

INCORPORATING TAPHONOMY INTO COMMUNITY-BASED PALEOENVIRONMENTAL RECONSTRUCTIONS: CAN DIATOM PRESERVATION DISCRIMINATE AMONG SHALLOW LAKE SUB-ENVIRONMENTS?

GABRIELA S. HASSAN, LUCIANA A. ROJAS, AND CLAUDIO G. DE FRANCESCO

*Instituto de Investigaciones Marinas y Costeras (IIMyC), CONICET-Universidad Nacional de Mar del Plata, Facultad de Ciencias Exactas y Naturales, Juan B. Justo 2550, Mar del Plata, Argentina
email: ghassan@mdp.edu.ar*

ABSTRACT: The value of taphonomic signatures as a source of paleoenvironmental information has been recognized at local and regional environmental scales. In environmentally heterogeneous shallow lakes, the habitat complexity provides an opportunity to evaluate the potential use of taphonomy to uncover environmental differences among within-lake sub-environments. In this contribution, the composition and preservation of diatom assemblages from five sub-environments (free-floating and attached macrophytes, water column, open waters, and littoral sediments) were analyzed in a Pampean shallow lake (Nahuel Rucá, Argentina). Sub-environments differed in depth, macrophyte coverage, and water composition, being these differences reflected both by the composition and preservation of diatom assemblages. Diversity, fragmentation, and dissolution were higher in planktonic and open-waters sedimentary assemblages, whereas fragmentation dominated in littoral sediments. Epiphytic assemblages were the least diverse and showed the best preservation. Compositional and taphonomic indices were significantly correlated, suggesting common environmental controls on the species composition and preservation at local scales. The joint analysis of compositional and taphonomic variations in the recent sedimentary record of Nahuel Rucá demonstrated the usefulness of taphonomic analyses to uncover subtle paleoenvironmental variations, which could be overlooked if only traditional compositional analyses are performed. We concluded that both taphonomic analyses and a holistic consideration of ecologically meaningful taxa should be considered in order to improve paleoenvironmental reconstructions in environmentally heterogeneous shallow lakes.

INTRODUCTION

Paleoenvironmental research focuses largely on the use of biological remains as proxies of past environmental conditions (Battarbee 2000). In doing so, paleoenvironments are usually inferred from the composition of fossil assemblages, whose environmental significance can be qualitatively or quantitatively addressed in modern settings (Smol 1992; Birks 1998). As such, the quality of paleoenvironmental reconstructions relies on an accurate assessment of the completeness of the fossil record, which is in its vast majority biased and dampened to some degree (Kidwell and Flessa 1995). Taphonomic processes can add or remove information during the decay of organisms, their incorporation into death assemblages, burial, and early diagenesis during fossilization (Behrensmeier et al. 2000). During the last decades, paleoenvironmental research has grown increasingly aware of the problems and potentialities of taphonomic biases, and a number of articles signaling the impact of preservation on past environmental inferences have been published for several biological indicators (e.g., Mitchell et al. 2008; Ryves et al. 2009; Jackson 2012; De Francesco et al. 2013; Hassan et al. 2014).

Although traditionally defined as the study of postmortem information loss, our present view of taphonomy emphasizes not only the biases, but also the positive contributions of preservational processes and the biologically meaningful information that is contained in time-averaged, ecologically mixed assemblages (Behrensmeier and Kidwell 1985). Among these, taphofacies analysis (i.e., facies defined on the basis of diagnostic taphonomic traits; Speyer and Brett 1986) has been a major

focus for working on the postmortem sedimentology and biology of death remains (Behrensmeier et al. 2000). These studies underscore the non-random relationship between taphonomic signatures (i.e., the summary description derived from the full suite of taphonomic attributes) and environmental conditions in modern settings, highlighting the feasibility of reconstructing paleoenvironments from taphonomic analyses (Parsons and Brett 1991). Accordingly, contemporary taphofacies studies have focused both in understanding how individual taphonomic processes alter dead remains, and the scales at which unique taphonomic signatures can be recognized (Staff and Powell 1990). Overall, these positive contributions of taphofacies analyses have emphasized the relevance of analyzing taphonomic signatures as a working tool for complementing compositionally based paleoenvironmental research both in marine (e.g., Tomašových and Zuschin 2009 and references therein) and continental settings (e.g., Tietze and De Francesco 2017 and references therein).

The scale of analysis of taphonomic signatures is highly variable, as variability in death-assemblage structure and preservation is usually observed at different spatial scales, varying from local changes over centimeters to regional variation over kilometers or more (Staff and Powell 1990). At local scales, variability can be promoted by subtle gradients in environmental or sedimentological parameters, but also by taphonomic factors acting during and after deposition (e.g., Earle et al. 1988; Charles et al. 1991; Link et al. 1994; Adler and Hübener 2007). The interaction between these factors can produce large within-habitat variability that can even obscure regional tendencies if it is overlooked (Hassan 2015a). This local variability can be significant in shallow lakes, in which the extensive

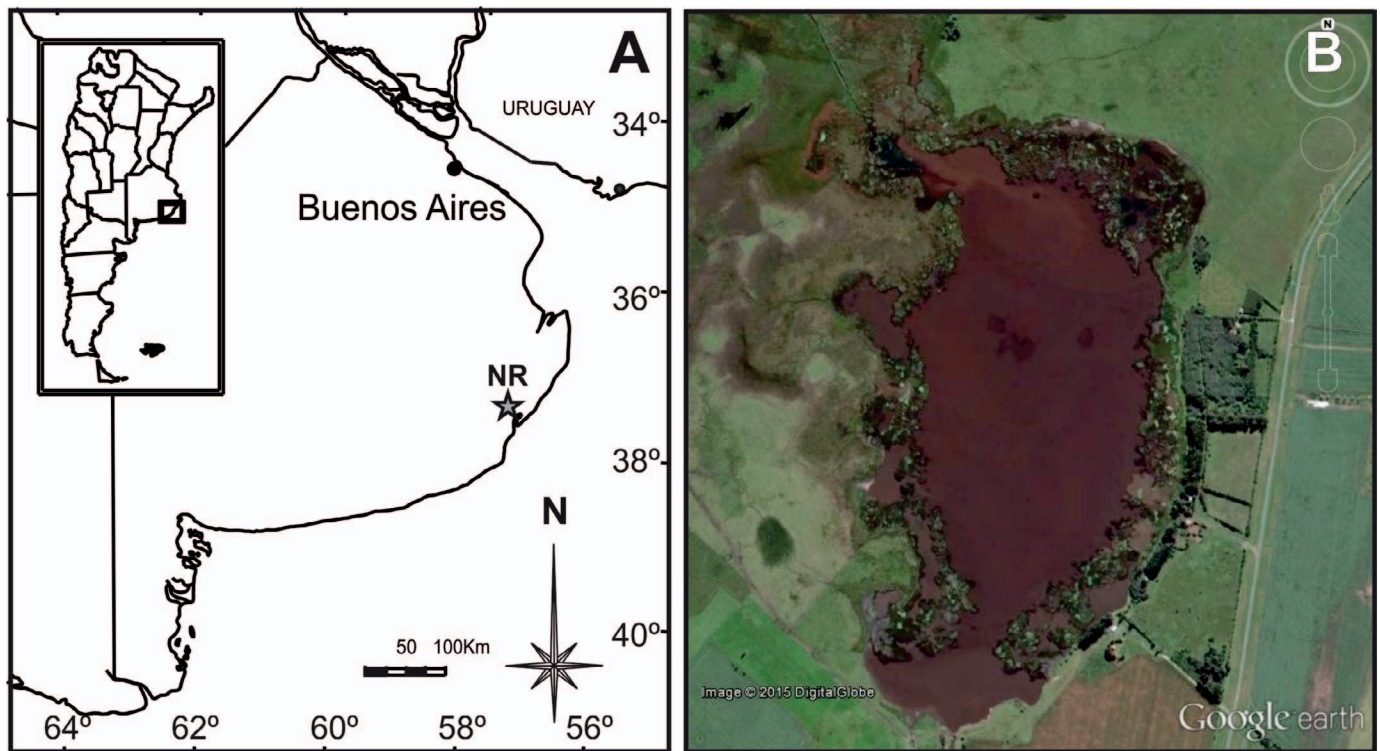


FIG. 1.—Map of the study area. **A**) Location of Nahuel Rucá Lake in the Buenos Aires province (Argentina). **B**) Satellite image of the lake.

development of the littoral zone relative to the pelagic zone provides a wide suite of available microhabitats that promote the growth of diverse and productive periphytic and benthic communities (Wetzel 2001). The development of pelagic communities can also be promoted in these lakes, as the occurrence of intermittent mixing events allows the resuspension of planktonic taxa, preventing their sinking (Bennion et al. 2010). Given their environmental variability, it is highly probable for these within-lake compartments to pose differential environmental constraints for death-assemblage preservation, which could imprint distinctive taphonomic signatures on their respective biological remains. Besides its paleoenvironmental potential, the study of within-lake taphonomic signatures has been largely overlooked in shallow lake taphonomic research, which is scarce and mainly focused on regional gradients (e.g., Ryves et al. 2006; Tietze and De Francesco 2017).

Diatoms (Bacillariophyceae) are one of the most ubiquitous biological indicators used to assess paleoenvironmental changes in shallow lakes. They occupy a variety of habitats within these lakes, developing distinctive and stable populations in pelagic, epiphytic, and benthic habitats (Bennion et al. 2010). Besides compositional differences, this environmental variability often results in variable diatom valve preservation, which may be conditional upon their life form; for example, floating remains (such as plankton) may tend to be easily reworked and distributed through the lakes sub-environments, whereas epiphytic and benthic taxa may more easily sink and become incorporated into the sediments near their source areas (De Nicola 1986; Frey 1988; Heggen et al. 2012; Hassan 2015b). Moreover, as diatom dissolution and breakage are strongly dependent on the chemical and physical properties of the environment (e.g., Haberyan 1985; Ryves et al. 2013), differential preservation among within-lake sub-environments could lead to distinctive taphonomic signatures of potential paleoenvironmental application. Thus, recognizing within-lake taphofacies can be a useful tool for identifying subtle environmental differences from fossil diatoms in shallow lakes. Whether diatom assemblages are useful to

discriminate between within-lake taphofacies is still unknown, as is the potential applicability of local variability in compositional and taphonomic data for the identification of past sub-environments.

In the present contribution, the composition and preservation of epiphytic and planktonic diatom assemblages were analyzed and compared with surface-sediment and fossil remains in an environmentally heterogeneous shallow lake from the Argentinean Pampas. The taphonomic signature of diatom valves from each lake sub-environment was analyzed and their potential use as an indicator of past changes in lake dynamics was quantitatively evaluated and compared to assemblages species composition. The potential applicability of within-lake diatom taphofacies to the identification of past sub-environments was then evaluated through the comparison of contemporary and fossil (last ca. 700 cal. years BP) diatom assemblages, in order to provide actualistic tools for the comprehension of past shallow lake dynamics.

