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Research Paper

Phytoplankton and Epipelon Responses to Clear and Turbid Phases in a Seepage Lake (Buenos Aires, Argentina)

key words: shallow lake, alternative states, algae, total phosphorus, chlorophyll *a*

Abstract

Annual changes in the algal density and concentrations of chlorophyll *a*, total phosphorus, and organic matter were analyzed in water and sediments at four sites characterized by the presence or absence of submerged and emergent macrophytes, during turbid- and clear-water conditions to determine the contribution of the algal components of the plankton and the epipelon and to identify the most typical species in each community. Three states were recognized: one turbid and two clear, with different submerged macrophyte cover. The peaks of phytoplankton and epipelon occurred in the turbid phase, whereas the highest proportion of true epipelic algae in sediments was reached in the second clear phase. The Oscillatoriaceae dominated during the turbid phase in the water and throughout the entire year within the sediments.

1. Introduction

In shallow lakes where alternative equilibrium states can occur, the importance of the relationships between epipelic and pelagic algae has recently been highlighted (Vadeboncoeur *et al.*, 2002). In such lakes the structure and biomass of epipelon varies in relation to spatial heterogeneity created by the presence or absence of emergent and submerged macrophytes. According to Cyr (1998), the biomass of benthic algae varies among sites and according to depth in small oligotrophic and mesotrophic lakes.

The benthic assemblages are made up of autochthonous species plus others incorporated from the plankton and periphyton. Thus, changes in environmental conditions can promote an increase in the density of those algae that can develop in both the sediment and the water column, giving them a competitive advantage over the algae that can live in only one of those lake habitats. The seasonal distribution of algal productivity observed by Hansson (1996) in North American lakes, and by Barko *et al.* (1977) and Flöder *et al.* (2006) in small ponds, suggests an exchange of algal organisms between the planktonic and epipelic populations.

The phosphorus in shallow lakes tends to accumulate in the sediments and in the macrophytes (Søndergaard *et al.*, 2003; Rooney and Kalff, 2003). Thus, the nonplanktonic algae

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(epipelic and periphytic) can prevail over the planktonic algae inhabiting the pelagic zone when there is enough light (HWANG *et al.*, 1998), such as during periods of a clear-water phase with submerged macrophytes (FLÖDER *et al.*, 2006). The settling and resuspension of these algae are mechanisms that, in combination with the submerged macrophytes, regulate the total phosphorus (TP) concentrations in the water column. In lakes rich in epipelon, water-column TP remains relatively constant and low throughout the year (LIBORIUSSEN and JEPPESEN, 2003) with the epipelic algae diminishing the release of phosphorus from the sediments (HANSSON, 1988; DOODS, 2003). The sediments colonized by microalgae may reduce the nutrient concentrations in the overlying water column directly by taking them up for growth and indirectly by oxidation of the sediment surface layer, thus immobilizing the nutrients within the sediments (HANSSON, 1988; WETZEL, 2001; DOODS, 2003). Nevertheless, LIBORIUSSEN and JEPPESEN (2003) postulate that the benthic algae of shallow lakes contribute only weakly to the maintenance of clear phases and that this effect is less stable than that associated with submerged macrophytes.

DOKULIL and TEUBNER (2003), as well as ROONEY and KALFF (2003) separate lakes dominated by macrophytes (or lakes with high inorganic turbidity) from those dominated by pelagic algae with a critical total phosphorus:chlorophyll-*a* ratio in the water column. MOSS (1994) previously proposed several classes of clear phases for shallow lakes according to the biomass of submerged macrophytes present. The algae and the macrophyte beds promote a bottom-up control, while the macrophytes also serve to regulate the action of grazers (JEPPESEN *et al.*, 1997; LAURIDSEN *et al.*, 1999). Emergent aquatic macrophytes can furthermore influence the pelagic total phosphorus concentration by reducing the degree of sediment resuspension (HORPPILA and NURMINEN, 2001).

In the Salado River basin, three main categories of shallow lakes are recognized: interconnected lake systems, backwater pond systems, and seepage lakes. Whereas limnological investigations have focused principally on river-connected lakes (CLAPS *et al.*, 2002; GABELLONE *et al.*, 2001; SOLARI *et al.*, 2002a, 2002b, 2003), the seepage lakes of this region have not previously been studied. In these latter environments, the role of external factors in effecting internal biological regulation is very different from that observed in backwaters and flushing lakes.

The objective of this study was therefore to determine the contribution of planktonic and epipelic algal components in this seepage lake, in terms of density and biomass, and to ascertain the relation of their dynamics to alternative states of equilibrium. We also intended to discriminate between typical epipelic species, which develop in sediments, from those which develop in the water column. This paper thus examines the annual changes in algal densities within the water column and in the sediments plus the concentrations of chlorophyll *a*, TP, and organic matter at four sites (with and without submerged and emergent macrophytes) during turbid- and clearwater conditions.

2. Study Area

The shallow Lacombe Lake is located 164 km south of the city of Buenos Aires (35°50′ S–57°53′ W). Its area is approximately 130 ha with a maximum length of 1,750 m and a maximum width of 1,500 m (Fig. 1). The shoreline length is 5.6 km, while the maximum depth during the sampling period was 2.5 m. In this lake the fluctuations in water level over a given year and between years are determined by local rains and the input of groundwater. The mean annual rainfall for this shallow lake is 1,079 mm (period: 1970–2002). During the present sampling period, the rainfall was 1,336 mm in 2001 and 1,375 mm in 2002, which were among the five rainiest within the last 32 years. The predominant winds were from the northeast, south-southwest, and east-southeast, with an average velocity of 11 km h^{-1}.

