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Distribution of epiphytic diatoms on five macrophytes from a Pampean shallow lake: host-specificity and implications for paleoenvironmental reconstructions

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Epiphytic diatoms are an important component of death and fossil assemblages in macrophyte-dominated shallow lakes. In the Argentinean Pampas, the lack of studies on the composition, diversity and distribution of epiphytic diatoms limits the extent of the paleoenvironmental inferences that can be made from their fossil record. We studied the composition of epiphytic diatom biofilms living on five macrophytes in a Pampean shallow lake (Nahuel Rucá, Buenos Aires Province). Samples of emergent, free-floating, rooted-floating and submersed macrophytes were collected in triplicate over one year and analyzed for diatoms. Epiphytic assemblages on the free-floating species *Azolla filiculoides* and *Ricciocarpus natans* were dominated by *Lemnicola hungarica*, whereas the remaining macrophytes (the emergent *Schoenoplectus californicus*, the submersed *Ceratophyllum demersum* and the rooted-floating *Hydrocotyle ranunculoides*) were dominated by *Cocconeis placentula*. Although all assemblages were dominated by epiphytic taxa, low proportions of planktonic and benthic taxa were also recorded. Composition, diversity, richness and evenness of diatom assemblages found on free-floating macrophytes differed significantly from the rest of the samples analyzed. The strong association of the epiphytic diatom, *L. hungarica*, with free-floating macrophytes, together with the high dominance of *C. placentula* on emergent and submersed plants provides a potential method for inferring past fluctuations in aquatic vegetation coverage in the palaeolimnological record of Pampean shallow lakes.

Keywords: epiphytic diatoms, shallow lakes, macrophytes, Pampas, Argentina

Introduction

Epiphytic diatoms are an important component of the aquatic biocoenosis in macrophyte-dominated shallow lakes (Toporowska et al. 2008). These lakes usually have extensive littoral zones, where the productivity of the epiphytic algae frequently exceeds that of the phytoplankton (Wetzel 2001, Bennion et al. 2010). Epiphytic assemblages are vital in several aspects of shallow lake dynamics, acting as mediators between freshwater nutrient status and primary productivity, and dominating the diets of aquatic herbivores (see references in Emson 2015). Because of their importance, they have been widely used as indicators of shallow lake water quality (e.g., Bennion 1994, Bennion et al. 2001, Poulíčková et al. 2017) and in paleolimnological research (e.g., Charles & Smol 1994, Cantonati et al. 2014). Surprisingly, despite their importance and abundance, little is known about key aspects of their biology, such as biogeographical patterns, population dynamics and substratum preference (Emson 2015). Research focused on these aspects of epiphytic diatom assemblages is very scarce and scattered (e.g., Tiffany & Lange 2002, Rodríguez et al. 2011, Desianti 2012, Al-Handal et al. 2014, Emson 2015, Letáková et al. 2016),

leading to a lack of the key empirical information needed to assess their paleoenvironmental significance in many regions of the world (e.g., Hassan 2015).

The Argentinean Pampas represents one of the largest wetland areas of South America (Quirós et al. 2002). This is a vast region in which the prevailing flat geomorphology promotes the occurrence of numerous shallow lakes, whose littoral zones are densely populated by emergent and submersed macrophytes, forming a ring that entirely surrounds the lakes and clearly differentiates littoral from open water areas (García-Rodríguez et al. 2009, Stutz et al. 2012, Hassan 2013). In this context, Pampean shallow lakes provide suitable microhabitats for the development of diverse assemblages of epiphytic diatoms, which constitute a significant part of the total diatom assemblages inhabiting these lakes, as evidenced by the death assemblages (Boucot 1953) preserved in surface sediments (Hassan 2015). However, few studies describe epiphytic diatom assemblages in these lakes (Claps 1991, Pozzobon & Tell 1995, Tesolín & Tell 1996, Sánchez et al. 2010, Rodríguez et al. 2011), contrasting noticeably with the attention paid to phytoplanktonic (e.g., O'Farrell et al. 2003, see Vouilloud 2003 and references therein), epipellic (e.g., Gómez 1998,

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Vouilloud 2003) and sedimentary (Hassan et al. 2009, 2011, Hassan 2015) assemblages. Hence, the ecology and distribution of diatom assemblages inhabiting aquatic macrophytes from shallow lakes of the Pampean region remain largely undocumented (Rodríguez et al. 2011).

Pampean shallow lakes constitute an excellent source of paleoenvironmental information in southern South America (García-Rodríguez et al. 2009). Over the last decade, a series of studies conducted on these lakes have provided Holocene paleoenvironmental reconstructions based on pollen, non-pollen palynomorphs, plant macrofossils (Stutz et al. 2010, 2012), molluscs (De Francesco et al. 2013) and diatoms (Hassan 2013, Hassan et al. 2014). Studies on surface sediment diatom distribution (Hassan et al. 2009, 2011, 2014) and preservation (Hassan 2015) have also been conducted, providing ecological and taphonomical information applicable to the interpretation of fossil assemblages. This information, however, was based only on the study of sedimentary assemblages, and did not provide data on ecological aspects of the epiphytic diatom assemblage. Given the high prevalence of epiphytic diatom frustules on death assemblages observed in sediments, this lack of information on their environmental significance places limitations on the paleoenvironmental significance of sedimentary assemblages in Pampean shallow lakes.

In the present study, the distribution of epiphytic diatom assemblages on the dominant macrophytes, *Azolla filiculoides* Lamarck, *Ricciocarpus natans* (Linnaeus) Corda, *Hydrocotyle ranunculoides* Linnaeus, *Schoenoplectus californicus* (Meyer) Soják and *Ceratophyllum demersum* Linnaeus was analyzed in Nahuel Rucá Lake, a shallow lake located in the southern Pampas of Argentina. These macrophyte species are abundant in the littoral zone, forming a complete ring of vegetation that surrounds the entire lake (Stutz et al. 2010). They are very abundant and represent the diversity of life forms exhibited by macrophytes in the lake: emergent, submersed, rooted-floating and free-floating. The main aim of this research is to provide information on epiphytic diatom diversity and ecology, and to

assess for host-specificity of diatom distribution that could be useful for the reconstruction of past environmental fluctuations during the Holocene.

Materials and methods

Study area

Nahuel Rucá (37°37'2.28" S-57°25'29" O) is a shallow, freshwater lake located in the southeastern Argentinean Pampa plain, close to the Atlantic coast (Fig. 1). As with most Pampean lakes, Nahuel Rucá is very shallow (max. depth = 90 cm; Table 1). It has a surface of approximately 245 ha (Cristini & De Francesco 2012). Its shallowness and small size favour the interaction between sediments and the water column through wind-driven turbulence. Like

Table 1. Summary of environmental characteristics of Nahuel Rucá (modified after Hassan, 2015).