MATERIAL AND METHODS

Field and Laboratory methods

Study Area.—Sampling was conducted in Lake Nahuel Rucá ($37^{\circ}37'S$ - $57^{\circ}25'W$; Fig. 1), a very shallow (max. depth = 60–90 cm; Hassan 2015b) and small (245 ha) lake located in the southern Pampas of Argentina. This shallowness favors the interaction between sediments and the water column through wind-driven turbulence. The lake plant community is characterized by several species of emergent, floating and submersed macrophytes (Stutz et al. 2010). The dominant species is the emergent bulrush *Schoenoplectus californicus* (C.A. Mey.) Soják, which forms a complete ring around the lake (Fig. 1). Other emergent macrophytes that grow into the shallowest zones are *Zizaniopsis bonariensis* (Balansa and Poitr.) Speg., *Hydrocotyle bonariensis* Comm. ex Lam., *H. ranunculoides* L.f., *Alternanthera philoxeroides* (Mart.) Griseb., *Solanum glaucophyllum*

TABLE 1.—Summary of environmental characteristics of Nahuel Rucá (modified after Hassan 2015b). Values are mean \pm SD; minimum and maximum values are given in parentheses. *Only one measurement available.

Conductivity (mS/cm)	0.8 \pm 0.5 (0.3–1.6)
Salinity (ppt)	0.4 \pm 0.2 (0.1–0.8)
pH	8.1 \pm 0.3 (7.4–8.5)
Dissolved oxygen (ppm)	7.5 \pm 2.7 (2.1–10.8)
Temperature ($^{\circ}$ C)	16.3 \pm 7.3 (7.2–25.5)
CO ₃ ²⁻ (mg L ⁻¹)	–
HCO ₃ ⁻ (mg L ⁻¹)	529.0 \pm 230 (303–849)
Cl ⁻ (mg L ⁻¹)	144.0 \pm 82 (91–266)
Hardness (mg L ⁻¹ of CaCO ₃)	250.0 \pm 127 (173–438)
Ca ²⁺ (mg L ⁻¹)	30.7 \pm 16.5 (18.1–53.2)
Mg ²⁺ (mg L ⁻¹)	41.7 \pm 29.7 (18.8–85.4)
SO ₄ ²⁻ (mg L ⁻¹)	108.9 \pm 61.5 (27.4–169)
SiO ₂ (mg L ⁻¹)	17.7 \pm 1.3 (16.8–18.6)
PO ₄ ³⁻ (mg L ⁻¹)	161.3 \pm 88.7 (98.6–224.0)
NO ₃ ⁻ (mg L ⁻¹)	67*
Depth (Open waters samples, cm)	78.7 \pm 8.8 (60–90)
Depth (Littoral samples, cm)	40.0 \pm 14 (15–65)
Secchi depth (cm)	16.7 \pm 9.6 (5–40)

Desf., *Bacopa monnieri* (L.) Wettst., *Polygonum punctatum* Elliott, *Ranunculus apiifolius* Pers., *Triglochin striata* Ruiz and Pav. and *Phyla canescens* (Kunth) Greene (Stutz et al. 2010). Near the shore, the floating species (i.e., duckweeds) *Ricciocarpus natans* (L.), *Azolla filiculoides* Lam., *Lemma valdiviana* Phil. and *Wolffiella lingulata* (Hegelm.) form a dense cover (Stutz et al. 2010). *Myriophyllum elatinoides* Gaudich. and *Ceratophyllum demersum* L. develop submersed both in the deep (open water) and littoral zones of the lake (Stutz et al. 2010).

When compared against other lakes worldwide, Pampean shallow lakes show limnological characteristics that depart from most of those located in temperate regions, such as having higher phosphorous, nitrogen, and chlorophyll-a concentrations and much lower transparency, and therefore they stand as upper extremes of the trophic-state gradient (Diovisalvi et al. 2015). This is the case of Nahuel Rucá, which exhibited very eutrophic, turbid, and alkaline conditions during the sampling period (Table 1). Its sediments are composed mainly by fine sands (30–60%) and mud (~40%; Cristini et al. 2017, fig. 3), with maximum organic matter contents ranging between 30 and 60% (Cristini et al. 2017). Overall, given its environmental characteristics, Nahuel Rucá exhibits the typical physical and chemical characteristics of Pampean shallow lakes, constituting a good model for the study of these environments. Moreover, the availability of previous works on environmental characteristics (Cristini et al. 2017) and diatom assemblages (Hassan 2015b; Rojas and Hassan 2017) from this lake demonstrate its environmental heterogeneity and variability in diatom composition, signaling its usefulness as natural laboratory for the study of within-lake taphofacies identification.

Field Methods.—The dataset was constructed to allow comparison among the three main sub-environments inhabited by diatoms in shallow lakes: sediments, water column, and dominant macrophytes. Sediment and water-column samples were collected between December 2009 and September 2010 as part of a previous study on live-dead agreement (Hassan 2015a). In order to cover temporal variability in community composition, sampling was carried out on a seasonal basis over a year. During each visit, 12 sediment samples were randomly collected with a 7-cm diameter piston core, from both littoral (six samples) and open-water (six samples) areas. The upper centimeter of each core was sliced in the field and preserved with alcohol 96%. Additionally, six 1 L samples of subsurface water were collected with a Van Dorn sampler in the same

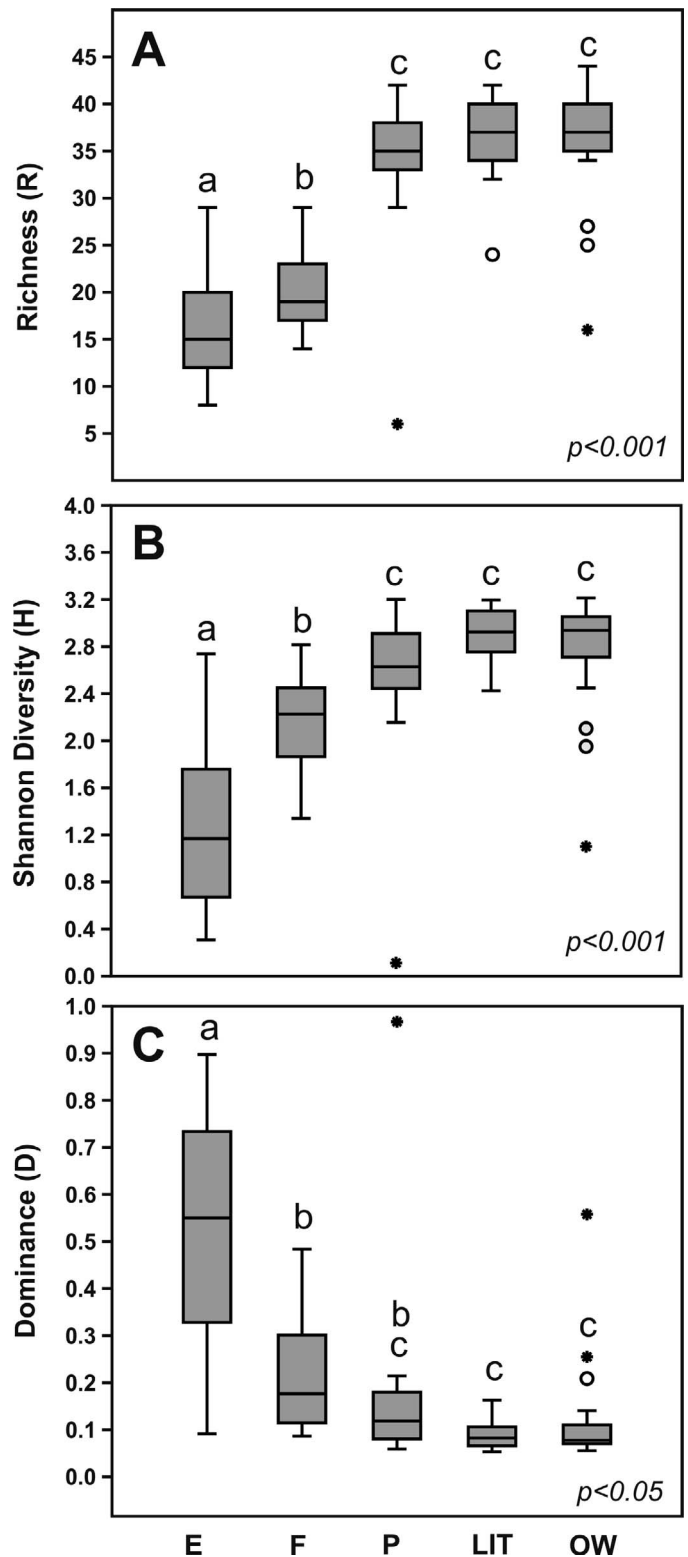


FIG. 2.—Boxplots showing the 25–75 percent quartiles (box), median (horizontal line), minimum and maximum values (error bars). A) Richness. B) Shannon Diversity. C) Dominance indices comparing diatom assemblages from emergent/submersed macrophytes (E), free-floating macrophytes (F), plankton (P), littoral sediments (LIT) and open waters sediments (OW) from Nahuel Rucá Lake. Same letters indicate no significant differences at the p-value listed in each plot, according to ANOVA tests.