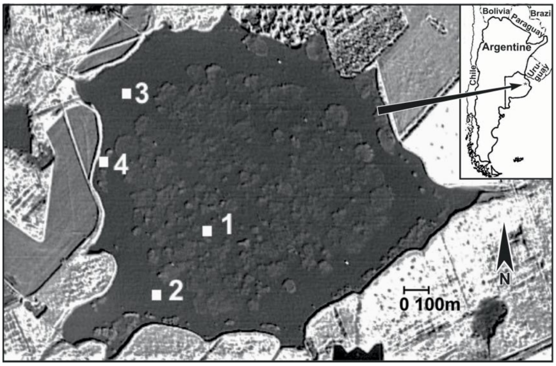

Figure 1. Location of the sampling stations in Lacombe Lake.

The water body is colonized by emergent (*Scirpus californicus* STEUD) and submerged (*Stukenia pectinata* [L.] BOER, and *Myriophyllum quitense* KUNTH) macrophytes. Sport fishing takes place all year round for the planktivorous *Odontesthes bonariensis* CUVIER et VALENCIENNES and the predatory *Hoplias malabaricus*. BLOCH. Extensive cattle breeding and agriculture are developed within the surrounding area.

3. Methods

Four sampling stations were established in Lacombe Lake according to the spatial distribution of the aquatic macrophytes (emergent and submerged) present. Station 1 (St. 1) was located near the center of the lake, 340 m from the shoreline, with a depth ranging between 1.70 and 2.50 m and with dense stands of *Scirpus californicus* and a variable abundance of submerged macrophytes present. Station 2 (St. 2) was situated in the southern sector of the lake at the edge of emergent-macrophyte stands, approximately 160 m from the shoreline, with a depth ranging from 1.70 to 2.60 m and submerged macrophytes also present. Station 3 (St. 3) was located in the northern sector, 180 m off shore, with a depth between 1.68 and 2.50 m, and without emergent macrophytes, though with abundant submerged ones. Station 4 (St. 4), at the northwestern sector, was nearest to the shoreline, with a depth ranging from 0.58 to 1.40 m and with dense beds of submerged macrophytes (Fig. 1). A single water inflow sample was obtained from an intermittent channel that flowed into the lake to assess the influence of this water source when runoff occurred (September, November, and December 2001). A representative time sequence of rainfall for the shallow lake's basin was obtained from a local precipitation gauge located at 200 m from the lake and making daily measurements.

The water and sediment samples were taken at three to four week intervals during the period of July 2001 to June 2002. At St. 1, St. 2, and St. 3 (deep stations), vertical profiles of the water column consisting in five layers at each site were performed. At St. 4, the shallowest site, subsuperficial samples were obtained. The following measurements were made with a Horiba Multimeter U-10: temperature, conductivity, and turbidity. On every sampling occasion, the water depth at each sampling station was recorded with a graduated scale and the water samples obtained during midmorning by means of a suction pump. The water samples were placed in 1 L acid-cleaned polyethylene bottles, transported back to the laboratory in an ice-cooled isolation box, and stored in the dark at 5–8 °C prior to analysis. The TP was determined by the ascorbic-acid method after digestion with acidic persulfate (method 4500-P B, APHA 1995). The chlorophyll-*a* concentration was measured by spectrophotometric analysis of samples collected on Whatmann GF/C filters (method 10200 H, APHA 1995) and calculated according to LORENZEN (1967). The concentrations of total suspended solids (dry weight) were assessed by method 2540 D of APHA (1995). The concentrations of particulate organic matter (LOI) were determined by weight loss on ignition at 550 °C (method 2540 E, APHA 1995). The results of total phosphorus, LOI, chlorophyll *a* concentration, and phytoplankton density from each sampling station, with values obtained monthly, were integrated and normalized to a unit of area following the formulae of WALSBY (1997). The extent of the euphotic zone was calculated from the Secchi depth, the chlorophyll-*a* concentration, and the extinction coefficient according to the method of Scheffer (1998).

At each sampling station, replicate sediment samples of 2 cm in depth were obtained with a core sampler of 3.5 cm diameter. In these samples, the chlorophyll *a* and LOI were analyzed as in the water samples. The calculations of chlorophyll *a* were made following Lorenzen (1967) and Varela (1981). The TP was analyzed according to Andersen (1979), while the epipelic algae were counted according to Cattaneo (1983).

Duplicate phytoplankton samples were counted by means of the settling technique (Utermöhl, 1958) and the percentage cover of the macrophyte beds of *Stukenia pectinata* and *Myriophyllum quitense* estimated in ten parcels of one m^2 area at each station. Emerged and submerged macrophyte sections were also collected for qualitative periphyton samples.

Regression analyses were performed to test relationships between the TP and the chlorophyll in the sediment and the water. In order to confirm the existence of three phases in the lake, the mean values of selected variables from the four stations on each sampling occasion were used in the k-means, a nonhierarchical-clustering procedure, through squared Euclidean distances for the measured distances (Dufrene and Legendre, 1997). The ANOVA results within clusters comprise a portion of the results of the k-means method.

4. Results

The sampling period was characterized by three exceptional rainfalls (Fig. 2) that promoted an increase in the water level and a reduction in conductivity (Fig. 3).

Water transparency fluctuated between 0.3 and 0.97 m (Fig. 3), with the highest mean turbidity in the water column being recorded during the first three months of sampling (range: 96 to 108 NTU). This period was followed by a notable decrease in turbidity, after which point the turbidity was maintained at <31 NTU during the rest of the sampling period (Fig. 4).

The main growth period of the submerged macrophytes, including S*tukenia pectinata* and *Myriophyllum quitense*, occurred from October 2001 to February 2002. These plants decreased notably during the following autumn, but experienced a regrowth at the end of the sampling period (June 2002), mainly owing to *S. pectinata* development. The shallowest station (St. 4) had the maximum macrophyte development, reaching 100% cover in February. At St. 3 and St. 1, the maximum cover was close to 50%, in summer as well. St. 2 was the sector with the lowest percentage cover, there reaching the maximum values in June (25%; Fig. 4).

