.5)	9.8 (0.4)	9.8 (0.4)	9.9 (0.0)	9.8 (0.3)	9.7 (0.5)
Conductivity ($\mu\text{S cm}^{-1}$)						
St. 1	2373 (836)	2376 (838)	2379 (841)	3540 (479)	2353 (87.8)	1884 (449)
St. 2	2350 (836)	2351 (838)	2357 (838)	3516 (469)	2291 (21.4)	1871 (465)
Dissolved oxygen (mg L^{-1})						
St. 1	9.3 (1.4)	9.0 (1.4)	8.7 (1.3)	8.9 (0.9)	9.6 (0.2)	8.9 (1.7)
St. 2	9.8 (1.7)	9.1 (1.2)	8.6 (1.5)	8.6 (1.0)	10.2 (0.6)	9.1 (1.8)
Suspended solids (mg L^{-1})						
St. 1	22.3 (22.2)	21.7 (18.7)	25.9 (27.0)	55.3 (24.1)	13.1 (3.0)	12.5 (4.7)
St. 2	26.8 (34.5)	31.5 (38.8)	28.7 (34.5)	79.7 (37.7)	14.6 (4.7)	11.4 (5.3)
Particulate organic matter (mg L^{-1})						
St. 1	19.9 (20.0)	19.8 (17.8)	23.0 (25.9)	50.7 (22.7)	9.8 (2.6)	11.3 (4.9)
St. 2	20.5 (24.4)	24.5 (27.1)	23.9 (27.2)	60.8 (25.2)	10.0 (3.2)	10.4 (5.3)
Dissolved polyphenols (mg L^{-1})						
St. 1	4.3 (2.0)	4.6 (2.2)	4.4 (2.1)	6.9 (3.5)	4.6 (1.4)	3.7 (0.5)
St. 2	4.7 (2.1)	4.8 (2.0)	4.5 (2.0)	6.2 (3.3)	5.4 (1.0)	3.9 (0.6)
Total phosphorus ($\mu\text{g L}^{-1}$)						
St. 1	250 (151)	276 (133)	266 (125)	308 (46)	495 (118)	179 (47)
St. 2	258 (113)	270 (130)	267 (140)	319 (50)	483 (70)	179 (42)
Soluble reactive phosphorus ($\mu\text{g L}^{-1}$)						
St. 1	28 (29)	30 (32)	29 (30)	18 (7)	72 (54)	21 (10)
St. 2	27 (30)	29 (37)	31 (39)	15 (5)	79 (65)	20 (6)
Nitrates + nitrites ($\mu\text{g N-NO}_3 \text{ L}^{-1}$)						
St. 1	196 (84)	180 (81)	193 (101)	162 (108)	224 (128)	191 (61)
St. 2	183 (102)	168 (77)	162 (57)	154 (83)	228 (137)	162 (48)
Phytoplanktonic chlorophyll <i>a</i> (mg m^{-3})						
St. 1	31.7 (20.7)	28.4 (15.5)	29.0 (19.1)	49 (11)	30 (24)	21 (12)
St. 2	33.8 (27.9)	35.4 (24.8)	30.8 (23.7)	65 (13)	38 (31)	19 (10)
Percentage of incident light (%)						
St. 1	79 (12)	26 (13)	5 (4)	20 (25)	28 (30)	40 (30)
St. 2	71 (10)	28 (13)	6 (5)	22 (27)	27 (29)	41 (30)

3.2. Epiphyton structure and dynamics

Most of the epiphytic-community variables manifested two general tendencies (Figs. 2 and 3). First, during the turbid period the vertical profiles exhibited similar values throughout the range

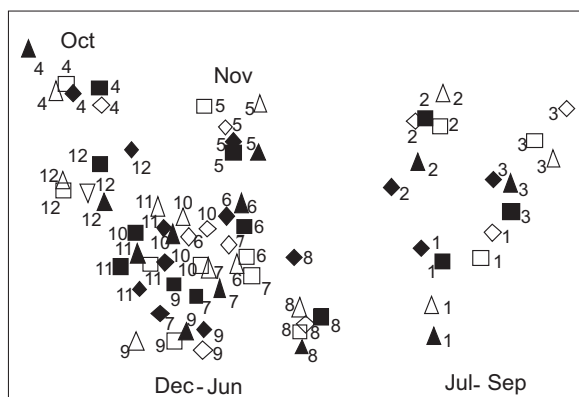


Fig. 1. MDS plot. Ordination of samples according to site, depth level, and sampling occasion. Numbers, sampling occasion: (1) July; (2) August; (3) September; (4) October; (5) November; (6) December; (7) January; (8) February; (9) March; (10) April; (11) May; (12) June. Geometric figures, depth levels: triangle, L1 (5-cm depth); diamond, L2 (60-cm depth); square, L3 (100-cm depth). Sampling stations: black, St. 1; white, St. 2.