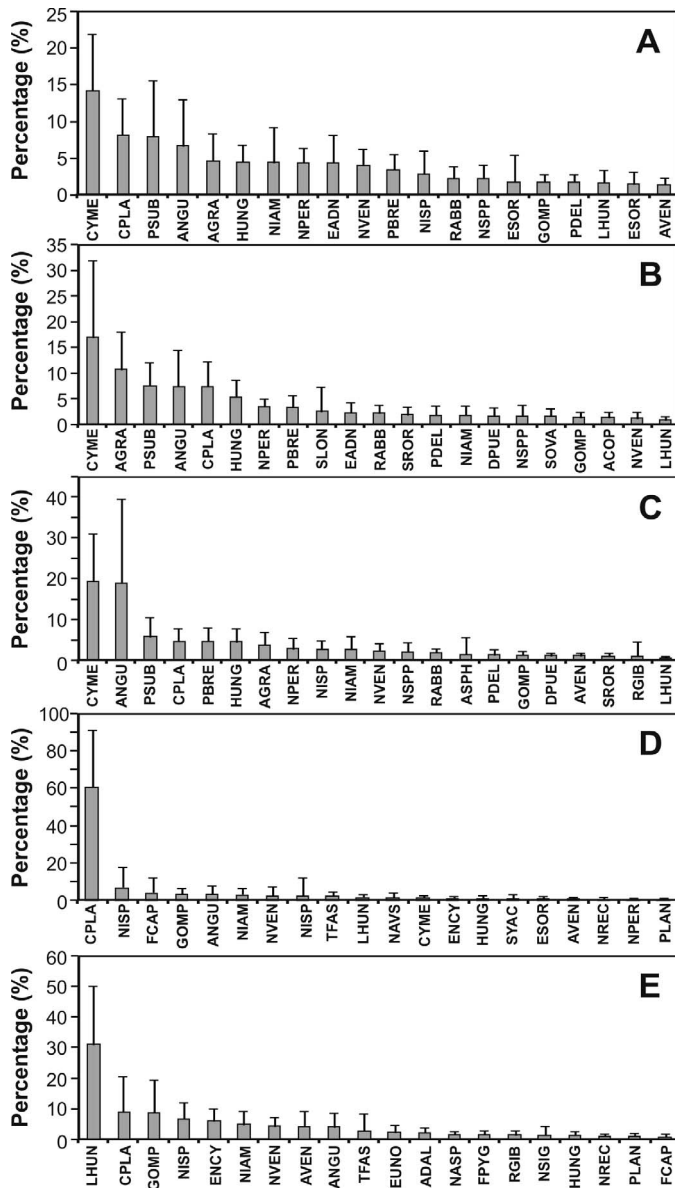


FIG. 3.—Relative abundances of the dominant* diatom taxa in samples. **A)** Open waters sediments. **B)** Littoral sediments. **C)** Plankton. **D)** Emergent/submersed macrophytes. **E)** Free-floating macrophytes. *Taxa showing the highest 20 average relative abundances in each sub-environment. Abbreviations: ACOP = *Amphora copulata*; ADAL = *Adlafia bryophila*; AGRA = *Aulacoseira granulata*; ANGU = *A. granulata* var. *angustissima*; ASPH = *Anomooneis sphaeropora*; AVEN = *Amphora veneta*; CPLA = *Cocconeis placentula*; CYME = *Cyclotella meneghiniana*; DPUE = *Diploneis puella*; EADN = *Epithemia adnata*; ENCY = *Encyonema* sp.; ESOR = *Epithemia sores*; EUNO = *Eunotia* sp.; FCAP = *Fragilaria capucina*; FPYG = *Fallacia pygmaea*; GOMP = *Gomphonema* spp.; HUNG = *Hippodonta hungarica*; LHUN = *Lemnicola hungarica*; NASP = *Navicula* spp.; NIAM = *Nitzschia amphibia*; NISP = *Nitzschia* sp.; NPERE = *Navicula peregrina*; NREC = *N. recens*; NSIG = *Nitzschia sigma*; NVEN = *Navicula veneta*; PBRE = *Pseudostaurastrum brevistriata*; PSUB = *P. americana*; PDEL = *Planolithidium delicatulum*; PLAN = *P. lanceolatum*; RABB = *Rhoicosphenia abbreviata*; RGIB = *Rhopalodia gibba*; SLON = *Staurastrum longirostris*; SOVA = *Surirella ovalis*; SROR = *S. rorata*; SYAC = *Synedra acus*; TFAS = *Tabularia fasciculata*.

sampling points where open waters sediments were sampled. Macrophytes, on the other hand, were sampled between August 2013 and September 2014 in order to complement this previous sampling (Rojas 2016; Rojas and Hassan 2017). Five macrophyte taxa were selected and sampled during the whole year in three sampling points from the littoral zone: *A. filiculoides*, *C. demersum*, *H. ranunculoides*, *R. natans*, and *S. californicus*. 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*). At each sampling point, pieces of *S. californicus* stems were removed using scissors, while whole specimens of the remaining macrophytes were collected by hand and stored in 96% alcohol. Overall, the final data set comprised a total of 129 samples (48 of surface sediments, 24 of water, and 57 of macrophytes) which covered both the temporal and spatial variability in diatom composition existing in the lake.

Laboratory Methods.—Water samples were centrifugated to allow floating diatoms to decant, and the supernatant was discarded before chemical processing. The resulting samples, as well as sediment and macrophyte samples, were oxidized with 30% hydrogen peroxide at 80°C until no further reaction was observed, washed several times with distilled water and stored. After complete homogenization, a subsample was transferred to a coverslip and air-dried, and permanent slides were made using Naphrax®. On each slide, at least 300 diatom valves were counted across random transects using a Leica DM500 light microscope (LM) at 1000× magnification. Taxa were identified to the lowest possible taxonomic category following Lange-Bertalot et al. (1996), Krammer and Lange-Bertalot (1997, 1999, 2004a, 2004b), Metzeltin and Lange-Bertalot (1998, 2007), Rumrich et al. (2000), Metzeltin et al. (2005), Levkov (2009), and Sar et al. (2009).

Preservation of the whole assemblages was evaluated under 1000× magnification using 300 diatom valves per sample. Two taphonomic variables: (1) degree of fragmentation and (2) dissolution (sensu Ryves et al. 2009) were determined in each sample in a three-grade scale. For each variable, specimens were classified as good (0 = best preservation; < 10% alteration), fair (1 = intermediate, between 10 and 50% alteration), and poor (2 = poorest; > 50% alteration) both for fragmentation and dissolution independently. The dominant species *Cyclotella meneghiniana* Kützing, *Aulacoseira granulata* (Ehrenberg) Simonsen, *A. granulata* var. *angustissima* (Muller) Simonsen, *Cocconeis placentula* Ehrenberg, *Hippodonta hungarica* (Grunow) Lange-Bertalot, Metzeltin and Witkowski and *Lemnicola hungarica* (Grunow) Round and Basson were selected as target taxa and evaluated for both taphonomic variables. As diatom preservation is strongly dependent on valve morphology and, consequently, on taxonomy (Barker 1992; Ryves et al. 2009), the use of these target taxa allowed to assess changes in preservation independently of the assemblage composition. Given their morphological differences, the raphe and rapheless valves of both monoraphid taxa (*L. hungarica* and *C. placentula*) were analyzed separately.

Data Analyses

Compositional Comparisons.—Previous analyses of epiphytic diatoms inhabiting Nahuel Rucá lake (Rojas 2016; Rojas and Hassan 2017) showed strong differences in composition between free-floating and the rest of the host macrophytes (emergent, submersed, and rooted-floating). 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* (Rojas and

Hassan 2017). Hence, in order to simplify the comparisons with sedimentary and planktonic assemblages, epiphytic assemblages were clustered into two groups for analytical purposes: assemblages living on *A. filiculoides* and *R. natans* (free-floating assemblages, F) and those living on *S. californicus*, *H. ranunculoides*, and *C. demersum* (attached macrophytes, E). In order to compare the specific composition of diatom assemblages among epiphytic, planktonic, and sedimentary sub-environments, different aspects of assemblages structure were considered. First, the raw number of taxa (S), Shannon-Wiener Diversity (H') and Dominance (1-Simpson index) indices were calculated (standardized at a sample size of $n = 300$ individuals). Differences in richness, diversity, and dominance between the three assemblages were evaluated through ANOVA tests, which allowed testing the null hypothesis of no difference among indices means, after checking for the assumptions of homoscedasticity and normality with Levene's and Shapiro-Wilk tests, respectively. Diversity indices and further ANOVA tests were performed using the software PAST version 3.14 (Hammer et al. 2001).

Second, a PCoA (Principal Coordinates Analysis) was performed in order to summarize the multivariate data into a bidimensional plot. PCoA is a multivariate technique that extracts orthogonal directions of variation from a multivariate data set, but is not restricted to using Euclidean distances, and can be based on Bray-Curtis distances (Lepš and Šmilauer 2003). Species were fitted as vectors in PCoA axes 1 and 2 space (which points in the direction of maximal correlation with species abundance) using the function "add.spec.scores" from the package BiodiversityR version 2.8-0 (Kindt 2017). Analysis of Similarities (ANOSIM) was applied to the data in order to test if the composition of diatom assemblages varied significantly among the groups (Birks 2012). PCoA and ANOSIM were performed using R version 3.3.0 (R Development Core Team 2016).

Taphonomic Comparisons.—For each target taxon, all valves counted in each lake sub-environment were pooled and randomly resampled 100 times using Monte Carlo random permutations, with a minimum sample size of 50 valves. Permutations were performed using the "sample" function in R version 3.3.0 (R Development Core Team 2016). The obtained taphonomic variables were used to calculate the *F* dissolution (F_d) and breakage (F_b) indices (Ryves et al. 2009, 2013), which compare the ratio of undamaged valves (undissolved/unbroken) to all valves counted. The indices vary from 0 to 1, with $F = 1$ indicating all valves are perfectly preserved and $F = 0$, indicating all valves appear dissolved/broken under LM. To maximize potential information from more dissolved valves, the Diatom Dissolution Index (DDI; Ryves et al. 2006) was applied, which compares the assemblage to its dissolution endpoint:

$$DDI = \frac{\sum_{s=3}^{s=1} ns * (S - 1)}{N * (Smax - 1)}$$

where n is the number of valves in the preservational stage, S (good, fair, or poor), and N is the total number of valves classified. $Smax$ is the highest dissolution stage that valves in the assemblage can reach. DDI varies from 0 (perfect preservation) to 1 (all valves at the highest dissolution stage). Additionally, the Diatom Fragmentation Index (DFI) was also calculated by applying the same equation to fragmentation data (Hassan et al. 2014).

Differences in the degree of preservation (F_d , F_b , DDI, and DFI indices) of total diatom assemblages between epiphytic, planktonic, and sedimentary assemblages were evaluated through Kruskal-Wallis tests, followed by Mann-Whitney post-hoc comparisons, which allowed testing the null hypothesis of no difference between indices medians, using the software PAST version 3.14 (Hammer et al. 2001). This non-parametric test was applied as the normality and homoscedasticity assumptions required by ANOVA were not met by the data, according to Levene's and Shapiro-Wilk tests.

Comparison of Taphonomic and Compositional Patterns.—Two approaches were applied to evaluate the relationship between compositional and taphonomic data. First, the correlation between inter-sample taphonomic distances (Manhattan distances among every pair of sites, calculated from the matrix of four taphonomic indices) and species compositional similarities (Bray-Curtis dissimilarities among proportional assemblages composition for every pair of sites) was evaluated in order to establish if the relation between both datasets is positive (Tomašových and Zuschin 2009). The analysis was based on Pearson linear correlation coefficients, and performed using the software PAST v. 3.14 (Hammer et al. 2001). Second, Procrustean Rotation Analysis (PRA, Peres-Neto and Jackson 2001) and the associated PROTEST permutation test (Jackson 1995) were used to evaluate the concordance of PCoA ordinations of compositional (based on Bray-Curtis distances) and taphonomic (based on Manhattan distances) datasets. PRA allows comparing two separate ordinations, as it holds one set of sample coordinates fixed and finds the best fit of the second set of points to this using rotations, re-scalings, and translations (Birks 2012). PROTEST is a permutation-based procedure (Jackson 1995), which assesses the degree of concordance between two matrices, producing a correlation-like statistic derived (m_{12}) and an associated P value indicating the likelihood of the relationship occurring by chance (Bae et al. 2014). Vector residuals represent the distance of each sampling site between the two superimposed ordinations, and indicate the degree of similarity in the position of each site between both ordinations (Bae et al. 2014). In order to assess for differences in PRA concordance among the five lake sub-environments, the length of the vector residuals among these was tested using Kruskal-Wallis analysis of variance followed by Mann-Whitney post-hoc tests (Zar 2010), using the software PAST v. 3.14 (Hammer et al. 2001). PRA and PROTEST were carried out in R version 3.3.0 (R Development Core Team 2016), using the package "vegan" version 2.4-2 (Oksanen et al. 2017).