Water chemistry	
Conductivity (mS/cm)	0.8 ± 0.5 (0.3–1.6)
pH	8.1 ± 0.3 (7.4–8.5)
Dissolved oxygen (ppm)	7.5 ± 2.7 (2.1–10.8)
Temperature (°C)	16.3 ± 7.3 (7.2–25.5)
CO ₃ ²⁻ (mg L ⁻¹)	0
HCO ₃ ⁻ (mg L ⁻¹)	529 ± 230 (303–849)
Cl ⁻ (mg L ⁻¹)	144 ± 82 (91–266)
Hardness (mg L ⁻¹ of CaCO ₃)	250 ± 127 (173–438)
Ca ²⁺ (mg L ⁻¹)	30.7 ± 16.5 (18.1–53.2)
Mg ²⁺ (mg L ⁻¹)	41.7 ± 29.7 (18.8–85.4)
SO ₄ ²⁻ (mg L ⁻¹)	108.9 ± 61.5 (27.4–169)
SiO ₂ (mg L ⁻¹)	17.7 ± 1.3 (16.8–18.6)
PO ₄ ³⁻ (mg L ⁻¹)	161.3 ± 88.7 (98.6–224.0)
NO ₃ ⁻ (mg L ⁻¹)	67 ^a
Physical characteristics	
Depth (open water samples, cm)	78.7 ± 8.8 (60–90)
Depth (littoral samples, cm)	40 ± 14 (15–65)
Secchi depth (cm)	16.7 ± 9.6 (5–40)

Note: Values are mean ± SD; minimum and maximum values are given in parentheses.

^aOnly one measurement available.

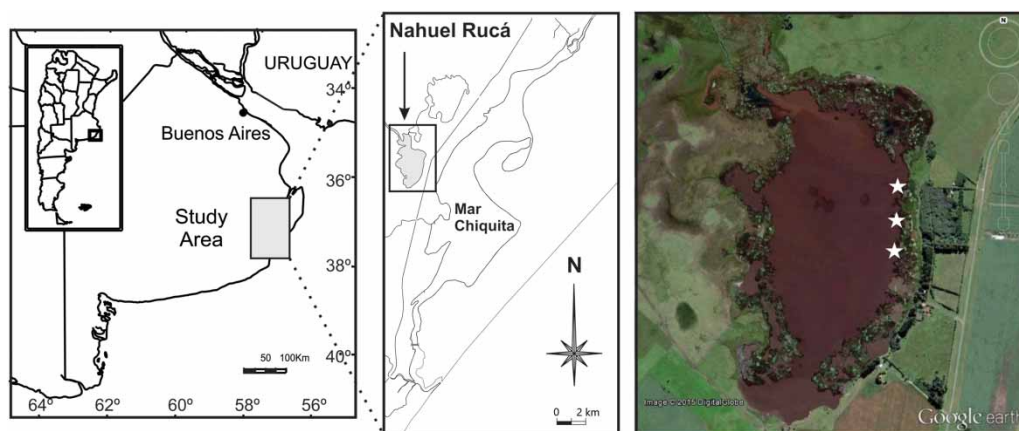


Fig. 1. Map of the study area showing the location of Nahuel Rucá lake and the three sampling stations.

most lakes on the continental plain in the southern part of the Pampean region, it shows a typical lenticular profile and tends to have a rounded to slightly elongated shape (Diovisalvi et al. 2015).

The plant community in Nahuel Rucá is characterized by several species of emergent, floating and submersed macrophytes. The dominant species is the emergent *Schoenoplectus californicus*, which forms a complete ring around the lake (Fig. 1). Other emergent macrophytes grow into the ring of *S. californicus* in the shallowest water/soil interface zones: *Zizaniopsis bonariensis* (Balansa & Poitrasson) Spegazzini, *Hydrocotyle bonariensis* Commerson ex Lamarck, *H. ranunculoides*, *Alternanthera philoxeroides* (Martius) Grisebach, *Solanum glaucophyllum* Desfontaines, *Bacopa monnieri* (Linnaeus) Wettstein, *Polygonum punctatum* Elliot, *Ranunculus apifolius* Persoon, *Triglochin striata* Ruiz & Pavón and *Phyla canescens* (Kunth) Greene. Near the shore, the free-floating *R. natans*, *A. filiculoides*, *Lemna valdiviana* Philippi and *Wolffiella lingulata* Hegelmaier form a dense carpet. The submersed species *Myriophyllum elatinoides* Gaudichaud-Baupré and *C. demersum* develop in the deepest parts of the lake, but can be also found near shore (Stutz et al. 2010).

Pampean shallow lakes show some limnological features that depart from most of those located in temperate regions, such as higher concentrations of phosphorus, nitrogen and chlorophyll *a* as well as lower transparency and, therefore, they represent extremes of the trophic-state continuum (Diovisalvi et al. 2015). This is the case of the studied lake, which exhibited hypereutrophic, turbid and alkaline conditions during the sampling period (Hassan 2015). The environmental characteristics of Nahuel Rucá Lake were measured seasonally and summarized as mean \pm standard deviation (Table 1; see Hassan 2015 for methodological details). The sediments are muddy and organic, with a maximum organic matter content of 60% (Cristini & De Francesco 2012).

Field and laboratory methods

Samples were collected once every three months between August 2013 and September 2014. During each field trip, macrophyte samples were collected from three sampling points (Fig. 1). The selected macrophyte taxa were chosen to represent the dominant species observed during the sampling period, as well as to cover the whole variability of life forms: emergent (*S. californicus*), submersed (*C. demersum*), rooted-floating (*H. ranunculoides*) and free-floating (*A. filiculoides* and *R. natans*). According to a previous study (Federman 2003), *S. californicus* is the dominant macrophyte in Nahuel Rucá, covering 23.5% of the lake surface, followed by *R. natans* (18.7%) and *A. filiculoides* (16.44%). The percentage of the lake covered by macrophytes during the sampling period was calculated

by examining Google Earth[®] satellite images using klm polygons, which indicated 50.2% coverage. However, this methodology did not allow us to distinguish between the different macrophyte taxa, although the extent of the macrophyte cover during the sampling period was comparable to that reported for 2003 (58.6%; Federman 2003). Data on the percentage of cover of *H. ranunculoides* and *C. demersum* were not available, but they were incorporated into the study as they formed conspicuous patches among emergent macrophytes during the sampling period and represented root-floating and submersed habitats.