of depths, while during the clear-water period the profiles became characterized by marked gradients with increasing depth, with more pronounced differences occurring between sections S7 and S10. The profiles of the transitional period corresponded to those of either the one or the other phase. Second, pronounced variations in the vertical profiles occurred over time beginning in October 2001 with lesser fluctuations ensuing from March 2002 onwards—in both instances, the changes were related to rainfalls taking place during those two months. Species richness, the chlorophyll-*a* concentration (Fig. 2), total biovolume, and the Shannon-Wiener diversity index (H' ; Fig. 3) likewise followed both of these patterns.

Table 2

Average and standard deviation (in brackets) of the photosynthetic active radiation (PAR) ($\mu\text{E m}^{-2} \text{d}^{-1}$) in both sampling stations of Lacombe Lake taking in account the annual estimation for each level of the vertical profile and the estimations of the three regimes recorded in the shallow lake.

	Mean (n = 12)	Regime		
		Turbid (n = 3)	Transitional (n = 2)	Clear (n = 7)
St. 1				
L1	12,650 (7949)	5012 (1861)	15,622	15,075 (8358)
L2	4571 (3602)	565 (91)	4111	6419 (3290)
L3	898 (861)	13 (16)	388	1423 (837)
St. 2				
L1	12,809 (7873)	5520 (2191)	15,324	15,214 (8416)
L2	4747 (3679)	853 (236)	3791	6689 (3420)
L3	983 (967)	33 (16)	322	1578 (832)