Application to the Fossil Record.—Fossil data on Nahuel Rucá diatom assemblages composition and taphonomy (DDI and DFI profiles) from a 70 cm core covering the last ca. 700 cal. yrs BP was obtained from Hassan et al. (2014). Diatom compositional zones in the sequence were defined using constrained hierarchical clustering based on Bray-Curtis distance matrices, with clusters constrained by stratigraphic order. The statistical significance of the diatom zones was assessed using the 'broken stick' model (Bennett 1996) with the package "rioja" version 0.9-9 (Juggins 2016). Two approaches were applied in order to assess the usefulness of the obtained contemporary compositional and taphonomic data for reconstructing past environmental changes in Nahuel Rucá Lake. First, the average distance between fossil and contemporary compositional data from littoral and open water assemblages was calculated based on Bray-Curtis. For each fossil level, a LIT/OW Index was calculated as the difference between average Bray-Curtis similarities to littoral and open waters samples, respectively. The index was constructed as a measure of whether the fossil assemblage was more likely produced by a diatom community living in the littoral or open-waters zones, and was then used to assess for changes in the dominance of littoral or open waters sub-environments, being positive values indicative of dominant littoral conditions. Additionally, the minimum Bray-Curtis distance (MIN BC) between fossil and modern samples was calculated. Second, taphonomic comparisons among fossil and contemporary samples were conducted by plotting the DDI and DFI values obtained for the target taxa *Cyclotella meneghiniana* in a bivariate plot. Similarity in diatom valves preservation among assemblages was inferred by the qualitative analysis of samples proximity in the plot. All analyses and graphs were performed in R version 3.3.0 (R Development Core Team 2016).

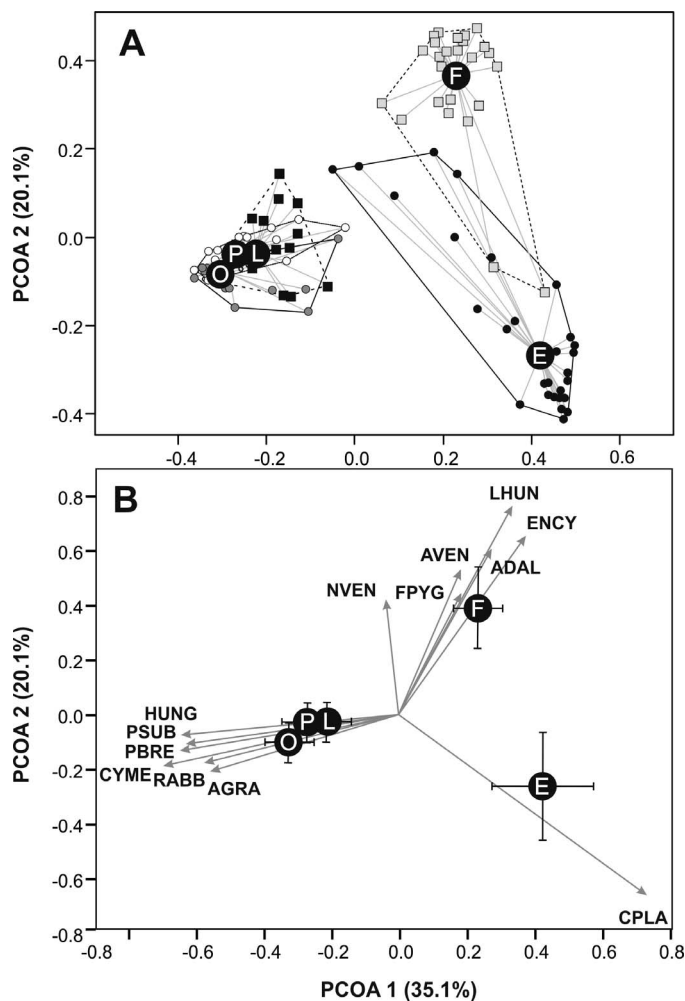


FIG. 4.—First two axes of Principal Coordinates Analysis (PCoA). **A**) The ordination of sites grouped by lake sub-environment. **B**) A joined plot of each sub-environment centroid and standard deviations (error bars) plus the fitted vectors of dominant diatom species. Symbols: gray circles = open waters sediments (O); black squares = littoral sediments (L); white circles = plankton (P); black circles = emergent/submersed macrophytes (E); gray squares = free-floating macrophytes (F).

RESULTS

Compositional Comparisons

Richness and Diversity Indices.—Richness, diversity, and dominance of diatom assemblages significantly differed among sub-environments (Fig. 2). Overall, planktonic and sedimentary assemblages showed similar values for all indices and differed from the epiphytic ones. Richness and Shannon diversity were lower in epiphytic assemblages than in planktonic and sedimentary ones. Dominance, on the other hand, was significantly higher in epiphytic assemblages, whereas it exhibited the lowest values in sediments. Within epiphytic assemblages, free-floating assemblages were the least diverse and also exhibited the highest dominance of all macrophytes.

Assemblages Composition.—A total of 112 diatom taxa were identified in the 127 samples analyzed. Sub-environments differed in assemblage composition, particularly in their dominant taxa (Fig. 3). The first two axes of the PCoA ordination plot explained a 55.2% of the total variance in the dataset. The PCoA plot revealed noticeable differences in

the species composition of assemblages among the five sub-environments considered (Fig. 4A). Both epiphytic assemblages showed considerable separation in the ordination space, whereas planktonic and sedimentary assemblages showed more overlap (Fig. 4A).

Further plotting of species scores on the PCoA plot revealed that differences among these groups of samples were controlled by differences in the proportional abundances of dominant taxa in each sub-environment (Fig. 4B). PCoA axis 1 separated epiphytic from the other three assemblages mainly as a consequence of the dominance of *Cyclotella meneghiniana*, *Aulacoseira granulata*, *Rhoicosphenia abbreviata*, *Hippodonta hungarica*, *Pseudostaurosira brevistriata*, and *P. americana* in sedimentary and planktonic samples. PCoA axis 2 separated epiphytic assemblages on free-floating vegetation from the rest of the macrophytes, given their differences in the percentages of the dominant taxa *L. hungarica*, *Encyonema silesiacum*, and *C. placentula*. These differences were particularly significant for *L. hungarica*, which reached high abundances in free-floating macrophytes (mean: $33 \pm 4\%$), but was present in much lower percentages in the rest of the macrophytes (mean: $3.5 \pm 1.7\%$), as well as in littoral (mean: $1.7 \pm 2\%$), open-waters (mean: $0.77 \pm 0.15\%$), and planktonic assemblages (mean: $0.44 \pm 0.1\%$; $p < 0.0001$). Results of ANOSIM test indicated that the observed differentiation between both free-floating and emergent/submersed epiphytic assemblages was also significantly different between them ($p < 0.0001$). Differences between planktonic and sedimentary assemblages were also significant; although only when lower significance levels were considered ($p < 0.05$).

Taphonomic Analyses

DDI vs. DFI scatterplot signaled fragmentation as the main taphonomic factor influencing the preservation of diatom assemblages in Nahuel Rucá. DDI values ranged between 0 and 0.14, while DFI reached values of up to 0.45 (Fig. 5A). Examination of F_d indicated that most valves were pristine, as they did not exhibit any dissolution mark. Values of F_b , on the other hand, were more variable, and indicated the occurrence of valve fragmentation (Fig. 5B).

Taphonomic comparison of the different sub-environments analyzed exhibited significant differences in the preservation of diatom valves (Fig. 5A–5C). Overall, epiphytic assemblages (both free-floating and attached) showed the best preservation, displaying low DDI and DFI values (Fig. 5B, 5C). Littoral assemblages exhibited low DDI values, when compared to open waters and plankton valves (Fig. 5B), but presented significant differences with those assemblages when fragmentation was analyzed (Fig. 5C).

The examination of DDI results of target taxa indicated patterns of preservation similar to those of total assemblages (Fig. 6). Most target taxa showed higher DDI values in open-waters (*C. meneghiniana*) and planktonic assemblages (*Aulacoseira* spp., *H. hungarica*, Fig. 6A), whereas than evidences of dissolution in epiphytic assemblages were almost negligible for *C. placentula*, but significant for *L. hungarica* (Fig. 6B). Results of DFI, on the other hand, showed differences among diatom taxa. Fragmentation of the planktonic taxa *C. meneghiniana*, *A. granulata*, *A. granulata* var. *angustissima*, and the benthic *H. hungarica* did not show evident differences among the substrates analyzed (Fig. 6A), whereas than the epiphytic *C. placentula* and *L. hungarica* showed higher fragmentation in sedimentary and planktonic assemblages, displaying better preservation in epiphytic assemblages (Fig. 6B). *Lemnicola hungarica* also showed preservational differences between the raphe and rapheless valves, the latter being less susceptible to both dissolution and fragmentation (Fig. 6B).

Comparison of Taphonomic and Compositional Patterns

Correlation between variation in total assemblages preservation and variation in species composition was significantly positive ($r = 0.34$, $p <$