At each sampling site, pieces of *S. californicus* stems were removed using scissors. The other macrophytes were collected by hand and stored in 90% alcohol. As no individuals of *H. ranunculoides* were found in autumn, only nine samples of this macrophyte were included in the dataset. In the laboratory, samples were oxidized with 30% hydrogen peroxide at 80°C and washed several times with distilled water. The pieces of macrophyte tissue were entirely submersed in the hot peroxide until no evidence of vegetal tissue remained. This procedure was chosen in order to collect all the diatom material present in the sample and to avoid sampling biases produced by scraping the structurally different surfaces of the different life forms collected (e.g., *R. natans* and *S. californicus*). After homogenization of the digested diatom suspension, a subsample was transferred to a coverslip and air-dried, and permanent slides were made using Naphrax[®]. At least 300 diatom valves per slide were counted across random transects using a Leica DM500 light microscope (LM) at 1000 \times magnification. Additionally, each fresh sample was also mounted in Brunel aquatic mountant and examined using a light microscope (1000 \times magnification) in order to qualitatively assess the presence of dead diatom cells. We decided not to quantify the live–dead diatom ratio since the different macrophyte tissues posed different constraints on the observation of diatom cells. In some cases, it was hard to determine the presence of diatom chloroplasts in the raw material as the presence of organic material obscured the observations, and quantification would lead to uncertain ratios. For the qualitative evaluation of samples we focused on clearly identifiable dead remains, in order to assess their overall composition.

Diatom taxa were identified according to Lange-Bertalot et al. (1996), Krammer & Lange-Bertalot (1997, 1999, 2004a, b), Metzeltin & Lange-Bertalot (1998, 2007), Rumrich et al. (2000), Metzeltin et al. (2005), Levkov (2009) and Sar et al. (2009). Diatom taxa were characterized according to their life form, following the ecological classifications of Vos & de Wolf (1993), and modern data available for the Pampean region (e.g., Claps 1991, Gómez 1998, Hassan et al. 2009, 2011, Rodríguez et al. 2011). According to Vos & de Wolf (1993), the classification of diatom life forms includes six categories: euplankton, tychoplankton, epiphytic, benthos epipelon,

benthos epipsammon and benthos aerophilous. In order to simplify the description of the results, we grouped euplanktonic and tychoplanktonic taxa in a single category (plankton), whereas the three benthic categories were considered altogether as ‘benthos’. Given that some taxa exhibit variability in their reported life forms (such as *C. placentula*, which can occur both in the epiphyton and epilithon), a taxon was classified as epiphytic if it is capable of growing on macrophytes, even if it can also occupy other microhabitats.

Data analyses

Relative abundances, richness, Shannon-Wiener diversity, dominance and evenness were used to compare different aspects of the epiphytic diatom assemblages among the five macrophytes (Hammer et al. 2001, Magurran 2004). Significant differences in the median values of these indices were tested using Kruskal–Wallis analysis of variance followed by Mann–Whitney post-hoc tests (Zar 2010), the homogeneity of variances having previously been tested with a Levene’s test ($p > .01$).

Multidimensional Scaling (MDS) was used to summarize the multivariate data in a bidimensional ordination. The MDS plot was constructed based on Bray–Curtis similarities, which have proved to be adequate to deal with relative assemblage abundances (Birks 2012). An Analysis of Similarities (ANOSIM) was also performed on the data in order to test whether the diatom assemblage compositions varied significantly among the macrophyte groups (Birks 2012). ANOSIM was performed using Bray–Curtis as a distance measure. Finally, in order to identify which

diatom taxa were important in determining inter-group differences, a Similarity Percentage (SIMPER) analysis was performed. All the tests, analyses and graphs were performed using the software Past v. 3.11 (Hammer et al. 2001).

Results

Diatom assemblage composition

A total of 81 diatom species were identified in the 57 samples analyzed. Assemblages on the five macrophytes were dominated by epiphytic taxa, which constituted nearly 60–80% of the total diatom abundance. Small proportions of benthic and planktonic taxa were also recorded (Fig. 2; Table 2). Based on the examination of fresh material, dead valves belonged mainly to benthic taxa, and only to a lesser degree to epiphytic and planktonic species.

Assemblages inhabiting the free-floating taxa *A. filiculoides* and *R. natans* were clearly dominated by the epiphytic diatom *Lemnicola hungarica* (Grunow) Round & Basson, which accounted for up to 64% of the total diatom composition. The only exception was one sample of *A. filiculoides* collected during the winter, which almost lacked *L. hungarica* valves (<1%), and was dominated by *Cocconeis placentula* Ehrenberg (36%). The epiphytic species *C. placentula*, *Encyonema vulgare* Krammer and *Halamphora veneta* (Kützing) Levkov were sub-dominants within the *L. hungarica*-dominated assemblages. The benthic *Nitzschia amphibia* Grunow was the most abundant diatom among the non-epiphytic taxa in these samples (Fig. 3a, b).