Three periods could be distinguished on the basis of turbidity (2.19; $H = 142.75$; $P = 0.000$; Kruskal-Wallis test) that coincided with different levels of macrophyte development (Fig. 4): Phase 1 with high turbidity and without macrophytes, Phase 2 with low turbidity and with the highest macrophyte development, and Phase 3 with the lowest turbidity and least number

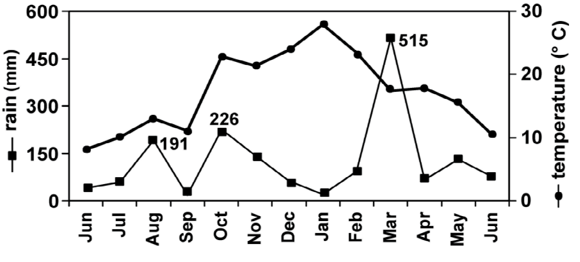

Figure 2. Monthly values of rainfall and water temperature in Lacombe Lake during the sampling period (June 2001 to June 2002).

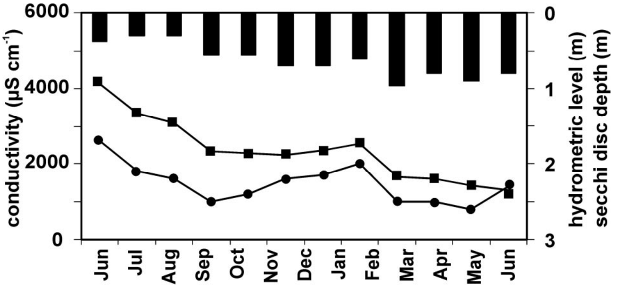

Figure 3. Hydrometric level (solid line with circles), conductivity (solid line with squares) and Secchi depth (black bars) recorded in the deepest station (St. 1) of Lacombe Lake during the sampling period (June 2001 to June 2002).

of macrophytes. During these three periods, no turbidity differences were found among the four sampling stations (3.19; $H = 1.09$; $P = 0.79$; Kruskal-Wallis test).

The euphotic zone extended to the bottom at the shallowest site (St. 4) during the entire sampling period. At the deep stations, light reached the bottom in October and thereafter at St. 1, from December onwards at St. 2, and only beginning in January at St. 3.

The LOI in the water was notably high during the turbid phase (Fig. 5), reaching maximum values in September. The maximum LOI concentrations in the sediments were recorded at St. 1 and St. 2 and showed roughly constant values in both stations (Table 1). At St. 3, the LOI in the sediments was lower than at the previous two sites and remained more variable throughout the annual cycle (Table 1). In the shallowest station (St. 4), the organic matter in the sediments and water were always less than those observed in the other lake sectors (Table 1).

The TP in the water underwent a similar trend in the deeper sectors of this shallow lake (stations 1, 2, and 3). The highest water TP concentration was recorded in October in all these sampling stations (Table 1) and later declined during the clear phase with the macrophytes present (Fig. 5). Thereafter, the lowest concentration was recorded at the beginning of the clear-water phase in the absence of macrophytes, even though a slight increase was observed during the last three months (Fig. 5). In the shallowest sampling station (St. 4), the maximum water TP concentration was measured in August 2001, with a minor increase being recorded during October and November.

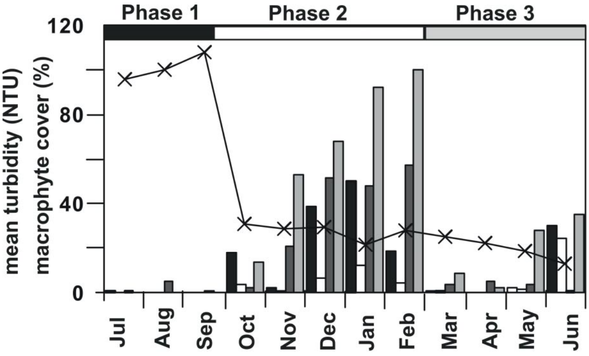

Figure 4. Mean turbidity (solid line) and percentage of submerged macrophyte cover at each sampling station, St. 1: black bars, St. 2: white bars, St. 3: grey bars, St. 4: light grey bars. The upper panel shows the temporal extent of each phase.

The TP concentrations measured in the sediments ranged from 556 µg cm^{-2} (St. 4, April) to 1,414 µg cm^{-2} (St. 2, September). At St. 3, the TP in the sediments was particularly variable during Phase 2. At St. 1 and St. 2, the minimum sediment TP concentrations (Table 1) were recorded during this phase in January (Fig. 5), a time when the highest percentage cover of submerged macrophytes (Fig. 4) along with dense stands of emergent macrophytes were also observed. High mean annual TP concentrations were found at both St. 1 and St. 2 (Table 1).

The maximum chlorophyll-*a* concentration in the water was measured at St. 1 (Table 1) in September, whereas maximum peaks were recorded on other sampling occasions at the other stations (in November at Sts. 2 and 4 and in December at St. 3). The minima at all stations were recorded in October (Fig. 5), with the lowest value occurring at St. 4 (Table 1).

The concentrations of chlorophyll *a* in the sediments were generally higher than in the water column (Table 1). The maximum sediment chlorophyll *a* concentrations were found at all stations during the clear water phase with macrophytes present (Fig. 5). The highest concentration recorded (Table 1) coincided with a major development of macrophyte cover (92%) at the shallowest sector (St. 4).

The chlorophyll concentration in the water correlated significantly with the TP concentrations there ($r = 0.29$; $P = 0.048$, $n = 48$), whereas the correlation between these two parameters in the sediment was not significant ($r = -0.24$; $P = 0.096$, $n = 48$). Moreover, the variation in the values for the TP concentrations in the water and for the sediment chlorophyll contents also showed no significant correlation between one another ($r = 0.12$; $P = 0.41$, $n = 48$).