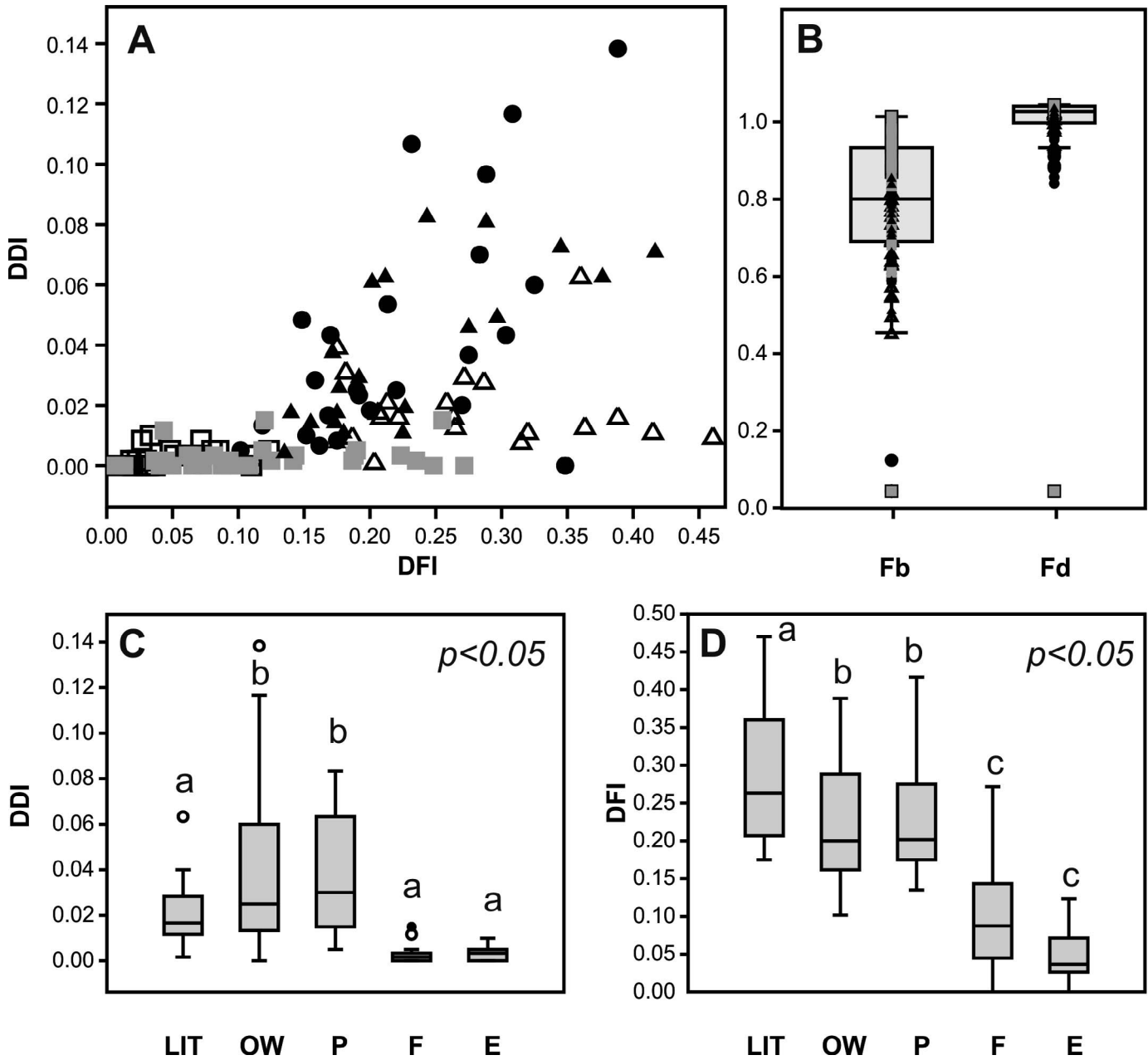
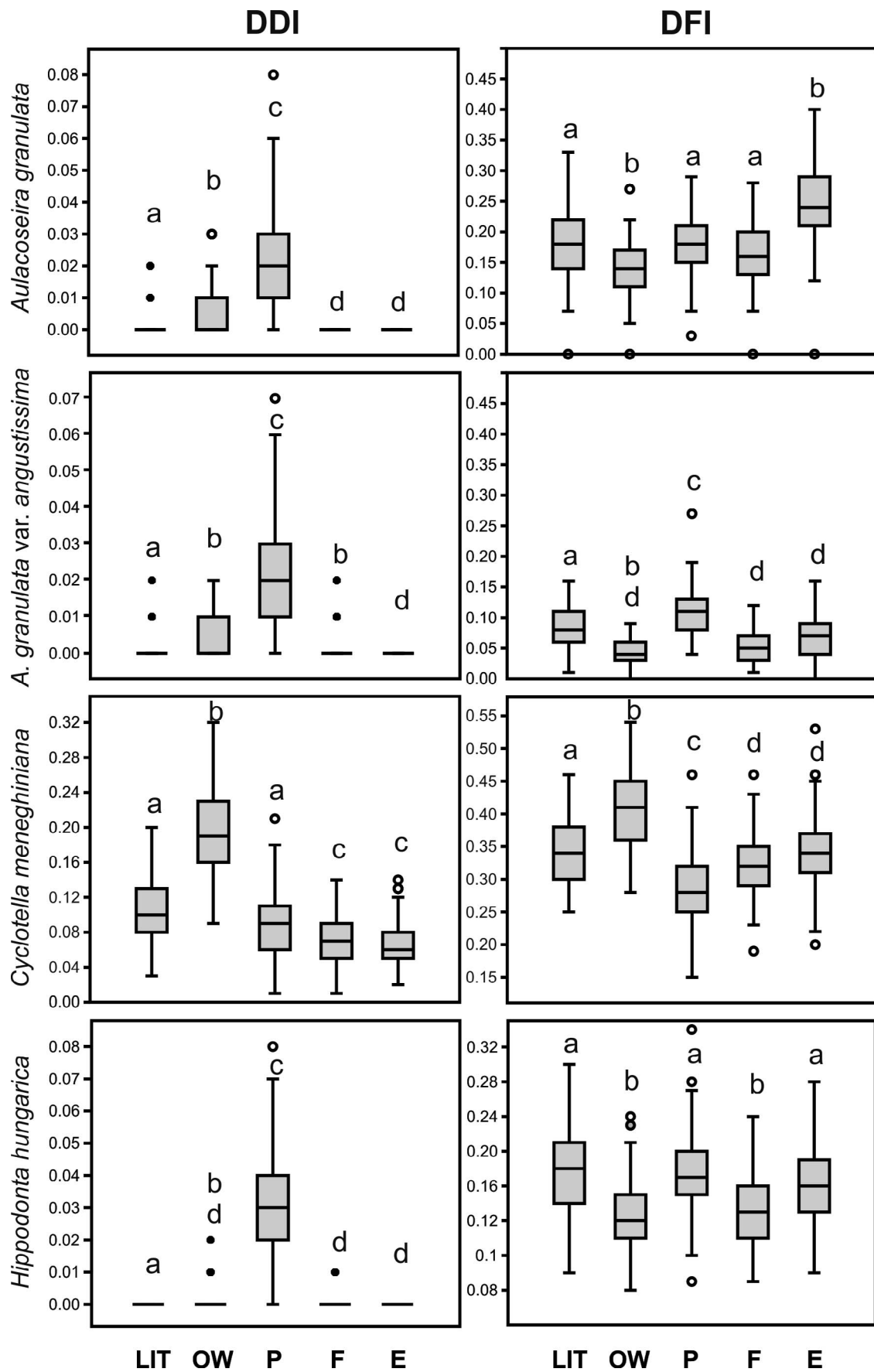


FIG. 5.—Results of taphonomic analyses based on total diatom assemblages. **A)** Plot of Diatom Dissolution Index (DDI) against Diatom Fragmentation Index (DFI). Symbols: black circles = open waters sediments; white triangles = littoral sediments; black triangles = plankton; gray squares = emergent/submersed macrophytes; white squares = free-floating macrophytes. **B)** Box and Jitter plots of F indices of dissolution (F_d) and fragmentation (F_b). **C)** Boxplots of DDI values for each lake sub-environment. **D)** Boxplots of DFI values for each lake sub-environment. Abbreviations: LIT = littoral sediments; OW = open waters sediments; P = plankton; F = free-floating macrophytes; E = emergent/submersed macrophytes. Same letters indicate no significant differences at the p-value listed in each plot, according to Kruskal-Wallis and Mann-Whitney post-hoc tests.

0.0001; Fig. 7). According to PRA and PROTEST results, the concordance of the PCoA plots for taphonomic and compositional data was highly significant ($m_{12} = 0.70$, $p < 0.001$). Examination of the PRA ordination plot allowed analysis of deviations in site position between both datasets (Fig. 8). Overall, sites showed variation in the PRA residuals, with some

samples having long vectors indicating low agreement (particularly some LIT and OW samples). The direction of vector displacement showed that epiphytic samples (both E and F) were more variable in their assemblage composition than in their taphonomic attributes, as they tend to converge to very good preservation. Sedimentary and planktonic samples (OW, LIT,

FIG. 6.—Boxplots of DDI and DFI indices calculated on selected target taxa. Abbreviations: LIT = littoral sediments; OW = open waters sediments; P = plankton; F = free-floating macrophytes; E = emergent/submersed macrophytes. Same letters indicate no significant differences at $p < 0.0001$, according to Kruskal-Wallis and Mann-Whitney post hoc tests.



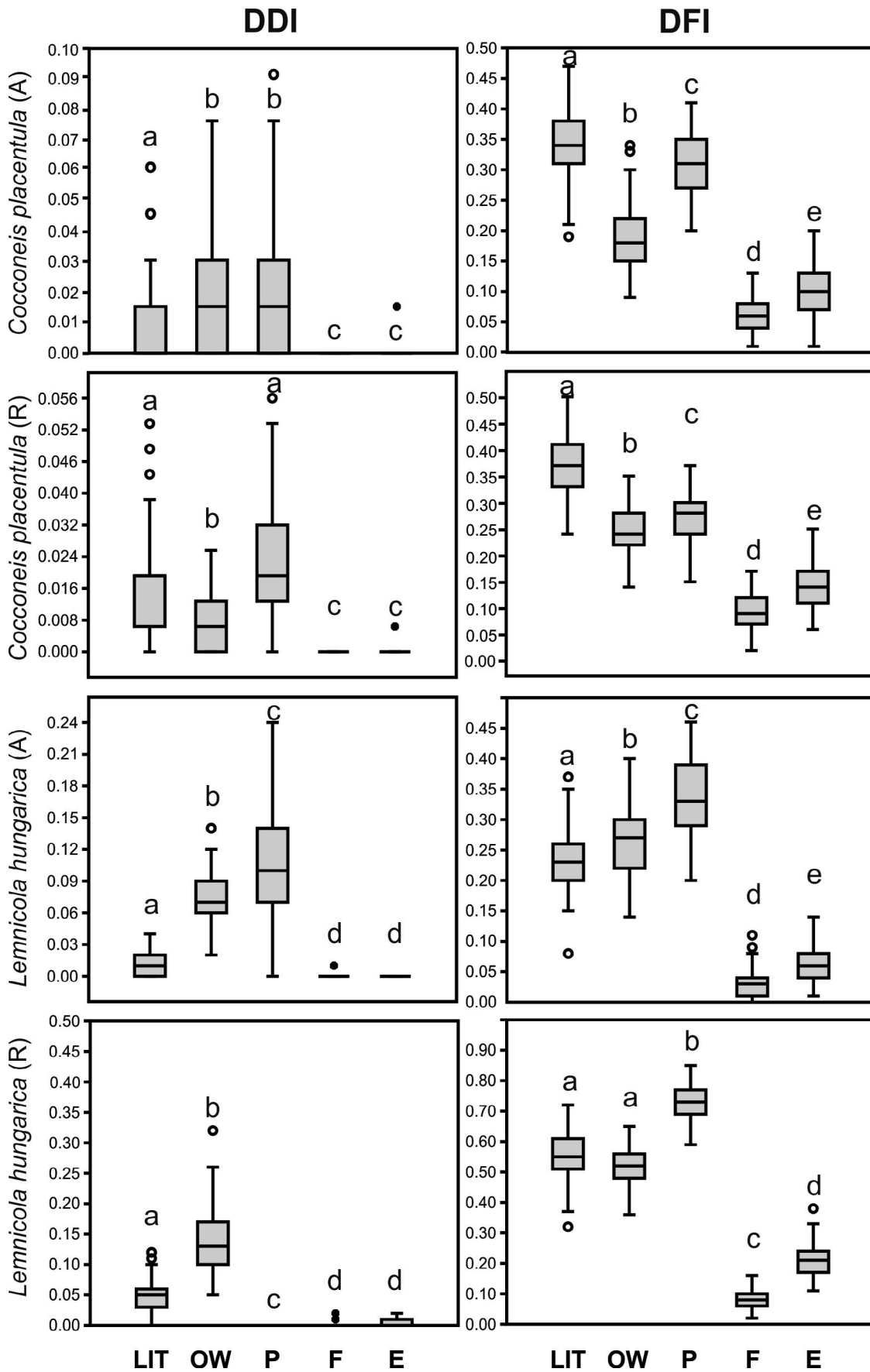


FIG. 6.—Continued.