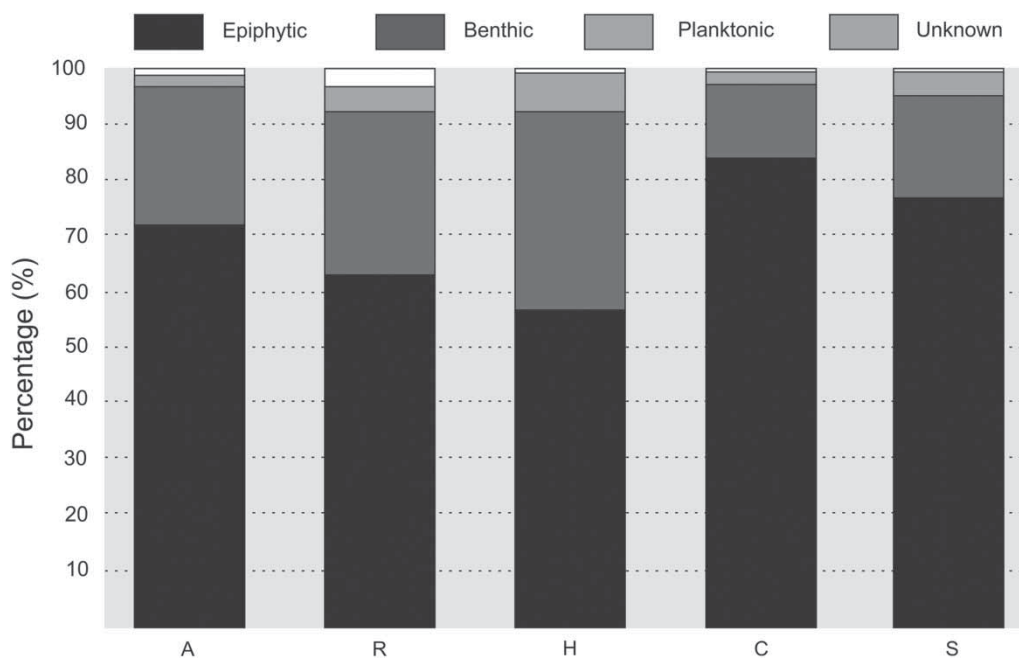


Fig. 2. Mean percentages of main diatom life forms found on the macrophytes *Azolla filiculoides* (A), *Ricciocarpus natans* (R), *Hydrocotyle ranunculoides* (H), *Ceratophyllum demersum* (C) and *Schoenoplectus californicus* (S).

Table 2. Complete list of diatom species, name codes and life forms.

Taxa	Code	LF
<i>Achnanthes exigua</i> Grunow	ACEX	B
<i>Adlafia bryophila</i> (Petersen) Moser, Lange-Bertalot & Metzeltin	ADBR	E
<i>Amphora copulate</i> (Kützing) Schoeman & Archibald	AMCO	E
<i>Amphora pediculus</i> (Kützing) Grunow	AMPE	B
<i>Anomoeoneis sphaerophora</i> Pfitzer	ANSP	B
<i>Aulacoseira granulata</i> (Ehrenberg) Simonsen	AUGR	P
<i>Aulacoseira granulata</i> var. <i>angustissima</i> (Müller) Simonsen	AGVA	P
<i>Bacillaria paxillifera</i> (Müller) Marsson	BAPA	B
<i>Biremis circumtexta</i> (Meister) Lange-Bertalot & Witkowski	BICI	ND
<i>Caloneis westii</i> (Smith) Hendey	CAWE	E
<i>Cocconeis placentula</i> Ehrenberg	COPL	E
<i>Craticula ambigua</i> (Ehrenberg) D.G. Mann	CRAM	P
<i>Ctenophora pulchella</i> (Ralfs) Williams & Round	CTPU	B
<i>Cyclotella meneghiniana</i> Kützing	CYME	B
<i>Diploneis puella</i> (Schumann) Cleve	DIPU	B
<i>Encyonema vulgare</i> Krammer	ENVU	E
<i>Entomoneis alata</i> (Ehrenberg) Ehrenberg	ENAL	B
<i>Eolimna muraloides</i> (Hustedt) Lange-Bertalot & Kulikovskiy	EOMU	ND
<i>Epithemia adnata</i> (Kützing) Brébisson	EPAD	E
<i>Epithemia sorex</i> Kützing	EPSO	E
<i>Eunotia exigua</i> (Brébisson) Rabenhorst	EUEX	B
<i>Eunotia</i> sp.	EUSP	ND
<i>Fallacia meridionalis</i> Metzeltin, Lange-Bertalot & García-Rodríguez	FAME	ND
<i>Fallacia pygmaea</i> (Kützing) Stickle & Mann	FAPY	B
<i>Fragilaria acus</i> (Kützing) Lange-Bertalot	FRAC	E
<i>Fragilaria brevistriata</i> Grunow	FRBR	B
<i>Fragilaria capucina</i> Desmazières	FRCA	E
<i>Fragilaria</i> sp.	FRSP	ND
<i>Gomphonema angustatum</i> (Kützing) Rabenhorst	GOAN	E
<i>Gomphonema laticollum</i> Reichardt	GOLA	ND
<i>Gomphonema parvulum</i> Kützing	GOPA	E
<i>Gomphonema pseudoaugur</i> Lange-Bertalot	GOPS	E
<i>Gomphonema truncatum</i> Ehrenberg	GOTR	A
<i>Gyrosigma acuminatum</i> (Kützing) Rabenhorst	GYAC	B
<i>Gyrosigma nodiferum</i> (Grunow) Reimer	GYNO	ND
<i>Halamphora veneta</i> (Kützing) Levkov	HAVE	E
<i>Hippodonta hungarica</i> (Grunow) Lange-Bertalot, Metzeltin & Witkowski	HIHU	B
<i>Lemnicola hungarica</i> (Grunow) Round & Basson	LEHU	E
<i>Mastogloia elliptica</i> (Agardh) Cleve	MAEL	B
<i>Navicula brasiliana</i> var. <i>platensis</i> Frenguelli	NABR	ND
<i>Navicula cincta</i> (Ehrenberg) Ralfs	NACI	B
<i>Navicula veneta</i> Kützing	NACR	E
<i>Navicula peregrina</i> (Ehrenberg) Kützing	NAPE	B
<i>Navicula recens</i> (Lange-Bertalot) Lange-Bertalot	NARE	B
<i>Navicula riediana</i> Lange-Bertalot & Rumrich	NARI	B
<i>Nitzschia subacicularis</i> Hustedt	NISU	E
<i>Nitzschia acicularis</i> (Kützing) W. Smith	NIAC	B
<i>Nitzschia amphibia</i> Grunow	NIAM	B
<i>Nitzschia clausii</i> Hantzsch	NICL	B
<i>Nitzschia communis</i> Rabenhorst	NICO	E
<i>Nitzschia filiformis</i> (W. Smith) Hustedt	NIFI	E
<i>Nitzschia filiformis</i> var. <i>conferta</i> (Richt) Lange-Bertalot	NFVC	E
<i>Nitzschia frustulum</i> (Kützing) Grunow	NIFR	E
<i>Nitzschia graciliformis</i> Lange-Bertalot & Simonsen	NIGR	ND
<i>Nitzschia inconspicua</i> Grunow	NIIN	E
<i>Nitzschia microcephala</i> Grunow	NIMI	B
<i>Nitzschia palea</i> (Kützing) W.Smith	NIPA	B
<i>Nitzschia reversa</i> W. Smith	NIRE	ND
<i>Nitzschia sigma</i> (Kützing) W. Smith	NISI	B
<i>Nitzschia</i> spp.	NISP	E

(Continued).

Table 2. Continued.