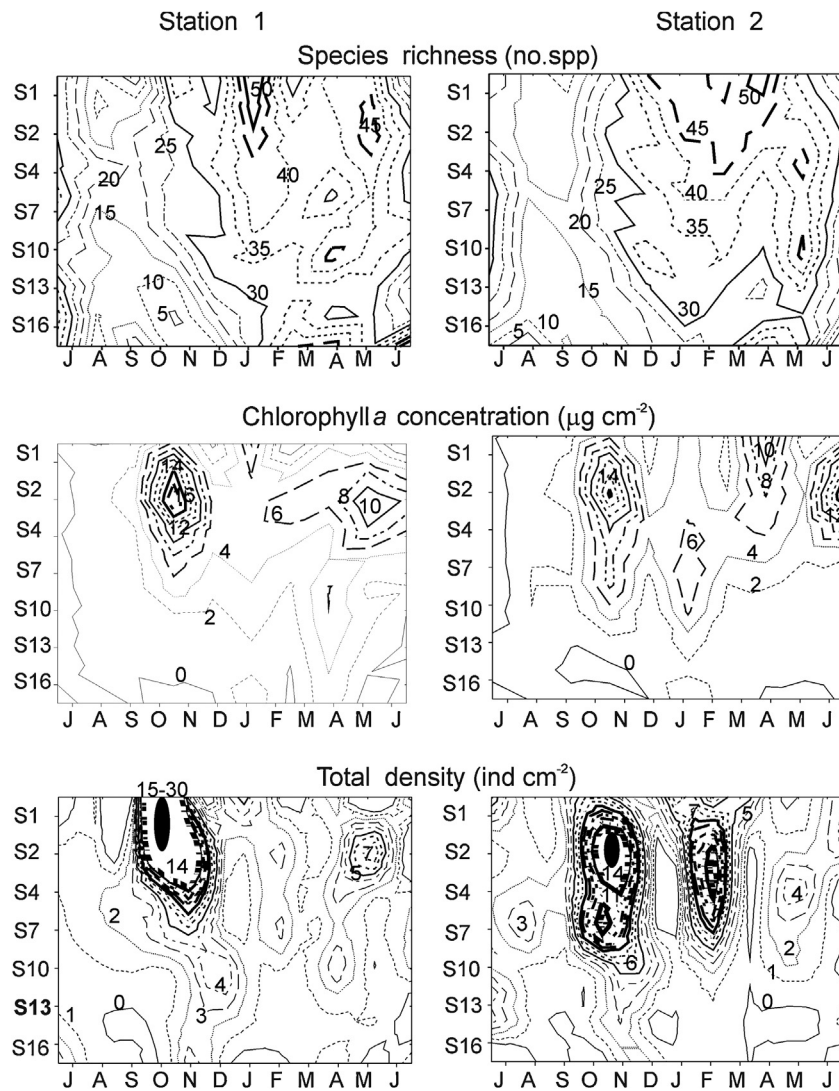


Fig. 2. Vertical profiles of the epiphyton species richness, chlorophyll-*a* concentration, and total density (individual values multiplied by 10^{-5}).

In contrast, the total algal density and the average biovolume per individual exhibited a different pattern.

The total algal density passed through another peak in February—one especially evident at St. 2, but not related to a pigment increase (Fig. 2). The vertical profiles of the total density were markedly variable over the study period, indicating on various occasions an abrupt diminution between the S7 and the S10 sections (Fig. 2). The profiles of average biovolume per individual were likewise homogeneous during the turbid period; but from December on the values increased abruptly over all the sections, indicating a structural difference among the profiles (Fig. 3). From January to March the higher values were usually associated with sections S7 or S10, but from April on the maxima became observed in the more surface-oriented sections 1 and 2 (Fig. 3).

The epiphyton communities present during the turbid- and the clear-water periods at both sampling locations differed sharply in species composition. Two vertical sections (S2, S13), were decided upon as being representative of the upper and the lower extremes, respectively, of the resulting vertical gradient since the data obtained from sections S1 and S16 had proved more variable.

Upon consideration of the species composition at level S2 of both sites, a complex of two *Gomphonema* species (the *G. parvulum*–*G. gracile* complex *sensu* Schoeman et al., 1984), with typical unicellular stalked morphology, was the most highly contributing taxon

with respect to the parameters of total density and total biovolume during the first four months (Figs. 4 and 5; upper panels). Other diatoms—such as *Halumphora veneta* (Kützing) Levkov and *Navicula veneta* Kützing, both adnate forms, as well as the filamentous chlorophyte *Oedogonium* aff. *sphaerandrum* Wittrock and Lundell, it affixed by means of a basal cell—also represented a large percentage of total density and total biovolume (Figs. 4 and 5). During October the communities were dominated by the *Gomphonema* complex, though certain compositional changes were detected in this month and became more marked in November—one of those being the appearance of large *Spirogyra* spp. adnate filaments that would structure the epiphyton communities up to the end of the sampling period. Diatoms continued to be prevalent, but in November other species, such as the adnate *Nitzschia amphibia* Grunow, started to dominate in terms of total density (Fig. 4). *Spirogyra* spp., however, ended up contributing almost the entire biovolume during the clear-water period from December onwards (Fig. 4).

Although in the deeper section S13 the principal features were similar to those observed in section S2—featuring, in both sections and at both sites, the replacement of the *Gomphonema* complex by *N. amphibia* along with a domination of *Spirogyra* spp. from December on—the composition varied in a different way and generally included greater contributions of cyanobacteria to the total density (Fig. 4; lower panels) and of diatoms