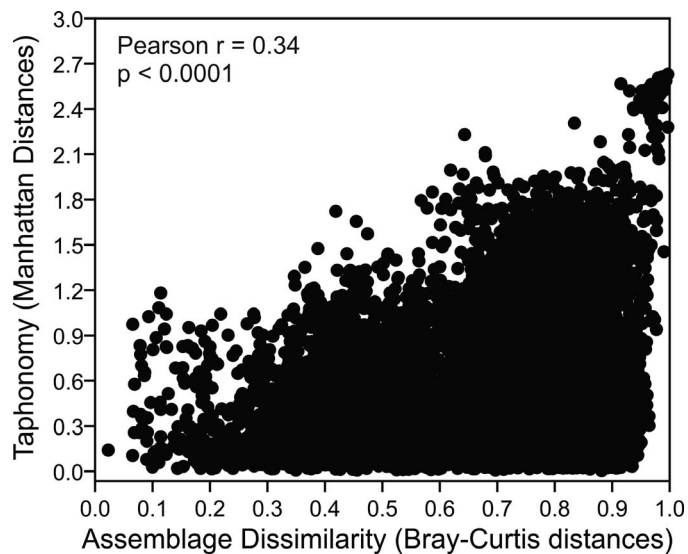


FIG. 7.—Pearson correlations between intersample distances based on taphonomic (Manhattan distances) and compositional (Bray-Curtis distances) datasets.

and P), on the other hand, showed the opposite tendency: samples were more dispersed when taphonomic attributes were used for ordination, while compositional data resulted in clustered sample ordinations. However, no significant differences in the mean residual distances between the five lake sub-environments were found when vector lengths were compared with the Kruskal-Wallis test ($p = 0.23$).

Application to the Fossil Record

Cluster Analysis and the subsequent broken-stick model allowed definition of seven significant diatom zones (DZ) in Nahuel Rucá core. Those taxa reaching abundances of 5% in at least one sample were presented in the stratigraphic plot, as they are usually considered the lowest abundance limit for excluding rare taxa in diatom-based paleo-reconstructions. Yet, in the present study, we also plotted the distribution of the ecologically meaningful taxon *Lemnicola hungarica*, even as it reached a maximum of 1.6% of total diatom abundance in the core. Significant relationships between *L. hungarica* and duckweed have been demonstrated for a variety of climatic conditions and waterbody types in many parts of the world, and it can be reliably considered as an indicator of past free-floating plant dominance (Emson et al. 2017; Rojas and Hassan 2017). Hence, including this taxon in the analysis allows evaluation of past duckweed coverage and avoids possible methodological biases in paleoreconstructions due to this conventional simplification (Fig. 9). Although the zones were defined on the basis of diatom compositional changes, examination of taphonomic profiles also showed noticeable differences in preservation among zones. Moreover, comparison of fossil and contemporary assemblages composition showed increased similarities between modern and fossil samples towards the top of the core, and allowed inferences on changes in the ratio between littoral and open waters during the last 700 cal. years BP (Fig. 9).

DZ I (70–58 cm) was dominated by brackish/freshwater taxa, such as *Cyclotella meneghiniana*, *Cocconeis placentula*, and *Nitzschia amphibia*, with low proportions of *Aulacoseira granulata* at the basal samples. MIN BC fluctuated around 0.6 in this zone. Examination of the LIT/OW index indicated a gradual tendency towards littoral-dominated conditions in this zone. The preservation of diatom valves was low, as shown both by high DDI and DFI values (Fig. 9).

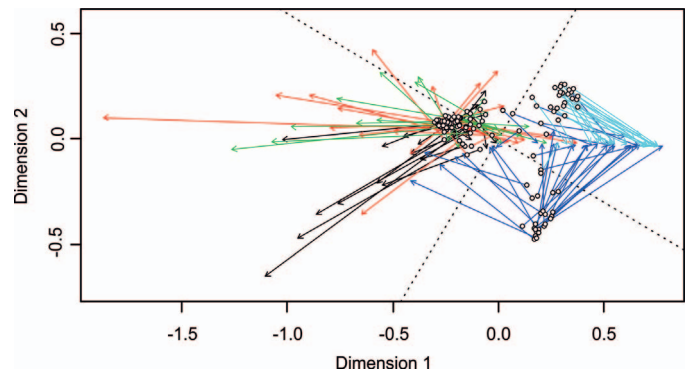


FIG. 8.—Procrustean concordance plot, generated by comparing PCoA ordinations based on compositional (Bray-Curtis distances) and taphonomic (Manhattan distances) datasets. The circles represent the position of samples based on compositional data, and the point of the arrow the position of samples based on taphonomic data. The distance between both is the Procrustean residual: the longer the arrow, the larger the difference between both ordinations. Different arrow colors indicate different lake sub-environments. Symbols: light blue arrows = free-floating macrophytes; blue arrows = emergent/submersed macrophytes; green arrows = plankton; black arrows = littoral sediments; red arrows = open waters sediments; dashed lines indicate the position of the rotated axes based on the taphonomic ordination of the samples.

DZ II (56–38 cm) presented increased percentages of the brackish and benthic *Pseudostaurosira americana*, while the epiphytic *C. placentula* diminished towards the top of the zone. MIN BC decreased from 0.6 at the base to 0.45 at the upper levels of the zone. The LIT/OW index indicated a gradual return to open-water conditions, which coincided with a noticeable diminution of valve dissolution (Fig. 9).

DZ III (36–32 cm), DZ VI (30–28 cm), and DZ V (26–24 cm) were characterized by rapid changes in diatom composition, shifting from levels almost entirely dominated by *C. meneghiniana* in DZ III, followed by a peak of *Staurosira longirostris* (up to 80% in DZ VI), which was later replaced by a more diverse assemblage, characterized by a tycho planktonic assemblage formed by *C. meneghiniana* and freshwater *Aulacoseira* spp. taxa. MIN BC showed a peak in DZ VI, reaching values of 0.8. The LIT/OW index also showed strong fluctuations along these zones, with a dominance of open-water associated conditions, linked to a new increase in the DDI and DFI values (Fig. 9).

DZ VI (22–18 cm) was dominated by a mixture of epiphytic diatoms, such as *Epithemia adnata*, *E. sorex*, and *C. placentula*. Low proportions of *L. hungarica* were also recorded in this zone, which was related to an increase in the littoralization, according to LIT/OW index. MIN BC ranged between 0.6 and 0.5. The preservation of valves improved significantly in this zone, as they showed the lowest DDI and DFI values from the whole sequence (Fig. 9).

DZ VII (16–10 cm) was dominated by *C. meneghiniana* and *A. granulata*, accompanied by *A. granulata* var. *angustissima*, *Hippodonta hungarica*, *Navicula peregrina*, and small proportions of *Pseudostaurosira brevistriata*, *P. americana*, *C. placentula*, and *L. hungarica*. MIN BC showed the lowest values of the whole sequence in this zone, ranging between 0.35 and 0.42. In these topmost sedimentary levels, diatom valves were well preserved, showing the same low DDI and DFI values that characterized DZ VI, and indicating a dominance of open-waters conditions at the point of extraction of the core according to the LIT/OW index (Fig. 9).

Comparison of taphonomic indices between contemporary and fossil assemblages allowed identification of modern analogs for past diatom preservation (Fig. 10). Several fossil samples showed high similarities to within-lake modern assemblages when preservation was considered. Among them, samples from the topmost zone of the core (DZ VII)

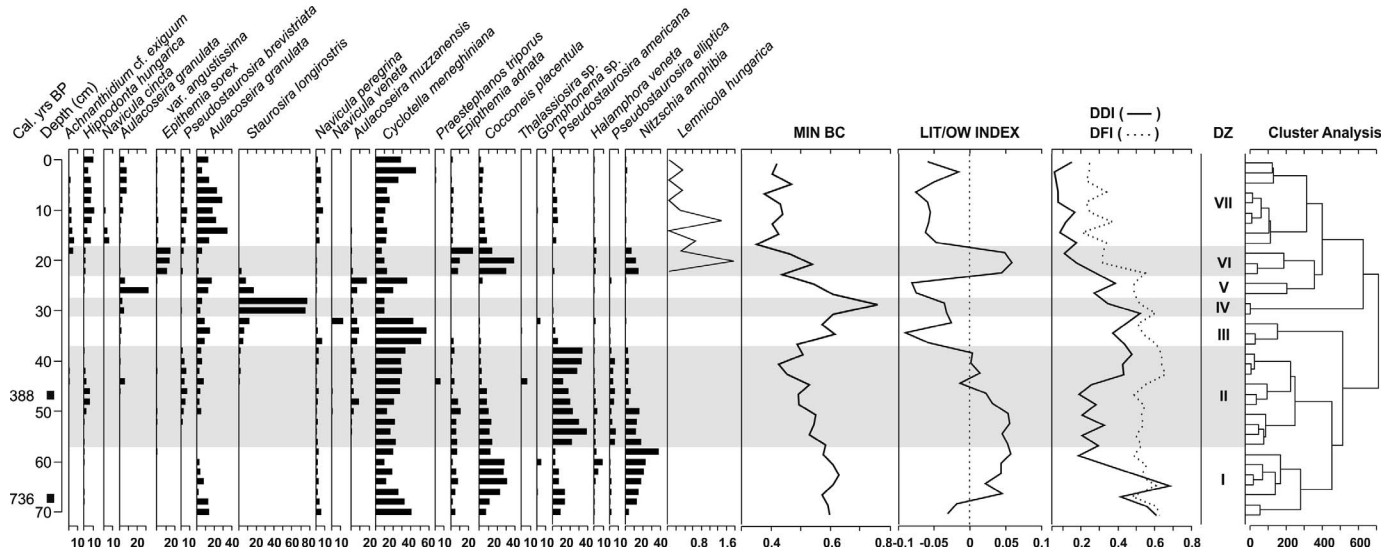


Fig. 9.—Relative abundance of the dominant diatom taxa (> 5%, black bars) and *Lemnicola hungarica* (line), MIN BC, LIT/OW, DDI and DFI indices plotted against depth in the Nahuel Rucá sediment core (See Material and Methods section for reference on indices calculation). Results of cluster analysis and associated Diatom Zones (DZ I to VII) are shown.

overlapped with modern planktonic and littoral samples, given the low values of DDI and DFI shown by diatom assemblages, which were the best preserved of the entire sequence. Most of the samples of DZ VI and DZ II overlapped with open waters modern samples, as they showed slightly higher DDI and DFI values (Fig. 10).