Taxa	Code	LF
<i>Nitzschia tryblionella</i> Hantzsch	NITR	E
<i>Nitzschia rostellata</i> Hustedt	NIRO	ND
<i>Pinnularia tabellaria</i> Ehrenberg	PITA	ND
<i>Placoneis abundans</i> Metzeltin, Lange-Bertalot & García-Rodríguez	PLAB	B
<i>Planothidium delicatulum</i> (Kützing) Round & Bukhtiyarova	PLDE	E
<i>Planothidium lanceolatum</i> (Brébisson) Lange-Bertalot	PLLA	E
<i>Pseudostaurosira americana</i> E.A. Morales	PSSU	B
<i>Rhoicosphenia abbreviata</i> (Agardh) Lange-Bertalot	RHAB	E
<i>Rhopalodia constricta</i> (W. Smith) Krammer	RHCO	ND
<i>Rhopalodia gibba</i> (Ehrenberg) Müller	RHGI	E
<i>Rhopalodia musculus</i> (Kützing) Müller	RHMU	E
<i>Staurosira brevistriata</i> (Grunow) Grunow	STBR	ND
<i>Staurosira longirostris</i> (Frenguelli) Metzeltin, Lange-Bertalot & García-Rodríguez	STLO	ND
<i>Stephanodiscus</i> sp.	STSP	ND
<i>Stephanodiscus vestibulis</i> Håkansson, Theriot & Stoermer	STVE	P
<i>Surirella rorata</i> Frenguelli	SURO	P
<i>Surirella striatula</i> Turpin	SUST	B
<i>Tabularia fasciculata</i> (Agardh) Williams & Round	TATA	E
<i>Tryblionella angustata</i> W. Smith	TRAN	B
<i>Tryblionella debilis</i> Arnott	TRDE	B
<i>Tryblionella hungarica</i> (Grunow) Frenguelli	TRHU	B
<i>Tryblionella kuetzingii</i> Álvarez-Blanco & Blanco	TRKU	B
<i>Tryblionella kuetzingii</i> Álvarez-Blanco & Blanco	TRKU	ND
<i>Tryblionella compressa</i> (Bailey) Poulin	TRCO	ND
<i>Ulnaria ulna</i> (Nitzsch) Compère	ULUL	E

Note: B: benthic; P: planktonic, A: aerophilous, E: epiphytic, ND: no data available.

The epiphytic *C. placentula* dominated the assemblages found on *H. ranunculoides* (Fig. 3c), *C. demersum* (Fig. 3d), and *S. californicus* (Fig. 3e). Abundances of *C. placentula* ranged between 20% and 85% on *C. demersum*. Samples from *H. ranunculoides* were more variable, showing assemblages clearly dominated by *C. placentula* (20–85%) and others in which it was co-dominant with the epiphytic *L. hungarica* and *Gomphonema* Ehrenberg spp., as well as the planktonic taxon *Aulacoseira granulata* var. *angustissima* (Müller) Simonsen. Together *N. amphibia*, the latter was among the most ubiquitous non-epiphytic taxon found in the assemblages on these macrophytes (Fig. 3c–e).

Richness and diversity indices

Overall, the species richness and diversity of Nahuel Rucá epiphytic diatom assemblages differed significantly among the macrophytes. Richness was higher on floating macrophytes (particularly *R. natans*) than on emergent species. The lowest richness was exhibited by *C. demersum*, while *H. ranunculoides* showed very variable values (Fig. 4a). Floating macrophytes (*A. filiculoides* and *R. natans*) were also characterized by significantly higher Shannon diversity values when compared to emergent and submersed taxa (*S. californicus* and *C. demersum*, respectively), while assemblages on *H. ranunculoides* were variable and did not differ from any other macrophyte taxa (Fig. 4b). Similar

patterns were shown by evenness and dominance indices, as assemblages on floating macrophytes were characterized by a significantly higher evenness and lower dominance than submersed and emergent taxa, whereas *H. ranunculoides* showed intermediate and variable values (Fig. 4c, d).

Multivariate ordination

The MDS analysis allowed the relative abundances of the epiphytic diatom assemblages from the macrophytes to be plotted in a two-dimensional space (Fig. 5). A small stress value (0.1531) was obtained when the Bray–Curtis distances were mapped, indicating that the data could be well represented in a two-dimensional space, and therefore no additional dimensions were needed.

The MDS ordination plot confirmed the considerable differences in the composition of assemblages between free-floating (*A. filiculoides* and *R. natans*) and emergent and submersed (*S. californicus* and *C. demersum*) macrophytes. Except for a single winter sample, all assemblages from free-floating macrophytes were ordered together on the left-hand side of the diagram, indicating similar epiphytic diatom assemblages. On the other hand, samples from *S. californicus* and *C. demersum* were closely grouped on the right-hand side of the diagram, and no evident seasonal changes were observed. Samples from *H. ranunculoides* showed a higher dispersion in their