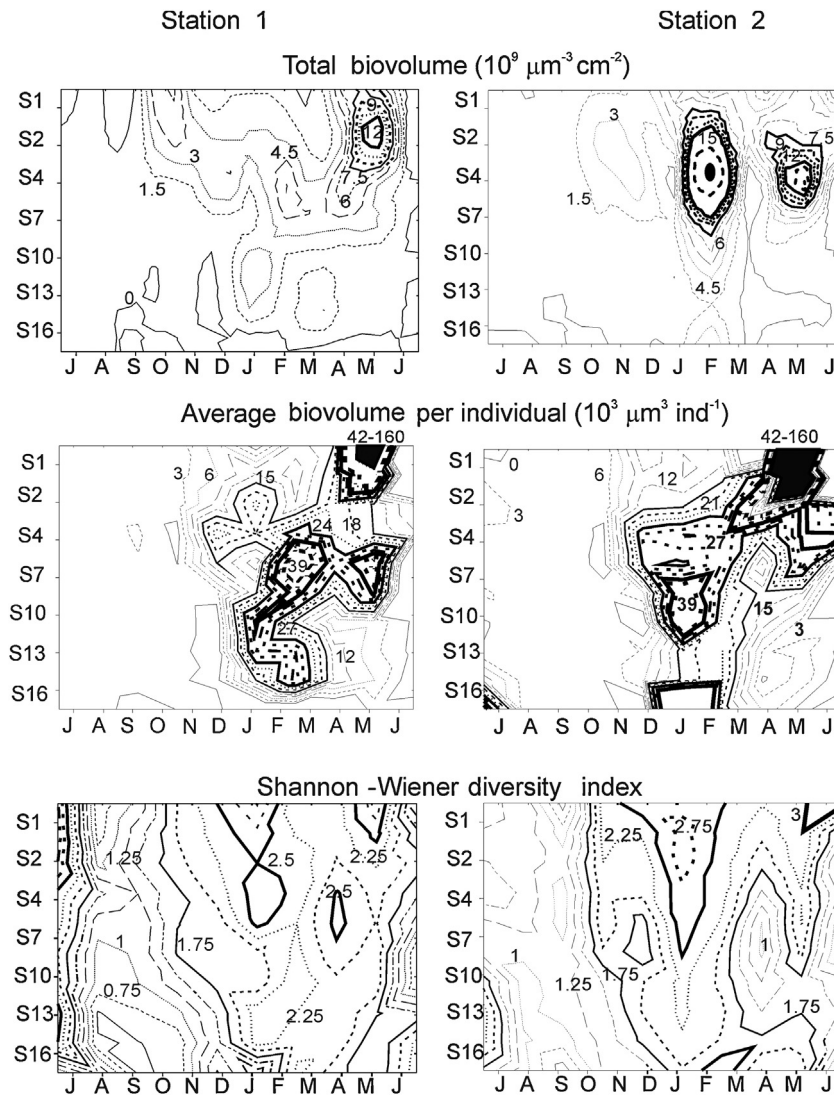


Fig. 3. Vertical profiles of the epiphyton total biovolume, average biovolume per individual, and Shannon–Wiener diversity index.

to the total biovolume (Fig. 5; lower panels). A codomination of the *Gomphonema* complex and *N. veneta*, however, was observed in July at both sites; while in August a total domination of the *Gomphonema* complex occurred. Further changes were recorded as of September, when the population of the small filamentous cyanobacterium *Heteroleibleinia pusilla* (Hansgirg ex Hansgirg) Anagnostidis and Komárek—it attached to the substrate with its mucilaginous sheath—started to increase. This species was abundant until November at St. 2 and up to December at St. 1 (Fig. 4). A domination of the *Gomphonema* complex was also noted with respect to total biovolume for the first three months (Fig. 5). During the clear-water period, although *N. amphibia* dominated, greater density contributions were recorded of, for example, *H. veneta* and *Heteroleibleinia–Leibleinia epiphytica sensu Kómarek and Anagnostidis* (2005), among others (Fig. 4). In terms of biovolume, *Spirogyra* spp. still dominated at this greater depth, but higher percentages of *N. amphibia*, *H. veneta*, and *Oedogonium inversum* Wittrock were observed compared to the corresponding values for section S2 (Fig. 5).

The variation in species composition along the vertical profile was gradual on all sampling dates, with no sharp compositional changes being detected among the different sections—i.e., the same species were present throughout the entire depth profile.

This constancy is partly reflected by Figs. 4 and 5, but also by the two ANOSIM analyses performed with the species-density and biovolume data for sections S2 and S13. Although the differences between these two sections were significant with respect to density (ANOSIM Test 4, significance level: 2.4%), the global *R* statistic was extremely low (*R*: 0.08), indicating that these differences were not pronounced. Furthermore, the differences between S2 and S13 with respect to species-biovolume data were not significant (ANOSIM Test 5; *R* statistic: 0.03, significance level: 13.8%).