A number of fossil levels, however, showed DDI and DFI values higher than that recorded in modern assemblages of the lake, lacking analogues in the dataset (Fig. 10). These levels corresponded mainly to DZ I and DZ III, which contained the most dissolved assemblages from the whole sequence, with DDI values ranging from 0.35 to 0.7 (Fig. 9). These most extremely

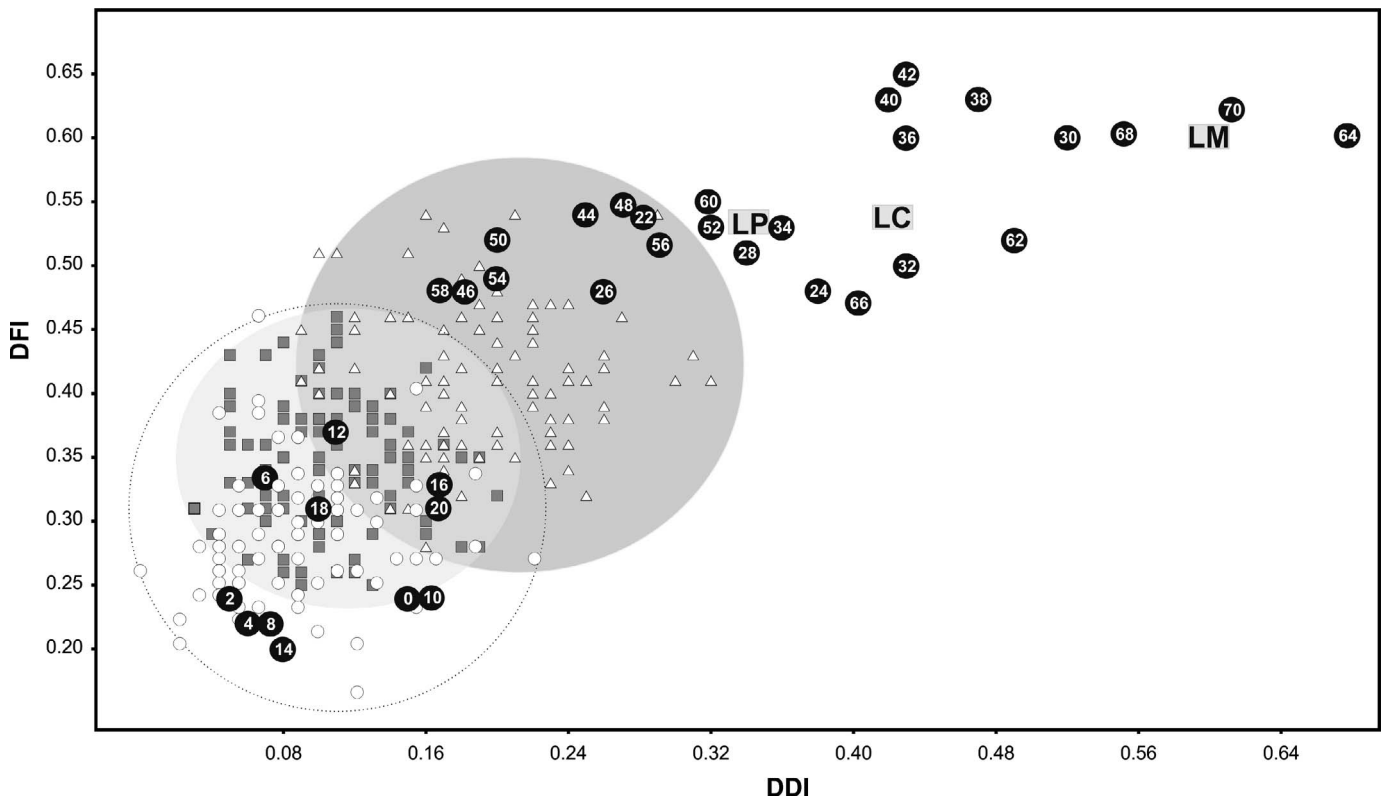


Fig. 10.—Plot of DDI vs. DFI indices for *Cyclotella meneghiniana* in contemporary and fossil samples. Symbols: gray squares = littoral samples; white circles = planktonic samples; white triangles = open waters samples; black circles = fossil samples from Nahuel Rucá core; LP = Puán Lake; LC = Cochicó Lake; LM = Monte Lake; large circles indicate areas where most littoral (light gray circle), planktonic (dashed circle), and open waters (dark gray circle) are located. Numbers indicate sample depth along the core.

dissolved levels had no analogs in the modern dataset, as valves of *C. meneghiniana* in modern Nahuel Rucá sediments reached maximum DDI values of ~ 0.3 (Fig. 6A). Therefore, in order to search for modern analogues for these poorly preserved fossil samples, taphonomic data from three previously studied Pampean brackish lakes with average salinities between 4 and 13 ppt (Puán, Cochicó, and Monte lakes; Hassan and De Francesco in press) were incorporated to the plot. Samples from these lakes covered the whole range of DDI and DFI values found in the fossil record, providing good analogues of past taphonomic conditions for those levels with no analogues in the within-lake dataset, as suggested by the observed closeness between samples in the plot (Fig. 10).

DISCUSSION

Compositional Comparison among Within-Lake Sub-Environments

Diatom assemblages showed significant differences in diversity and composition among within-lake sub-environments. Diversity and richness were higher in planktonic and sedimentary assemblages, whereas dominance showed higher values in epiphytic samples. These differences can be related both to the intrinsic characteristics of living communities and to differences in time-averaging among sub-environments. Sedimentary death assemblages constitute time-averaged representations of living communities and integrate dead-valve inputs over long periods of time, capturing demographic and environmental stochasticity and leading to assemblages with high species richness (Kidwell 2002; Tomašových and Kidwell 2009). These inputs can include not only autochthonous benthic valves (those inhabiting the bottom sediments), but also valves from other within-lake sub-environments, as epiphytic taxa living upon macrophytes or planktonic species inhabiting the water column, and consequently increasing diversity and richness in sedimentary assemblages (Smol 1981; Hassan 2015b). Moreover, the strong interaction between the bottom sediments and the water column in these wind-stressed shallow lakes can explain the similarity in diversity and richness shown by planktonic and sedimentary assemblages (Fig. 9). Given their very shallow depths, sediment mixing in these lakes is periodically induced by waves and bioturbation (Larsen and MacDonald 1993), leading to the consequent mixing and resuspension of associated diatom valves. Epiphytic biofilms, on the other hand, constitute sheltered environments bound by a mucilage that reduces the interaction between epiphytic communities and the surrounding environments (Hoagland et al. 1993). In addition, low species richness and diversity has been previously reported for diatom assemblages found on free-floating macrophytes, and attributed to the specific ecological and biological requirements of epiphytic diatoms to tolerate and thrive in the water-surface zone habitat, characterized by high light intensities, wind disturbance and temperature fluctuations (Emson 2015). Epiphytic assemblages in Nahuel Rucá were dominated by epiphytic diatom taxa, which contributed between 70% and 88% to the total diatom composition, and can be considered as autochthonous assemblages. The proportion of planktonic, tychoplanktonic and benthic diatom valves in epiphytic assemblages was low, as has been previously reported in other Pampean shallow lakes (e.g., Bauer et al. 2007; Rodríguez et al. 2011), suggesting a low input of allochthonous valves in epiphytic sub-environments when compared to sedimentary and planktonic assemblages.

Ordination of samples from the different sub-environments through PCoA also showed a strong compositional similarity between sedimentary and planktonic assemblages. Littoral, open waters and planktonic assemblages were mainly dominated by the tychoplanktonic species *C. meneghiniana*, *A. granulata*, and *A. granulata* var. *angustissima*. The dominance of these taxa both in the sediments and the water column may be explained by their life-form, as they occur intermittently in the water column after being swept up from the bottom (Smol and Stoermer 2010), favoring their lateral displacement among within-lake sub-environments.

This is particularly true for the heavy, silicified cells of *Aulacoseira* spp. that sink rapidly in non-turbulent water columns (Bradbury 1975). Increased turbulence in a lake can favor this genus over other planktonic species (Dong et al. 2008). Hence, the turbulence characterizing wind-stressed Pampean shallow lakes promotes the development of *Aulacoseira* spp. and populations of other tychoplanktonic species, causing their valves to be widely distributed both in benthic and planktonic habitats, as they are subjected to natural sinking-resuspension cycles.

Epiphytic taxa inhabiting macrophyte biofilms were also represented in low proportions in sedimentary and planktonic assemblages. As littoral habitats in Nahuel Rucá lake cover approximately 50% of the lake surface (Rojas and Hassan 2017), epiphytic assemblages would be expected to represent a similar percentage of sedimentary assemblages. This was not the case, as demonstrated by the low proportional abundances of the dominant epiphytes in sediments. This is the case of *L. hungarica*, which although dominating free-floating mats in percentages of 30–50%, only reached up to 5% in sedimentary assemblages. Comparable results have been recently reported by Emson et al. (2017) when studying diatom assemblages in duckweed-dominated ponds. In those environments, *L. hungarica* also occurred at relatively low percentages ($< 5\%$) in sediments, despite its marked dominance in life assemblages. Hence, our results support the potential of *L. hungarica* as indicator of past duckweed coverage, even when present at low percentages in sediments. This highlights the relevance of including rare diatom taxa (which are usually ignored in diatom stratigraphic plots) when reconstructing lacustrine paleoenvironments. In the case of *L. hungarica*, its presence (even at very low percentages) would be a reliably good indicator of duckweed coverage, a valuable information that is lost when using only the dominant species (i.e., those over 5% of total abundance; Emson et al. 2017), as is usually the case with diatom-based paleoenvironmental reconstructions.