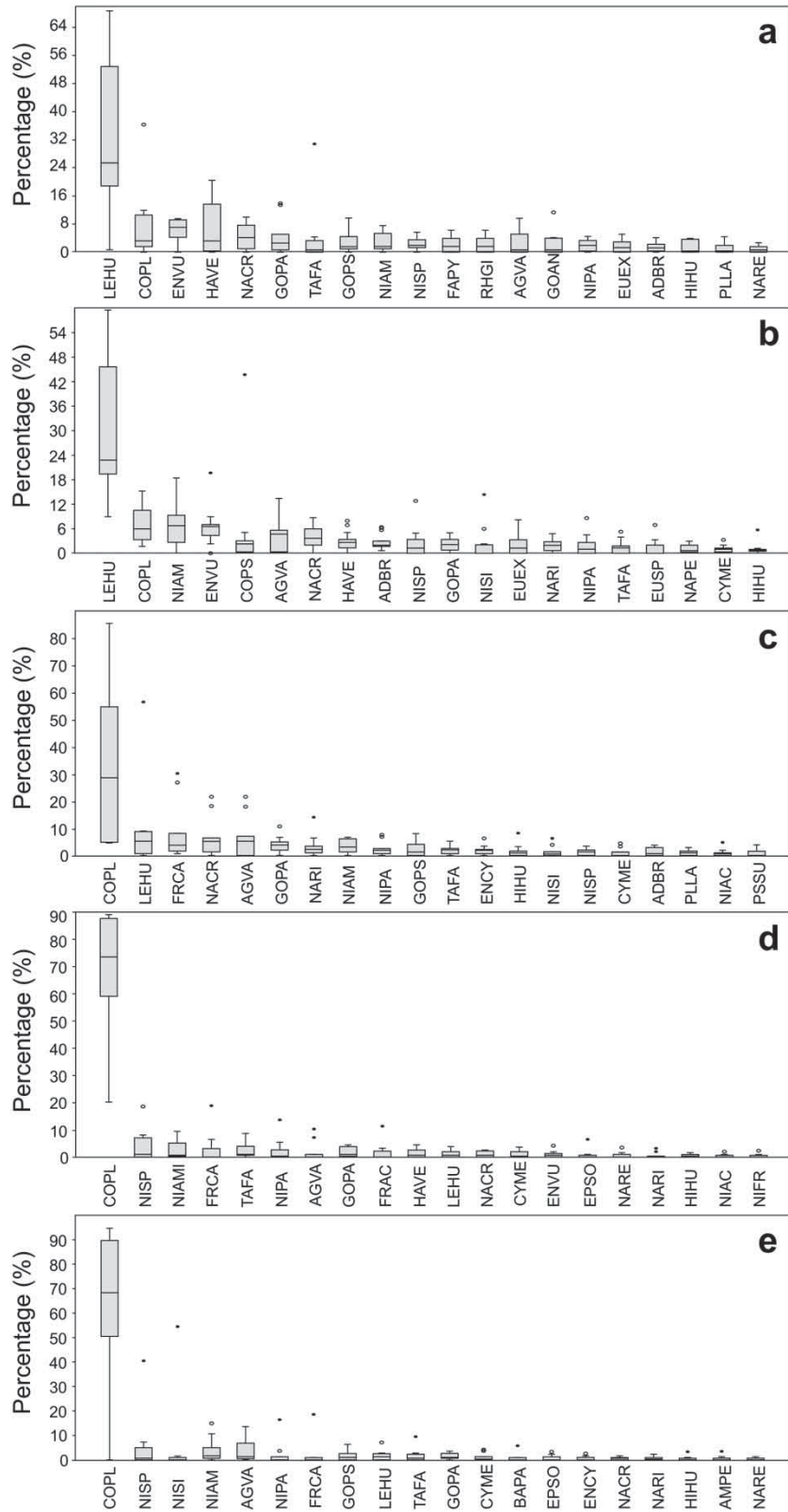


Fig. 3. Relative frequencies of the 20 dominant* diatom taxa on (a) *Azolla filiculoides*, (b) *Ricciocarpus natans*, (c) *Hydrocotyle ranunculoides*, (d) *Ceratophyllum demersum* and (e) *Schoenoplectus californicus*. Codes for diatom names are provided in Table 2. *Taxa with the 20 highest average relative abundances on each macrophyte.

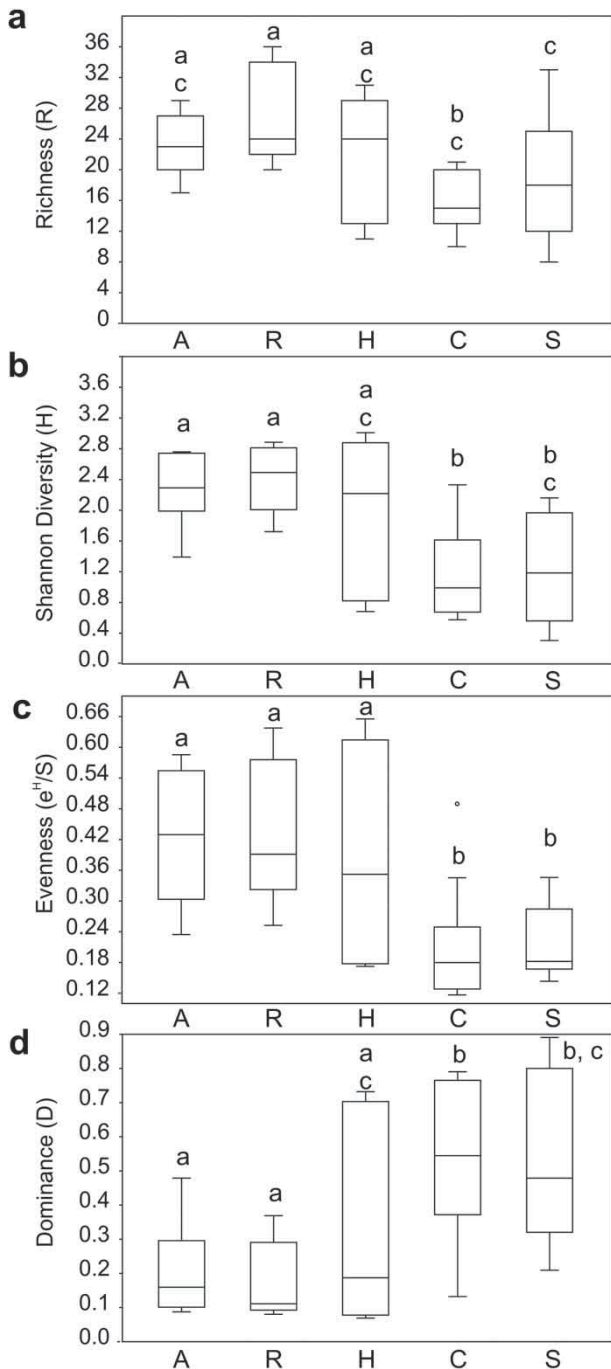


Fig. 4. Boxplots of (a) richness, (b) Shannon-Wiener, (c) evenness and (d) dominance indices comparing diatom assemblages from *Azolla filiculoides* (A), *Ricciocarpus natans* (R), *Hydrocotyle ranunculoides* (H), *Ceratophyllum demersum* (C) and *Schoenoplectus californicus* (S). Identical letters indicate no statistically significant differences at $p = .05$

distribution, and were located in the centre of the diagram, but showed partial overlap with both other groups of macrophytes (Fig. 5). This higher dispersion reflected the compositional variability in the epiphytic diatom assemblages on this macrophyte, which seemed to be partially

related to seasonality. Samples collected in summer were ordered close to the other free-floating macrophytes, while the rest of the samples were mainly grouped with the samples from emergent and submersed macrophytes.

The ANOSIM tests allowed the significance of the differences observed in the MDS plot to be assessed. The results indicated the presence of three groups: Group 1 was composed of *H. ranunculoides* samples, which significantly differed from the rest of the macrophytes ($p < .005$); Group 2 clustered the free-floating samples (*A. filiculoides* and *R. natans*), which differed significantly from Group 3, formed of *C. demersum* and *S. californicus* samples ($p < .0001$). According to the SIMPER analysis, the differences among these groups of samples were related to differences in the degree of dominance of *L. hungarica* and *C. placentula*, rather than to differences in the overall taxonomic composition of the assemblages. The group formed by *A. filiculoides* and *R. natans* (Group 2) showed an average dissimilarity of 69.3% with Group 1 (*H. ranunculoides*), *L. hungarica* and *C. placentula* contributing 20.7% and 20.2% to this difference, respectively. The average dissimilarity between Groups 2 and 3 was 81.3%, mainly from *C. placentula* (37.1%) and *L. hungarica* (18.8%). Finally, the observed dissimilarity between Groups 1 and 3 was 62.1%, to which *C. placentula* contributed a 37.1%, followed by *L. hungarica* (6.9%) and *Fragilaria capucina* Desmazières (6.8%).