As result of covariance analyses PAR values and temperature were the best correlated variables in the four cases detailed at Statistical analyses section. Since temperature showed negligible differences within the L1 through the L3 levels of the vertical profiles (Table 1), the epiphyton variables were tested for linear correlation with the PAR values estimated for each depth and date. In the first four comparisons (Set A) for each epiphyton variable, the data from all sections were included. Then sets of comparisons of each of the four parameters were performed successively, but each set with the data taken from a specific part of the vertical profile—i.e., Set B (data from S2 to S16), Set C (data from S4 to S16), Set D (data from S7 to S16), Set E (data from S10 to S16), and Set F (data from S1 to S7). The correlation coefficients were finally compared in a graph (Fig. 6) that revealed a high, statistically significant *r* ($p < 0.05$) for

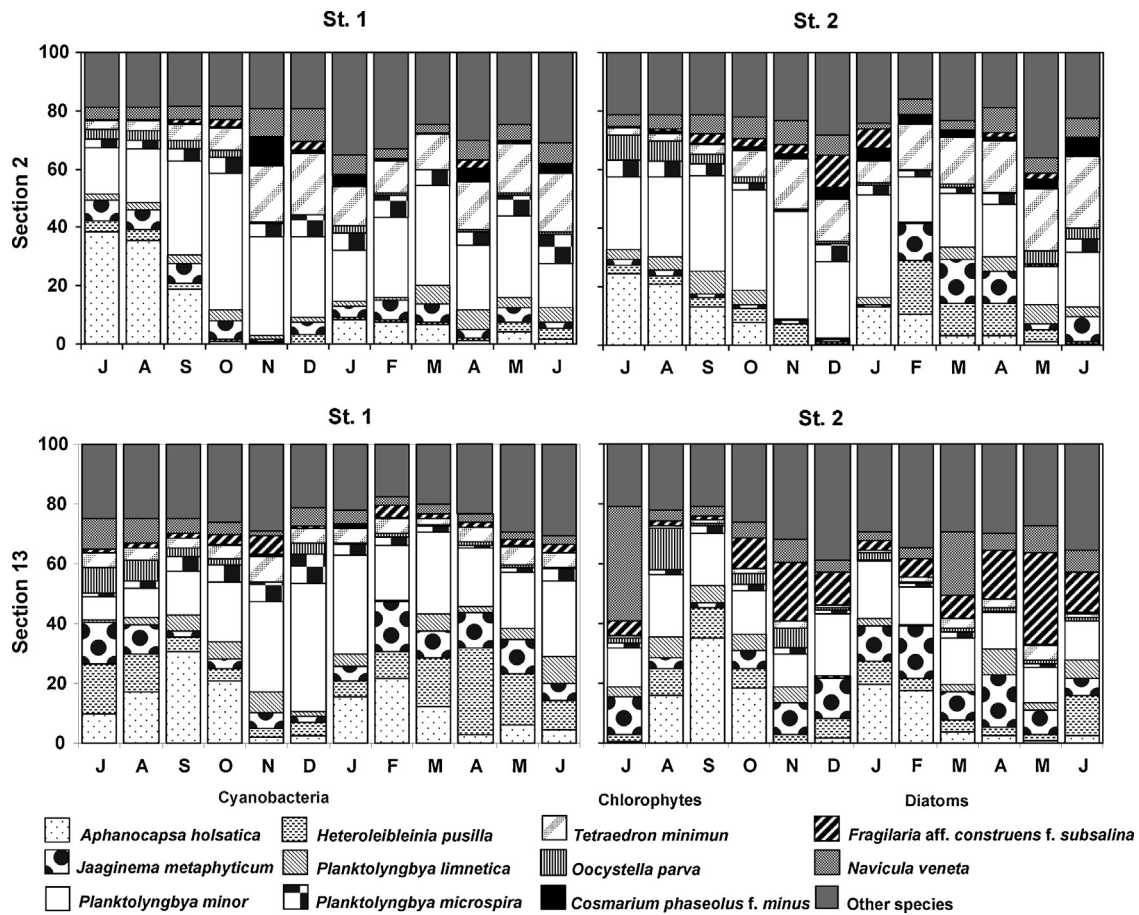


Fig. 4. Percent contribution of the most abundant species to total algal density in sections S2 and S13 at both stations for each sampling date. The species depicted represented 20% or more of the total density in any of the samples collected (for all dates or sections and at both stations).

most of the data sets. Except for one correlation coefficient (the density from Set F), all the r values were significant ($p < 0.05$). The coefficients of sets B and C were the highest, indicating that the elimination of the S1, and even the S2, data resulted in a better correlation with the PAR values. The effect of including S1 can also be seen when comparing sets E and F, whose data represent the lower and the upper portions of the profile. The correlation coefficients of Set E were higher than those of Set F and were all significant.