The TP : chlorophyll *a* ratio in the water was about 10 : 1 (Fig. 6). This ratio, however, was higher in October owing to the input of nutrients from runoff (Fig. 2). This phosphorus input was confirmed by independent measurements taken after the spring rains in a small channel that flowed into the lake for only a few months (477, 678, and 344 µg TP L^{-1} in September,

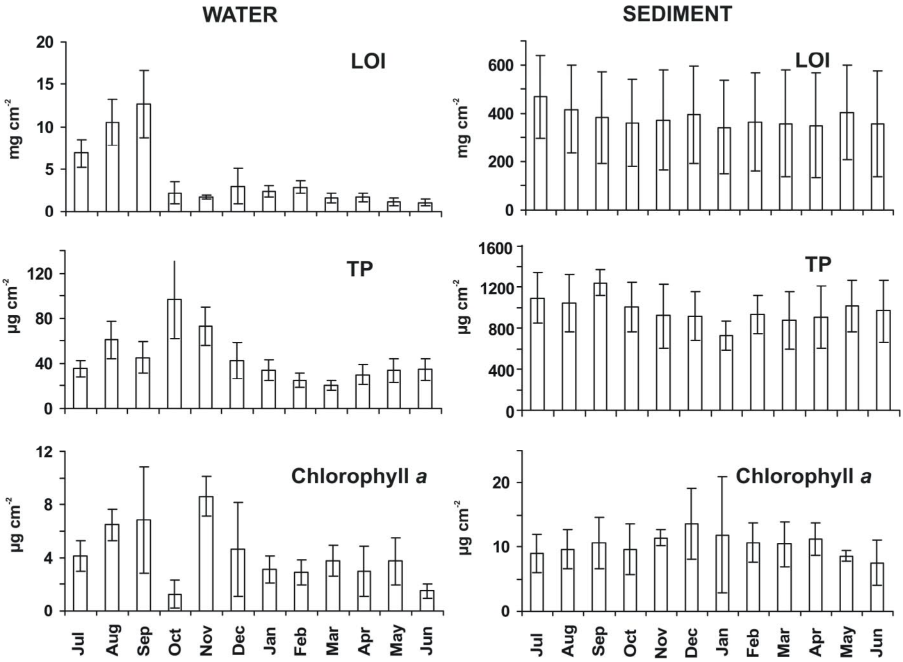

Figure 5. Mean and standard deviation of particulate organic matter (LOI), TP and chlorophyll *a* in water and in sediments, during the sampling period, including the four sampling stations.

Table 1. Mean, standard deviation (within parenthesis), minimum and maximum of variables measured in water and in sediments at each sampling station of Lacombe Lake during the sampling period.

	St. 1 *n* 12		St. 2 *n* 12		St. 3 *n* 12		St. 4 *n* 12	
	Mean (*SD*)	Min-Max	Mean (*SD*)	Min-Max	Mean (*SD*)	Min-Max	Mean (*SD*)	Min-Max
WATER								
TP ($\mu g\ cm^{-2}$)	47.6 (25.3)	23.9–114.6	47.8 (26.0)	20.1–111.0	50.7 (26.0)	22.2–114.9	30.7 (20.4)	14.1–82.9
LOI ($mg\ cm^{-2}$)	4.3 (4.2)	1.4–12.9	4.6 (4.9)	0.8–16.3	4.4 (4.4)	1.0–14.2	2.3 (2.4)	0.5–7.1
Chlorophyll *a* ($\mu g\ cm^{-2}$)	5.2 (2.9)	1.4–12.6	4.4 (2.5)	1.2–10.5	4.7 (2.8)	0.8–9.6	2.4 (2.1)	0.3–7.2
SEDIMENTS								
TP ($\mu g\ cm^{-2}$)	1154.5 (126.6)	927.8–1335.9	1112.8 (189.0)	712.1–1414.3	846.8 (188.5)	561.5–1159.1	758.9 (233.9)	556.2–1252.4
LOI ($mg\ cm^{-2}$)	588.5 (40.1)	530.3–673.1	481.5 (30.4)	431.1–543.7	274.1 (92.9)	136.0–502.7	175.5 (83.7)	82.2–347.7
Chlorophyll *a* ($\mu g\ cm^{-2}$)	6.9 (2.2)	3.8–12.1	10.5 (2.8)	6.0–14.4	11.6 (1.9)	9.2–15.9	12.1 (5.9)	2.9–25.3
DENSITY								
Phytoplankton (ind. $10^5\ cm^{-2}$)	10.7 (8.8)	2.0–31.2	9.4 (7.4)	1.9–26.7	10.1 (7.8)	2.6–26.7	8.3 (5.7)	1.3–21.0
Epipelic algae (ind. $10^5\ cm^{-2}$)	52.7 (35.7)	22.3–137.3	59.9 (27.8)	29.2–113.0	62.7 (27.1)	26.8–126.3	58.4 (26.6)	13.1–106.3
RICHNESS								
Phytoplankton (number of species)	48 (11.8)	22–63	50 (7.9)	36–63	41 (5.6)	31–48	25 (5.9)	16–33
Epipelic algae (number of species)	44 (6.6)	34–58	43 (7.9)	32–56	51 (9.1)	34–63	58 (5.6)	46–65

November, and December, respectively) since these TP concentrations were much higher than those measured in the lake during the same months.

The TP:chlorophyll *a* ratios in the sediment were always higher than those observed in the water. Some spatial differences in this parameter were observed in accordance with the presence of emergent macrophytes. The ratios at St. 1 and St. 2 were closer to the 100 : 1 line (Fig. 6) than those at St. 3 and St. 4, though at St. 3 the values fluctuated between 50 : 1 and 100 : 1.