Discussion

Data obtained from the analysis of epiphytic biofilms from five aquatic macrophyte taxa in Nahuel Rucá Lake allowed the description of abundant and diverse epiphytic diatom assemblages. Overall, these assemblages were dominated by epiphytic taxa throughout the sampling period, contributing between 70% and 88% total diatom composition. Minor proportions of non-epiphytic species were also present. These could represent reworked valves of allochthonous origin trapped in the epiphytic biofilms, as suggested by the presence of dead valves of non-epiphytic benthic diatoms. Several studies on Pampean shallow lakes reported the presence of planktonic, tychoplanktonic and benthic diatom valves in epiphytic assemblages, related to the strong interactions between water, sediments, and epiphytic habitats that characterize shallow lakes (e.g., Claps 1991, Tesolín & Tell 1996, Bauer et al. 2007, Rodríguez et al. 2011). Sediments in these lakes are subjected to frequent resuspension and mixing by wind and bioturbation, and can easily be trapped, both by macrophyte tissues and the mucilaginous matrix secreted by epiphytic algae (Tiffany & Lange 2002, Rodríguez et al. 2011, Al-Handal et al. 2014, Emson 2015). In particular, the high frequencies of the chain-forming planktonic diatom, *A. granulata* var. *angustissima*, can be attributed to the high abundances reached by this taxon during the summer. Its filamentous morphology favours its retention in epiphytic biofilms,

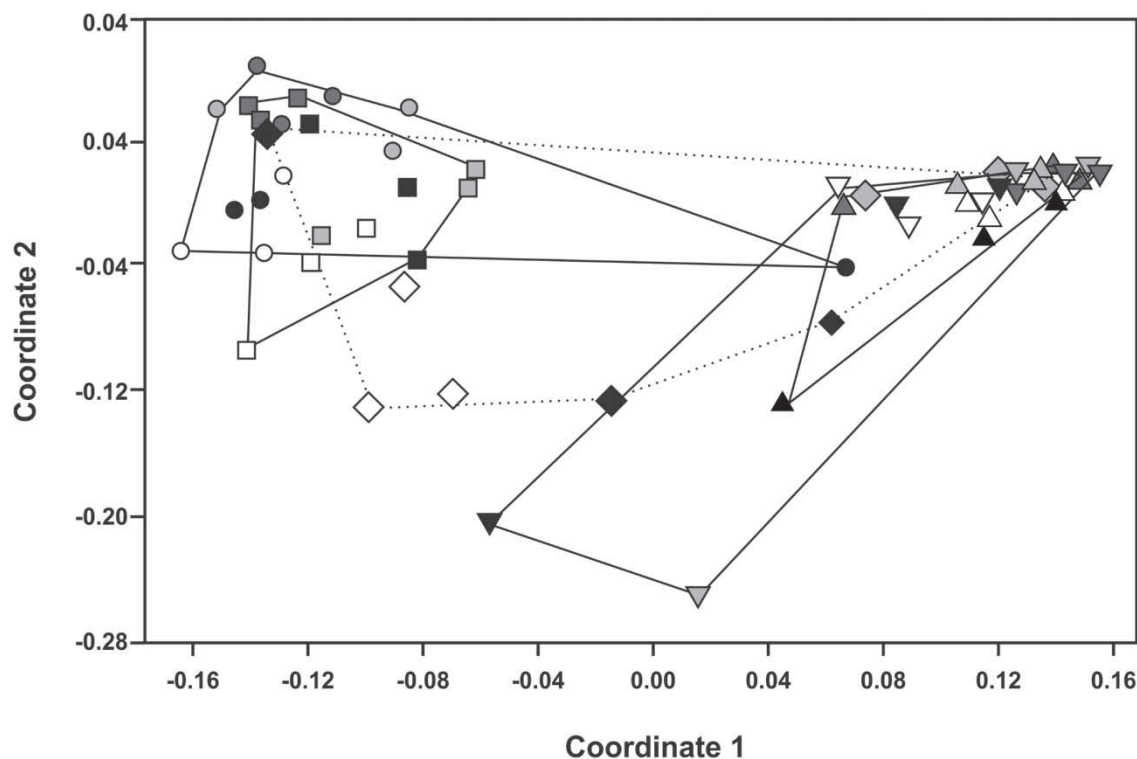


Fig. 5. First two axes of a multidimensional scaling (MDS) analysis based on Bray–Curtis similarities of samples from *Azolla filiculoides* (circles), *Riccioarpus natans* (squares), *Hydrocotyle ranunculoides* (triangles), *Ceratophyllum demersum* (triangles) and *Schoenoplectus californicus* (inverted triangles). Identical colours indicate the same season: winter (black), autumn (dark grey), spring (light grey) and summer (white).

leading to its frequent presence as an allochthonous component of that assemblage in Pampean shallow lakes (e.g., Bauer et al. 2007, Tesolín & Tell 1996).

The composition and diversity of the epiphytic diatom assemblages was directly related to the life form of the macrophytes, with assemblages inhabiting free-floating plants (*A. filiculoides* and *R. natans*) being significantly different from those living on emergent (*S. californicus*) and submersed (*C. demersum*) taxa. Several studies have demonstrated the occurrence of host-specificity in the diversity and specific composition of epiphytic diatom assemblages living on macrophytes (e.g., Buczkó 2007, Messyasz et al. 2009, Desinati 2012, Emson 2015, Letáková et al. 2016), although the nature of this association is not fully understood (Emson 2015). Experimental results have suggested that this relationship is physical rather than chemical, being mainly driven by the area, microstructure and complexity of the macrophyte surface, as well as by variation in light intensity between the two sides of the leaves (Cattaneo 1978, Harper & Garbary 1994, Al-Handal et al. 2014, Emson 2015). The epiphyton on emergent and submersed macrophytes probably receives light from almost all directions, while the attached assemblages on *A. filiculoides* and *R. natans* are subjected to shading by their own thalli or leaves, and by the surrounding floating mats, making light a more important limiting resource for epiphytic taxa on these macrophytes. On the other hand, water level exerts a stronger influence

on the assemblage attached to rooted macrophytes such as rushes, given the fixed life form of these plants (Rodríguez et al. 2011).