The four species that contributed most to the total biovolume in each taxonomical group (diatoms, chlorophytes, and cyanobacteria) were selected to test their relationship with the PAR incident light through Spearman-rank nonparametric-correlation analyses (Table 3). In accordance with the results obtained in the Pearson-correlation analyses, the data from the S1 section were not included. Almost all the correlation coefficients were statistically significant and were higher for the species that were predominant during the clear-water phase (e.g. *Spirogyra* spp., *Cosmarium sociale*, *O. inversum*, *N. amphibia*, *Heteroleibleinia mesotricha* and *Heteroleibleinia-Leibleinia epiphytica*). Lower values or non significant ones were obtained for species that were predominant during the turbid-water state or else that were present during the entire study period (e.g. *H. veneta*, *N. veneta*, *Jaaginema metaphyticum*, *Gomphonema* complex, *Leibleinia incospicua*).

4. Discussion

The variations in the biomass and specific composition of the epiphyton in the vertical dimension were similar at both sites. Cano et al. (2012) had observed this same similarity between the sites in

the average values for the epiphyton variables and had attributed this lack of difference to the low bulrush-stem densities recorded throughout the study period. This similarity between the two sites contrasts with observations made by other authors between the central and peripheral portions of stands of emergent macrophytes (Roos et al., 1981; Kairesalo, 1983; Cattaneo et al., 1998). Our preliminary data gathered in April and June 2001 (Cano, 2009), as well as those from later observations at La Rosita Lake (May 2005–April 2006), along with the data from a Czechoslovakian fishpond (Komárková, 1973), would suggest that macrophyte densities in excess of between 100 and 157 stems m^{-2} would be necessary to be able to observe a difference in epiphyton development.

The variations in epiphyton variables over time were coincident with the changes in the lake after the October and March rains. The perturbations in the spring led to a change from the turbid to the clear-water conditions in this ecosystem. Lower values for all epiphyton variables were accordingly recorded during the turbid period with higher figures occurring during the clear-water phase. This correspondence between epiphyton biomass and diversity and the water-transparency–equilibrium states had also been observed in relation to the chlorophyll-*a* concentrations of the epiphyton growing on artificial substrates by Sanchez et al. (2010) in both a clear-water (El Triunfo) and a turbid-water (El Burro) shallow lake, the two located in the same geographical region as Lacombe. In the present study, the species composition as well as the physiognomies of the communities likewise changed radically throughout the vertical profile in parallel to the alterations in the state of the ecosystem. The variations caused by the March rains were less pronounced than those produced by the October