The phytoplankton density reached the highest levels during the first three months of the annual cycle (Fig. 7). At the deep stations, this parameter decreased notably from mid spring to summer and then increased slightly during the autumn (Fig. 7). At St. 4 the phytoplankton

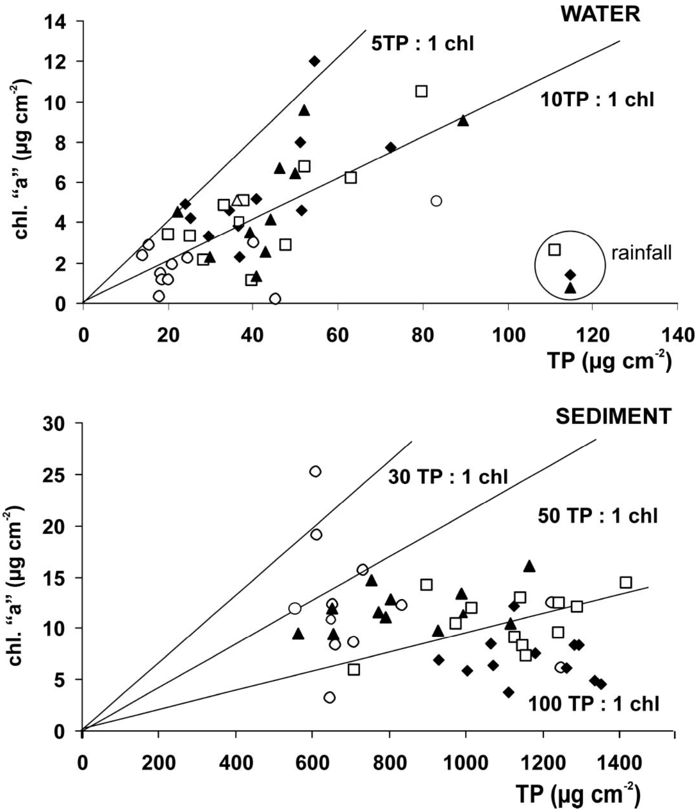

Figure 6. Ratio of TP: chlorophyll *a* in water (a) and in sediments (b) at the four sampling stations: black diamonds, St. 1; white squares, St. 2; black triangles, St. 3; white circles, St. 4.

density decreased in spring and then remained low, with slight variations, until the end of the sampling period (Fig. 7).

During the annual cycle ($n = 12$), the mean turbidity was strongly correlated with the integrated phytoplankton density (St. 1: $r = 0.77$, $P = 0.004$; St. 2: $r = 0.90$, $P = 0.0001$; St. 3: $r = 0.77$, $P = 0.003$; and St. 4: $r = 0.73$, $P = 0.007$) as well as the integrated LOI (St. 1: $r = 0.73$, $P = 0.007$; St. 2: $r = 0.62$, $P = 0.03$; St. 3: $r = 0.75$, $P = 0.005$; and St. 4: $r = 0.64$, $P = 0.025$).

The maximum epipelic algal density for the entire sampling period was recorded during the turbid phase at St. 1 (Fig. 7). In contrast, very low benthic algal abundances were recorded during the clear phase at this station. The epipelic algal density at St. 2 and St. 3 had three coincident peaks in the summer-to-autumn periods, though St. 3 always had lower values (Fig. 7). At the shallowest site (St. 4), the abundance was high from August until January, reaching a maximum in December (Fig. 7).

Significant differences among sampling stations were found with respect to the sediment LOI and TP, the water TP, and the water- and sediment chlorophyll concentrations (Table 2). Nevertheless, with respect to the variables measured in the water, these differences disappeared if St. 4 was excluded from consideration (Table 2).

According to the results from the k-means method (Table 3), the first group of the cluster comprised the winter months of July through September, the second the period from October

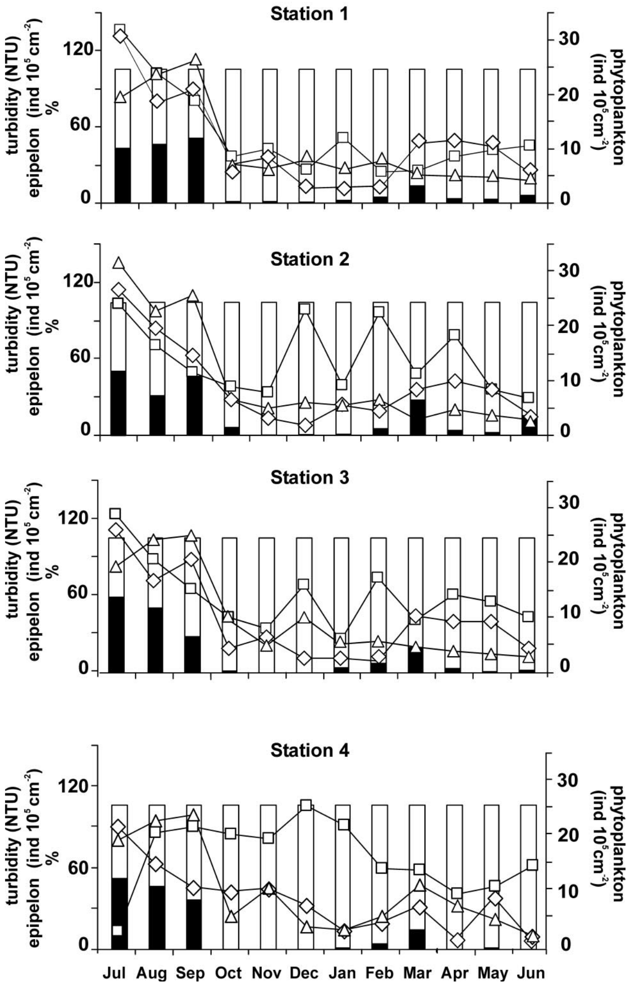

Figure 7. Density of planktonic (solid line with diamonds) and epipelic algae (solid line with squares) related to turbidity (solid line with triangles) at the four sites sampled in Lacombe Lake. Percentage participation of Oscillatoriaceae (black bars) respect to the other plankton algae (white bars) in the total phytoplankton density.

to February, and the third the months from March to June. The significant variables that grouped the sampling occasions in the clusters consisted in those related to hydrological conditions (conductivity and hydrometric level) as well as others that represented changes in the internal ecological function (turbidity, algal density, TP, and LOI).