Compositional dissimilarities between the different macrophyte groups were related to differences in the proportional abundances of the two dominant diatom taxa, *L. hungarica* and *C. placentula*, rather than to differences in the overall taxonomic composition of assemblages. Free-floating macrophytes were dominated by *L. hungarica*, a common, widespread diatom. It is typically found living attached to the roots of free-floating macrophytes, particularly of the Lemnaceae (Buczkó 2007). In a global study of 131 macrophyte samples from 63 sites covering North and South America, Europe, Southern Africa, Australia and Asia, *L. hungarica* clearly showed a strong affinity for free-floating plants and particularly for *Lemna minor* Linnaeus (Emson 2015). These observations agree with previous studies (Goldsborough 1993, Buczkó 2007) where *L. hungarica* was shown to dominate diatom assemblages of *L. minor*, while also being abundant on other duckweeds, such as *Lemna gibba* Linnaeus, *Spirodela polyrhiza* Linnaeus and *Wolffia arrhiza* (Linnaeus) Horkel ex Wimmer (Buczkó 2007). *Lemnicola hungarica* was always present on *L. minor*, *S. polyrhiza* and *Wolffia* sp. in a survey of 11 lakes from Oklahoma, although it was outnumbered by *C. placentula* in many samples (Desinati 2012). The affinity of *L. hungarica* for free-floating macrophytes was related to the physical protection offered by the floating

mat, reduced herbivory and an increase in nutrient availability, as the resulting anaerobiosis immediately below the mat can lead to the accumulation of reduced nutrient compounds (Goldsborough 1993). It has been suggested that, in order to adapt to the sub-optimal environment of a thick floating mat, diatoms must employ facultative or obligate heterotrophy (Goldsborough 1993, Emson 2015). Such adaptations have often been cited to explain the consistent abundance and dominance of *L. hungarica* in thick mats of duckweed, particularly in summer when light and nutrient conditions are least conducive to autotrophic productivity (Emson 2015).

Rooted and submersed macrophytes from Nahuel Rucá Lake were dominated by *C. placentula*, one of the most common cosmopolitan epiphytic diatoms in freshwater habitats (Jahn et al. 2009). These assemblages were characterized by low diatom diversity when compared to free-floating plants. *Cocconeis placentula* is considered a pioneer species with a widespread distribution on different macrophytes (e.g., Cattaneo 1978, Blindow 1987, Buczkó 2007, Emson 2015), as well as on stones and artificial substrata (Müller 1999). It often occurs in massive numbers across a broad ecological spectrum, growing from weakly acidic to alkaline pHs and tolerating high electrolyte concentrations (Müller 1999). It displays an opportunistic strategy, showing increases in abundance in the presence of intensive grazing by snails (Jones et al. 2000). High percentages of *C. placentula* in assemblages of low diversity and richness have been associated with high grazing pressure by snails and other invertebrates (Blindow 1987, Underwood & Thomas 1990, Underwood et al. 1992). Herbivory tends to be higher on submersed and emergent macrophytes than under the mats of free-floating plants, as this hypoxic environment tends to be less preferred by grazers (Goldsborough 1993, Meerhoff et al. 2003). Controlled experiments evidenced a low preference of grazers for *C. placentula*, most probably as a consequence of its adnate life form and strong attachment to the substrata (Underwood & Thomas 1990). This resistance to high grazing pressure, together with its wide environmental tolerance and opportunistic strategy, explains the low evenness and diversity exhibited by most samples from emergent and submersed plants containing *C. placentula*, as well as its ubiquity and predominance in death assemblages of Pampean shallow lakes (e.g., Hassan et al. 2009, Hassan 2015). Its high abundance can be related to the presence of dense populations of emergent and submersed macrophytes, although it seems to be outcompeted by *L. hungarica* in the physically stressful habitat provided by *A. filiculoides* and *R. natans*.

Epiphytic diatom assemblages from *H. ranunculoides* showed higher variability in composition and diversity than the other macrophytes studied. While some samples were clearly dominated by *C. placentula* (12–85%), others exhibited unusually high abundances of *L. hungarica* (8–25%), particularly during summer. This discrepancy

in assemblage composition in different samples from the same macrophyte can be partially attributed to seasonal variability. Litoral environments in Nahuel Rucá are characterized by a higher concentration of organic matter in the warmest seasons, and are more productive during the summer (Cristini et al. 2017). *Lemnicola hungarica* is a hypereutrophic diatom with a high affinity for nutrient-rich waters (Desinati 2012), which may explain its higher abundance during the warmest seasons. The high percentage of *L. hungarica* in a single winter sample can be attributed to contamination during sampling. Similar relatively high abundances of *L. hungarica* have been reported on samples of the attached-floating macrophyte *Hydrocharis morsus-ranae* Linnaeus and the submersed species *C. demersum* (Emson 2015). These samples were assumed to have been contaminated during sampling, as they were collected in the proximity of free-floating mats of macrophytes containing abundant *L. hungarica*.

The strong association of the epiphytic *L. hungarica* with free-floating macrophytes, together with the high dominance of *C. placentula* on emergent and submersed plants provides a potential method for inferring past fluctuations in aquatic vegetation coverage in the palaeolimnological record of Pampean shallow lakes. Previous studies demonstrated that the presence of *L. hungarica* can be utilized to track *Lemna* abundance shifts in surface sediment samples collected from duckweed-dominated and non-duckweed sites, as well as to infer known periods of *Lemna* dominance from the fossil record (Emson 2015). Although further work on how well sedimentary death assemblages represent epiphytic diatom assemblages is needed, previous work showing the presence of both *L. hungarica* and *C. placentula* in surface sediments of Nahuel Rucá Lake demonstrates that epiphytic diatoms are an important component of sedimentary assemblages in this lake (Hassan et al. 2011, 2014, Hassan 2015). Moreover, both taxa are represented in the Holocene record of the lake, with low proportions of *L. hungarica* registered in the top-most 20 cm (ca. 200 years BP), while *C. placentula* has been recorded over the last ca. 3700 years BP (Hassan et al. 2014). Thus, Nahuel Rucá Lake offers the opportunity of elucidating the dynamics of epiphytic diatom incorporation into the sedimentary record, and of assessing the impact of taphonomic factors on the contribution of diatoms from different microhabitats to the sediment record in shallow lakes.

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