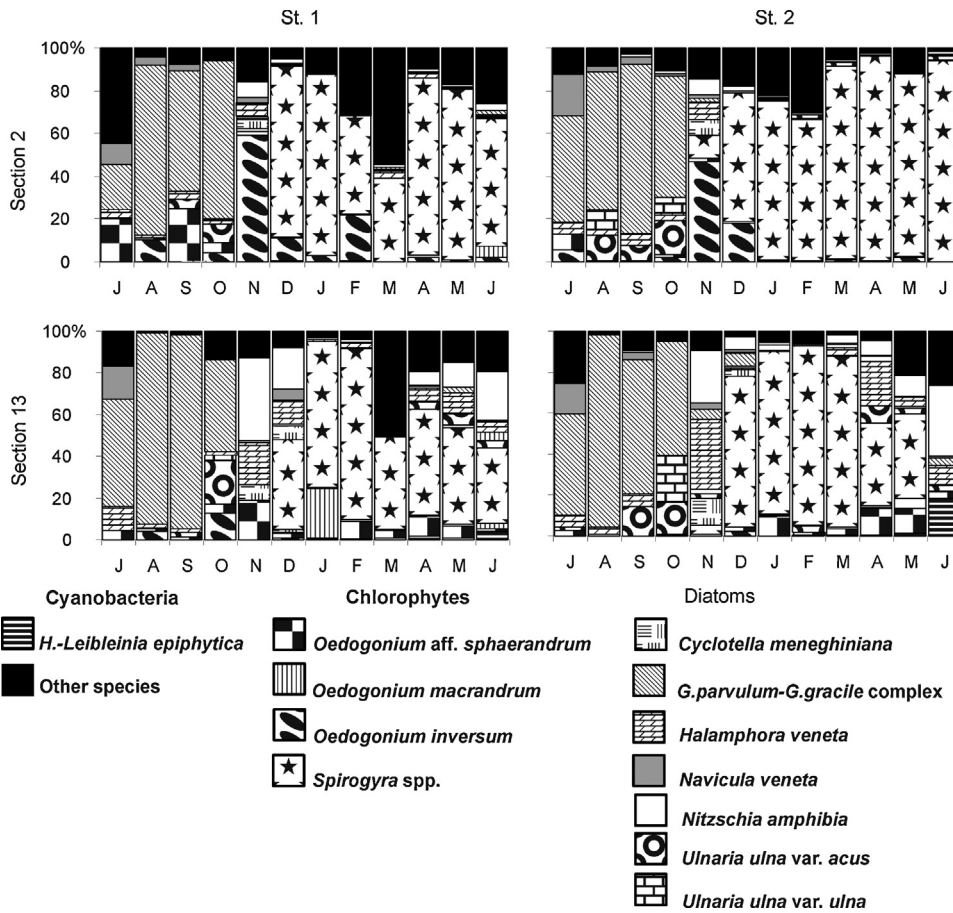


Fig. 5. Percentage representation of the species with the greatest contribution to the total biovolume in sections S2 and S13 at both stations. The species depicted represented 20% or more of the total biovolume of any of the samples collected (for all dates or sections and at both stations).

rainfall, here involving a preferential increase in the epiphyton biomass within the S2–S4 sections.

A general pattern exhibited by almost all the vertical profiles was a diminution in values of the epiphyton-descriptive variables with depth. Nonetheless, this decrease in those parameters was different whether the sample was taken during the turbid- or the clear-water period. The vertical profiles of the turbid period gave values that diminished gradually towards the deeper sections. In contrast, most of the vertical profiles from the clear-water period indicated pronounced differences between the S7 and the S10 sections; which samples, accordingly, corresponded to depths between 42 and 70 cm. Likewise, Galanti and Romo (1997) had

reported that a vertical zonation of the epiphyton on *Trapa natans* showed sharp differences below the 50-cm depth. These and other authors (e.g., Sultana et al., 2004) have related the epiphyton vertical variations to a diminution in light availability caused by vegetation. At Lacombe Lake the lower limit for foliage development of the two dominating species of submerged macrophytes (*Stuckenia striata* and *M. quitense*) coincided with this same depth range (Cano, 2009). This observation suggests that the conditions that affect the foliage distribution of these plants may also be influencing the vertical distribution of the epiphytes.

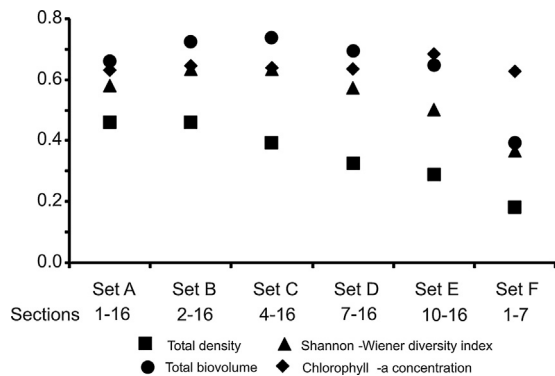


Fig. 6. Pearson-correlation coefficients, r , for epiphyton variables and the PAR incident light, taking in account different groups of sections along the vertical profile. All coefficients were significant.

Table 3

Spearman correlation analyses of selected species biovolume and PAR incident light. Significant correlation coefficients marked with an asterisk ($p < 0.05$).

Species	Taxonomic group	r_s
<i>Spirogyra</i> spp.	Chlorophyte	0.68*
<i>Cosmarium sociale</i>	Chlorophyte	0.59*
<i>Oedogonium inversum</i>	Chlorophyte	0.62*
<i>Oedogonium aff. sphaerandrum</i>	Chlorophyte	0.25*
<i>Nitzschia amphibia</i>	Diatom	0.64*
<i>Halamphora veneta</i>	Diatom	0.43*
<i>Gomphonema parvulum</i> – <i>G. gracile</i> complex	Diatom	–0.03
<i>Navicula veneta</i>	Diatom	0.25*
<i>Jaaginema metaphyticum</i>	Cyanobacteria	0.18*
<i>Leibleinia inconspicua</i>	Cyanobacteria	0.041
<i>Heteroleibleinia pusilla</i>	Cyanobacteria	–0.08
<i>Heteroleibleinia mesotricha</i>	Cyanobacteria	0.54*
<i>Heteroleibleinia</i> – <i>Leibleinia epiphytica</i>	Cyanobacteria	0.43*