176 species of phytoplankton were identified. The annual mean richness of the species in the deep areas was twice that recorded in the shallowest sector (Table 1). The specific composition was similar among all four sites with some temporal variations throughout the sampling period, especially as a result of the high proportion of Oscillatoriaceae in the water throughout the three first months (Fig. 7). During the turbid period, *Planktolyngbya limnetica* KOMÁRKOVÁ-LEGENEROVÁ et CRONBERG was the most abundant alga, followed by

Table 2. Results of the ANOVA and Kruskal-Wallis tests showing spatial differences. The tests for variables measured in water were repeated after excluding the shallowest station 4$^{(1)}$.

Test		Among sampling stations	
K-W	Log LOI water	$\chi^2 = 6.72$	$P = 0.08$
K-W	Log LOI water$^{(1)}$	$\chi^2 = 0.08$	$P = 0.96$
ANOVA	Log LOI sediment	$F = 50.48$	$P = 0.00$*
ANOVA	Log TP water	$F = 3.44$	$P = 0.03$*
ANOVA	Log TP water$^{(1)}$	$F = 0.100$	$P = 0.91$
K-W	Log TP sediment	$\chi^2 = 20.40$	$P = 0.00$*
ANOVA	Log Chl. water	$F = 4.28$	$P = 0.01$*
ANOVA	Log Chl. water$^{(1)}$	$F = 0.31$	$P = 0.74$
ANOVA	Log Chl. sediment	$F = 5.71$	$P = 0.00$*

Aphanocapsa delicatissima W. et G. S. WEST along with two species of *Oocystella* (*O. parva* HINDÁK and *O. nephrocytoides* HINDÁK). In October species of *Monoraphidium* dominated. During the clear period, with the development of submerged macrophytes, *Microcystis aeruginosa* KÜTZING was the most abundant, followed by *Cyclotella meneghiniana* KÜTZING and *Aphanocapsa holsatica* CRONBERG et KOMÁREK. Later, during the clear period with scarce submerged macrophytes, *Raphidiopsis mediterranea* SKUJA and *Coelosphaerium naegelianum* UNGER prevailed, while *Cryptomonas erosa* EHRENBERG and *Merismopedia minima* BECK were also frequently abundant.

The epipelic algae exhibited a total richness of 137 species, with the highest mean annual number of species being recorded at St. 4 (Table 1). The maximum richness of these benthic algae occurred in the clearwater phase without macrophytes at St. 4. *Planktolyngbya limnetica*, *Jaaginema metaphyticum* KOMÁREK, and *Heteroleibleinia pusilla* COMPÈRE were the most abundant taxa in the lake's sediments throughout the sampling period. The taxa that characterized each of the phases described were: in Phase 1, *Pseudoanabaena limnetica* KOMÁREK, *Leptolyngbya crassior* ANAGNOSTIDIS and *Oscillatoria* spp; in Phase 2, *Xenococcus minimus* GEITLER, *Cosmarium phaseolus* BRÉBISSON f. *minor* BOLD, and *Fragilaria* aff. *construens* var. *subsalina* HUSTED; and in Phase 3, *Oscillatoria janus* SKUJA and *Jaaginema subtilissimum* ANAGNOSTIDIS et KOMÁREK.

Table 3. Results of variance analysis within clusters obtained by the k-means method (probability ns: non significant, * < 0.05, ** < 0.1)

Variable	*P*
Turbidity (NTU)	**
Conductivity (µS cm^{-1})	**
Hydrometrical level (cm)	*
Chlorophyll "*a*" epipelon (µg cm^{-2})	ns
LOI. Sediment (mg cm^{-2})	*
Total Phosphorus Sediment (µg cm^{-2})	*
Density epipelon (ind. 10^5 cm^{-2})	**
Chlorophyll "*a*" Phytoplankton (µg cm^{-2})	ns
Total Phosphorus Water (µg cm^{-2})	ns
Density phytoplankton (ind. 10^5 cm^{-2})	**
LOI Water (mg cm^{-2})	**

The mean relative composition of algae in the sediments was 31% typical epipelic algae plus 69% allochthonous species. The maximum contributions of the various alga communities (mean annual percentage) among the four sites were: for the typical epipelic algae, 43% at St. 4 (the shallowest site); for the phytoplanktonic algae, 66% at St. 1; and for the periphytic algae, 21% at St. 4. The maximum representation of epipelic algae was recorded at St. 4 (62%, April), with the most abundant species being *F.* aff. *construens* var. *subsalina* (6.76×10^5 ind cm^{-2}), *J. metaphyticum* (4.96×10^5 ind cm^{-2}), *Planktolyngbya* aff. *undulata* KOMÁREK et KLING (3.62×10^5 ind cm^{-2}), and *H. pusilla* (1.19×10^5 ind cm^{-2}). The maximum participation of planktonic algae was observed at St. 1 (78%, July) with the most abundant species being *A. holsatica* (43.5×10^5 ind cm^{-2}), *Planktolyngbya limnetica* (26.9×10^5 ind cm^{-2}), *O. parva*, *Tetraedron minimum* HANSGIRG *sensu* SKUJA*, Spirulina laxissima* G. S. WEST, and *Merismopedia warmingiana* LAGERHEIM (all of them with 4.00 to 5.00×10^5 ind cm^{-2}). Finally, the maximum abundance of periphytic algae was recorded at the shallowest station, St. 4 (38%, March), with the following species being predominant: *Navicula cryptocephala* KÜTZING (6.85×10^5 ind cm^{-2}), *Navicula notha* WALLACE (2.01×10^5 ind cm^{-2}), and other species of *Navicula* (3.26×10^5 ind cm^{-2}).

5. Discussion

In the Lacombe shallow lake temporal and spatial variability were recognized in relation to alternative states of equilibrium and corresponding to the presence or absence of submerged and/or emergent macrophytes.