Jones et al. (1983) pointed out that the vertical zonation of epiphyton may reflect the adaptation of the species to light. The light penetration into the water column will vary with the density of the emergent and submerged macrophytes (Kiss et al., 2003) or with the amount of suspended matter (Scheffer, 1998). With respect to the former, emergent and submerged plants may not have had significant influences on the underwater light in Lacombe since their densities were never high (Cano et al., 2012). As regards the latter, Pearson-correlation analyses demonstrated the close relationship between the PAR in each section and the epiphyton-related variables. Pouličková et al. (2006) found a similar relationship between the percentage of incident light reaching different depths and the degree of epiphyton coverage. This relationship proved to be linear, or at least closely so, throughout most of the vertical profile. Nonetheless, the higher correlation coefficients obtained after discarding the upper sections indicated that at these more illuminated levels the epiphyton biomass or diversity was lower than expected. Turbulence and photoinhibition have been cited as major influences affecting periphytic communities at levels nearer the surface of the water (Kairesalo, 1983; Cattaneo, 1987; Hoagland and Peterson, 1990; Lalonde and Downing, 1991; Hill, 1996; Buczkó and Ács, 1997; Galanti and Romo, 1997; Albay and Akcaalan, 2003). Photoinhibition did not appear to be an influencing condition in Lacombe Lake, however, because neither did any specific compositional change occur, nor were physically damaged individuals found in the samples from the uppermost water layers.

In Lacombe Lake, during the turbid period, the epiphyton profiles should have shown their maximum development at the more surface-oriented sections, as the phytoplankton biomass had diminished the extent of light penetration in the water column. Under the turbid conditions, however, the vertical profiles of the different epiphyton variables nevertheless presented generally lower values for biomass and species richness in the upper sections than in the sections at greater depths. Moreover, the maxima in the chlorophyll-*a* concentrations for each sampling site and date had been recorded at sections S4 or S7. A possible explanation, therefore, is that under the turbid conditions light diminished gradually; but as a consequence of the absence of stands of submerged macrophytes, the water column became more unstable, especially near the surface. This increased degree of mixing would explain why the epiphyton displayed a higher biomass in the deeper but less well illuminated sections than in the upper ones. In fact, Lalonde and Downing (1991) also pointed out that turbulence may hamper epiphyton growth at levels closer to the water surface. Furthermore, according to those authors, during the clear-water period, the epiphyton profiles should exhibit a maximum degree of development at deeper levels since the light can penetrate more. This difference, though, was not observed in Lacombe Lake since, for example, the maxima for chlorophyll-*a* concentrations were usually recorded in section S2. Moreover, by this time submerged macrophyte stands were present and had reached a coverage of between 13 and 50% of the water surface (those values at St. 2 and St. 1, respectively; Cano et al., 2012). The development of those macrophyte stands was associated with not only the increase in transparency but also a stability of the water column at levels just below the surface. Therefore, during this clear-water period the negative effect of the water movement probably reached section S1 most of the time, but not the deeper sections from S2 on down. We have not found other environmental variables that produced differences in the vertical profile. The positive effect of the temperature during late spring–early summer that coincided with the transitional period and beginning of the clear period combined with the favourable effect of the improvement in light availability along the vertical profile. Previously, Cano et al. (2012) had observed that the total phosphorus concentrations were closely related to the increment in the average biomass of the epiphyton. Since we observed no

vertical differences in the phosphorus concentrations during the whole sampling period, we discarded that variable as a significant driver of variations in epiphyton vertical distribution. We conclude that the epiphytic vertical profiles are similar at both the peripheral and central parts of the bulrush stands because the bulrush density was not critical for the epiphytic algae light requirements. Those vertical profiles were different depending on whether the communities developed under a turbid- or a clear-water regime of the lake. The vertical distributions were characterized either by similar descriptive-parameter values over the whole profile during the turbid-water state or by a marked difference between the 45–through 65-cm depth under conditions of clear water. Finally, we summarized that the light-availability conditions followed by the movement of the water were the principal drivers influencing variations in the vertical distribution of epiphyton biomass. The species with high contributions to the overall biovolume were related to the incident light, and particularly those community members that were predominant in the clear-water period. These relationships are critical for gaining an understanding of the living strategies of the epiphytic species, those being responsive to the different regimes occurring at the lake along the length of the submerged stems of *Schoenoplectus*.

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