According to HORPPILA and NURMINEN (2001), the pelagic TP concentrations may depend on the degree of sediment resuspension, as affected by the presence or absence of emergent macrophytes. In Lacombe Lake, however, the TP concentrations and turbidity of the water did not show differences between sampling stations with and without emergent macrophytes, indicating that the prevention of resuspension was not an important effect of the emergent-macrophyte stands. Nevertheless, the TP concentrations in the sediments showed significant differences among the sampling stations and were always higher at stations with emergent macrophytes (*i.e.*, Sts. 1 and 2). This observation plus the fact that St. 1 had the lowest mean annual chlorophyll concentration in the sediment along with the highest density of emergent macrophytes explained the high sediment TP : chlorophyll *a* ratio recorded at St. 1 and St. 2. Since the emergent macrophytes would affect the sediment-phosphorus balance by phosphorus uptake as well as by sediment loading, the TP : chlorophyll *a* ratio varied throughout the study period in accordance with the macrophyte growth cycle. At St. 1 and St. 2, for example, the minimum sediment TP concentrations coincided with the maximum density of emergent macrophytes.

In Lacombe Lake, the variation of TP in the water was not related to the biomass of epipelic algae which suggests that these algae did not significantly liberate TP from the sediment, in contrast to the significant role in this fashion proposed for these algae by HANSSON (1988), WETZEL (2001), and DOODS (2003). We therefore agree with the proposal by LIBORIUSEN and JEPPESEN (2003) that epipelic algae are weak regulators of alternative states of equilibrium.

The epipelic chlorophyll was always higher than the planktonic chlorophyll consistent with the results of CYR (1998), who recorded annual mean values in sediments that were seven times higher than those measured in the pelagic zone. In Lacombe Lake, the chlorophyll-*a* estimations indicated that epipelic microalgae were the dominant algal association, in agreement with the results of LIBORIUSSEN and JEPPESEN (2003) in a clear shallow lake. The epipelic-chlorophyll concentration did not show differences among the three phases, which can be explained by two different factors acting throughout the study period: (1) input of chlorophyll from the sedimentation of phytoplankton during the turbid phase and (2) epipelic chlorophyll production promoted by the high light availability at the bottom during the clear phases. These influences could, in the end, prove more important than the dynamics of the sediment-TP content in determining the temporal differences in epipelon behaviour in a shallow seepage lake such as Lacombe.

Our results indicated a TP : chlorophyll *a* ratio in the water of about 10 : 1, much higher than the 3 : 1 ratio proposed by Dokulil and Teubner (2003). These authors postulated that the ratio observed by them might indicate the presence of certain conditions that affect phytoplankton development *e.g.*, light limitation by inorganic turbidity or macrophyte cover, allelopathic substances, or grazing. All these factors, except inorganic turbidity, could be responsible for the phytoplankton limitation in Lacombe Lake during the annual cycle. Likewise, in disagreement with the proposal by Rooney and Kalff (2003), the temporal variation in the TP : chlorophyll *a* ratio in our study was unrelated to the percentage of submerged macrophyte cover. If TP and chlorophyll concentrations are considered separately, significant differences among the three temporal phases were found, whereas the ratio between these two parameters remained essentially constant. The variability among these data during the study period did not permit a clear explanation for the constant TP : chlorophyll *a* ratio. The value for this ratio of 100 : 1 in the sediments indicated a clear nutrient excess with respect to the epipelic algae. For this reason, the mobilization of TP from the sediments to the water could not have been affected by algal activity.

In Lacombe Lake, different changes occurred during the three temporal phases as defined above.

Phase 1

This phase extended from winter to early spring and was characterized by high turbidity levels owing to bioseston as a result of the highest algal density recorded along with high LOI concentrations. Species of Oscillatoriaceae were the dominant group at this time possibly because, as established previously by Scheffer (1998), Nixdorf *et al.* (2003), and Nõges *et al.* (2003), these algae are adapted to conditions of low light. The most characteristic species of phytoplankton during this phase, *Planktolyngbya limnetica*, had also been found by Albay and Akcaalan (2003) as epiphyton in high abundance in a lake colonized by emergent macrophytes. These authors explained the successful growth of this species under those conditions on the basis of its wide tolerance to low water transparency. Nõges *et al.* (2003), in agreement with our results, recorded this same species at high density in phytoplankton in coincidence with a period of lower water level in a shallow lake. During this phase in Lacombe Lake, the benthic assemblages contain the maximum proportion of sedimentated planktonic algae (mostly cyanophytes). During this phase we also recorded high densities of *Pseudoanabaena limnetica* and *Aphanocapsa* spp. in the sediments; the former species, here constituting a characteristic epipelon of Lacombe Lake during this period, had also been identified as the planktonic dominant species during turbid states in several German lakes by Nixdorf *et al.* (2003).

The dominance by Oscillatoriaceae during the turbid phase (Fig. 7), along with the good correlations found between phytoplankton density and either turbidity or water LOI concentrations lend support to the existence of the positive feedback mechanism (maintenance of Oscillatoriaceae dominance) proposed by Scheffer (1998) as characteristic of this state. Later, coinciding with the decrease in turbidity, an evident change in the flora occurred wherein species with unknown adaptations to low irradiation came to predominate in the phytoplankton during the clear phases.

Phase 2

The beginning of the clear-water phase (in October; Fig. 2) was detected after heavy rainfalls, which events disturbed the system by raising the hydrometric level and nutrient incorporation, coinciding with an increase in water temperature and Secchi depth. Coops *et al.* (2003) found that the input of TP and increase in water level resulting from heavy rains produced a turbid state in European temperate lakes. This dissimilarity with our results could be explained by the relative shallowness of Lacombe Lake, which characteristic enables light penetration down to the bottom even under conditions of high water level. This change to a clear-water phase in the case of Lacombe Lake also occurred in conjunction with a seasonal temperature increase, one of the conditions favouring macrophyte growth. Lassen *et al.* (1997) proposed that certain stochastic phenomena in early spring determine whether shallow lakes will be dominated by phytoplankton or by macrophytes during a growth season, but the mechanisms that regulate the successful colonization of either macrophytes or phytoplankton are not as yet fully understood.

According to Scheffer (1998), a disturbance can reduce the turbidity to a value below a certain critical level needed for macrophyte colonization. In Lacombe Lake, the exceptional rainfall in October could have caused the shift to the clear-water state dominated by vegetation. Although this increase in water volume diluted the plankton, it did not diminish the TP concentrations in the water because of the input of nutrients through the accompanying runoff, as inferred from the high TP concentrations measured in a channel temporarily flowing into the lake at the same time.

During this phase, a marked decline in phytoplankton density was recorded (Fig. 7) along with the presence of a different algal assemblage, characterized by *Microcystis aeruginosa* and *Cyclotella meneghiniana.* By contrast, in an interconnected shallow lake of the Salado River basin (San Miguel del Monte Lake), *C. meneghiniana* had dominated during a clear phase containing submerged macrophytes, whereas *M. aeruginosa* had predominated during a turbid phase (Solari *et al.*, 2003). In Lacombe Lake, however, high densities of *M. aeruginosa*, occurred during the summer, probably because of its more rapid growth at temperatures above 20 °C, as noted by Reynolds (1984) and Chu *et al.* (2007). This species had also been documented during clearwater phases by Benndorf *et al.* (2002) in German shallow lakes. Nevertheless, Chen *et al.* (2003) found *M. aeruginosa* in highly turbid sectors of a stratified lake, where it was able to regulate its vertical position thus gaining a competitive advantage over other algae through the acquisition of better light conditions.

The lowest phytoplankton densities in all sampling stations were recorded in conjunction with the highest submerged macrophyte cover. According to Gross *et al.* (2003), the pelagic algae can be controlled by allelopathic substances elaborated by submerged macrophytes. Moreover, Körner and Nicklisch (2002) demonstrated the effect of such substances with algicidal activity that were released mainly by *Ceratophyllum demersum* L. and *Myriophyllum spicatum* L. With respect to the establishment of a clearwater state, allelopathy is one of several feedback mechanisms proposed by Scheffer (1998) that can affect the competitive balance in favour of algae other than Oscillatoriales. On the basis of the similarity in macrophytes present as well as the qualitative and quantitative change that occurred in the phytoplankton during this study, the conditions for the stabilizing mechanism proposed by the above authors could be occur in Lacombe Lake. However, we can not conclude about the significance of allelopathy in this lake because as other authors (Blindow *et al.*, 2002) pointed out the quantitative importance of this effect in the field is not known.

The maximum sediment-chlorophyll concentration was found in St. 4 coinciding with a macrophyte cover of 96%. Lassen *et al.* (1997) have demonstrated that maximum chlorophyll concentrations in sediments can be found even with 100% macrophyte cover in the shallow sectors of lakes. In such a situation, submerged macrophytes favour the development of benthic algae despite their shade by promoting an increase in water transparency as they facilitate grazing and prevent resuspension. On the basis of the formula given by Scheffer (1998), our results show that light always reached the bottom of Lacombe Lake during Phase 2, notwithstanding the failure of the calculation of the shading effect of the macrophytes on light penetration. Epipelic algae are favoured by high availability of both nutrients and light (Hansson, 1988; Hwang *et al.*, 1998 and Flöder *et al.*, 2006). Scheffer (1998) proposed that macrophytes can obtain many of their nutrients from the sediment rather than from the water column. In Lacombe Lake, whereas the sediment TP concentrations changed in relation to presence and distribution of macrophytes, the epipelon chlorophyll concentration was independent of the values for sediment TP.

Phase 3

According to Scheffer (1998), a small shift in critical turbidity resulting from a change in water level can bring about a switch from one state to the other if the lake is already close to the threshold for such a transition. The disturbance owing to the heavy rainfall in March that coincided with the senescence period of *Stukenia pectinata* led to the beginning of this third phase. The perturbation of an increase in water depth can precipitate the changeover to a mixed-phytoplankton state, in spite of stable turbidity levels. Since Lacombe is a flat-bottomed lake with a similar depth of water throughout its entire basin, a sudden increase in that depth can produce a simultaneous disappearance of all submerged macrophytes.

The phytoplankton density and species richness in this phase were higher than in Phase 2, whereas the average phytoplankton chlorophyll was lower. These differences possibly resulted from the intrinsic qualitative change in the phytoplankton as well as from a concomitant high grazing pressure associated with the maximum in biomass, abundance, and species richness of the zooplankton that also occurred during this last phase (Ardohain, 2008).

The maximum epipelic biomass levels at the deep stations were coincident with the largest participation of specifically epipelic algae. The diminution in both the submerged macrophyte cover and the phytoplankton density could favour the *in situ* growth of algal species during this last phase. In contrast, the maximum biomass at St. 4 was coincident with the largest proportion of periphytic algae in the sediments, probably related to the fact that the development of the submerged macrophytes had declined after their maximum level of coverage.

The increase in water level led to the disappearance of macrophytes, though not to an increased turbidity such as might have favoured the Oscillatoriaceae; this particular disturbance was thus able to induce a mixed-phytoplankton state. Nevertheless, submerged macrophytes and Oscillatoriaceae were still present at low density at different times within this phase. Consequently, this weak condition was capable of changing to either a turbid or a clear, macrophyte-dominated state, because of, for example, a high grazing pressure or a regrowth of submerged macrophytes.

During the entire study period the dominant species in the epipelon community were three Oscillatoriaceae, despite the changes in plankton composition and density over time and the enrichment of the sediments with the incoming plankton plus the epiphyton algae. Therefore, the benthic-algal system could be considered in a constant condition, though always dominated by these shade-tolerant algae. As a result, the Oscillatoriaceae could have a competitive advantage in repopulating the water column from the sediment inocula when the environmental conditions are favourable for them.

The changes recorded in epipelon and phytoplankton structure, in conjunction with significant differences found throughout the annual cycle, would argue for the existence of three different turbid- and clear-water phases within this typical shallow seepage lake.

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