The reasons for the under-representation of *L. hungarica* in surface sediments are uncertain, and should be addressed through experimental studies. As *C. placentula*, the epiphytic taxa dominating in rooted and submersed macrophytes, is well represented in sediments, these low *L. hungarica* abundances could be related to the particular characteristics of its frustule and/or the environmental conditions prevailing below the duckweed mats (Emson 2015). Comparison of DDI and DFI values of both species suggests preservation is the probable cause of this *L. hungarica* under-representation. Raphe valves of *L. hungarica* found in the plankton, open waters, and littoral sediments exhibited the highest DDI and DFI values among all taxa analyzed (up to 0.5 and 0.9, respectively), being the rapheless valves slightly better preserved (up to 0.24 and 0.5, respectively). These taphonomic indices are particularly high when compared to *C. placentula*, which showed maximum DDI and DFI values of ~ 0.1 and ~ 0.5 , respectively (Fig. 6B). It has been pointed out that epiphytic diatoms adapted to high grazing pressures, such as *C. placentula*, tend to develop highly silicified frustules which are difficult for grazers to break (Hamm et al. 2003). Consequently, these taxa are less susceptible to breakage and dissolution than less silicified taxa, becoming differentially preserved in sediments (Sawai 2001). *Lemnicola hungarica*, on the other hand, is adapted to the sheltered microenvironments below duckweed mats, where grazing pressures are lower, and consequently, less silicified valves are developed. As diatom preservation depends highly on the thickness, ornamentation, and surface/volume ratio of the frustules (e.g., Van Cappellen et al. 2002), differential preservation due to intrinsic factors could be exerting a significant bias in the representation of this taxa in shallow waterbodies, such as Nahuel Rucá Lake.

Taphonomic Comparisons

Fragmentation was identified as the main taphonomic factor influencing the preservation of diatom assemblages in Nahuel Rucá Lake. This result is not surprising, however, as diatom fragmentation is mostly induced by

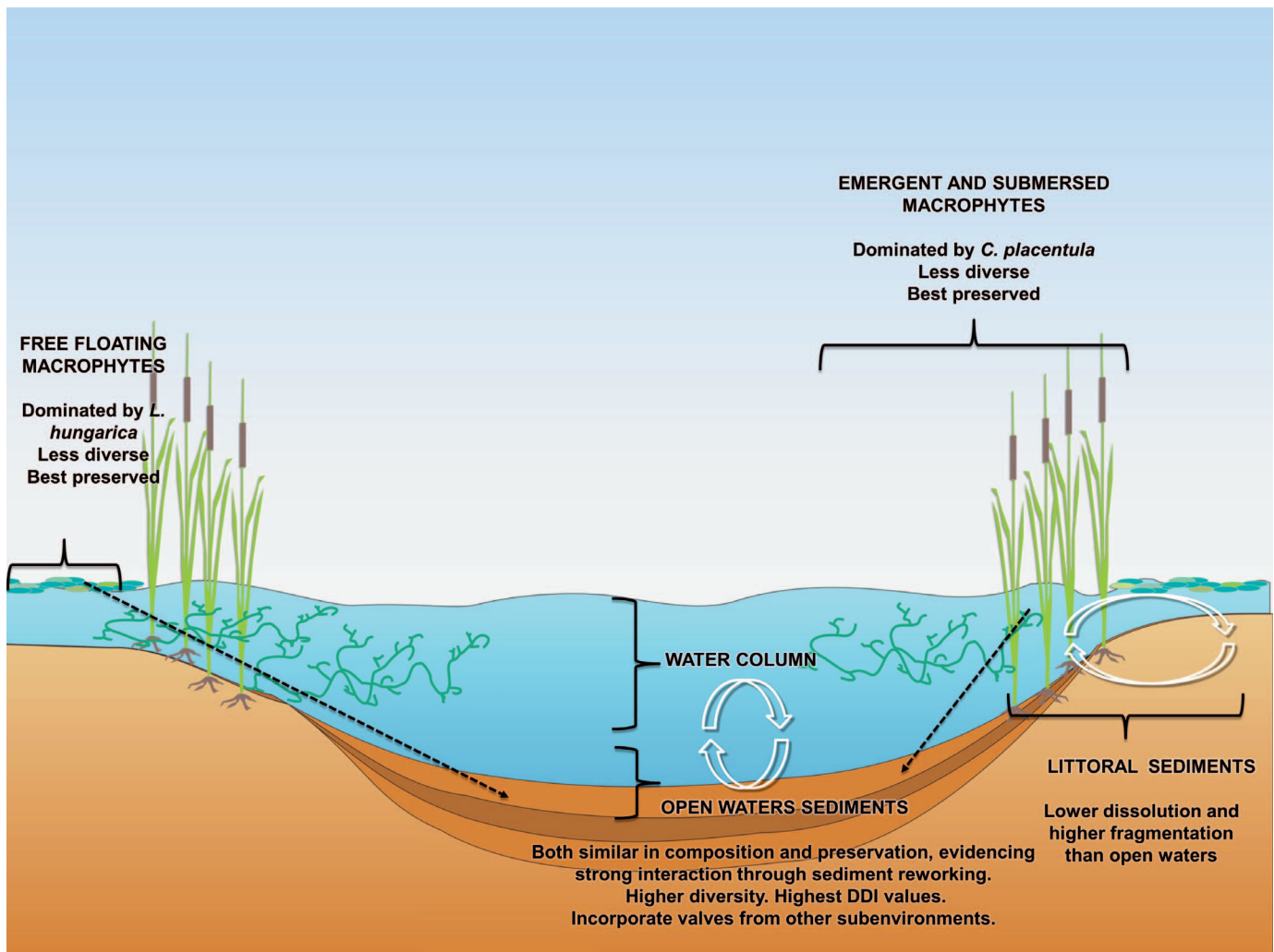


FIG. 11.—Summary of the taphonomic processes taking place in the different sub-environments of Nahuel Rucá Lake.

sediment reworking and resuspension, which have been already mentioned as a significant environmental trigger in these shallow, wind-stressed lakes. In fact, higher fragmentation has been associated with high energy environments, such as littoral and shallow lacustrine zones (Round 1964; Flower and Nicholson 1987). The effect of grazing has also proven to be significant in causing frustule breakage (Haberyan 1985). Therefore, biological and physical environmental variables, such as fetch, depth, wind speed, and grazers abundance may play a key role in explaining diatom fragmentation in Nahuel Rucá and other Pampean shallow lakes.

Dissolution effects, on the other hand, were less noticeable in the dataset, and examination of F_d indicated that most valves were pristine. Although dissolution significantly differed among sub-environments (being higher in plankton and open water sub-environments), the relatively low DDI values indicated a minor effect of this taphonomic factor on diatom preservation. These results agree with those expected for freshwater lakes, as dissolution is highly dependent on water chemistry, particularly on salinity and hardness (Barker 1992; Ryves et al. 2006; Roubeix et al. 2008). In Pampean shallow lakes, high salinity, carbonate, bicarbonate, and pH values, as well as low silica concentrations proved to be the main triggers of *Cyclotella meneghiniana* dissolution at regional scale (Hassan and De Francesco in press). In fact, the water composition of Nahuel Rucá (characterized by nearly circumneutral pH and low carbonate content)

represented good conditions for diatom preservation at regional scales, resulting in the lowest DDI and F_d indices among all the studied lakes (see Table 2; Hassan and De Francesco in press). Hereafter, as Nahuel Rucá is a freshwater lake (Cristini et al. 2017), dissolution of diatom valves is not a key factor for the preservation of assemblages.

Taphonomic comparison among sub-environments showed significant differences in the preservation of diatom valves, both in their dissolution and fragmentation (Fig. 11). Epiphytic assemblages (both free-floating and attached) showed the best preservation, as shown by the lowest DDI and DFI values of all the assemblages analyzed. These results were expected, however, as epiphytic assemblages were mostly composed of autochthonous valves which, being protected by the epiphytic biofilm structure and the sheltered areas among macrophytes (Rojas and Hassan 2017), tend to be less subjected to the taphonomic biases generated by physical and chemical environmental factors than planktonic and sedimentary assemblages. Benthic and planktonic sub-environments, on the other hand, constitute less stable habitats in which sediment reworking poses physical constraints to diatom preservation (Hassan 2015b), as was evident in the Nahuel Rucá dataset. Among these, littoral assemblages exhibited the lowest DDI values, as marks of dissolution were more evident in open waters and planktonic valves. This difference can be related to within-lake gradients in water chemistry characterizing the lake. Water chemistry

shows a horizontal zonation in Nahuel Rucá (Cristini et al. 2017), with a littoral zone characterized by lower pH and carbonate concentrations, conditions that would prevent diatom dissolution and favor preservation (Barker et al. 1994; Hassan and De Francesco in press). Open waters and water column, on the other hand, are characterized by higher pH and carbonate/bicarbonate concentrations (Cristini et al. 2017), which could explain the higher frequency of dissolution marks exhibited by diatom assemblages in these sub-environments. Therefore, despite being low, dissolution was significantly higher in open waters and plankton, being probably enhanced by the continuous reworking and mixing exerted by wind action in the lake.

Fragmentation marks were more frequent in littoral sub-environments. This result can be related to the very shallow depths characteristic of this environment (less than 60 cm), which would enhance the impact of sediment reworking on frustule breakage (Round 1964; Flower and Nicholson 1987). Moreover, given the high productivity associated to these densely vegetated areas, the littoral sub-environment can support abundant populations of macroinvertebrates (González-Sagrario and Ferrero 2013), which are mostly restricted to these shallow and vegetated zones (Tietze and De Francesco 2017; González-Sagrario et al. 2018). As diatom breakage is strongly related to grazing (Haberyan 1985), the highest DFI values found in the littoral sediments can be also explained by biological action through grazing activity. Examination of DFI results also showed differences in preservation among the different taxa analyzed: while tychoplanktonic taxa such as *C. meneghiniana*, *A. granulata*, and *A. granulata* var. *angustissima* were evenly fragmented among sub-environments, the epiphytic species *C. placentula* and *L. hungarica* showed higher fragmentation in sedimentary and planktonic assemblages. Thus, besides taxa life-form, examination of valve fragmentation constitutes a useful tool to differentiate between autochthonous and allochthonous taxa within epiphytic biofilms, with implications for environmental biomonitoring based on epiphytic communities in these shallow lakes.

Taphonomic Versus Compositional Patterns

The significant correlation between variation in total assemblages preservation and variation in species composition found in the present study suggests the existence of common environmental causes in the structuration of these patterns at local scales. This relation indicates that the same environmental factors can control both the assemblage structure (i.e., richness, diversity, and proportional abundances) and preservation (i.e., dissolution and fragmentation) of taxa in within-lake sub-environments. This was particularly noticeable in epiphytic assemblages, which were dominated by epiphytic species adapted to the special conditions of macrophyte mats, and also exhibited a distinctive taphonomic signature characterized by good preservation as a consequence of the protected conditions prevailing within mats. These results are coincident with patterns found at regional scales in Pampean shallow lakes, where *C. meneghiniana* preservation and assemblages composition were also significantly and positively correlated along a strong salinity gradient (Hassan and De Francesco in press). At these regional scales, diatom assemblage composition and preservation were strongly linked to salinity and ionic composition, which play a role not only in structuring living diatom communities but also in controlling the postmortem dissolution and fragmentation of valves (Barker et al. 1994; Ryves et al. 2006). In that study, dissolution proved to be a more sensitive indicator of salinity differences among lakes than shifts in relative abundances of diatom taxa, enhancing the paleoenvironmental significance of diatom taphonomic signatures at long environmental gradients (Hassan and De Francesco in press).

At the short environmental gradients covered in the present study, the link between preservation and composition also highlighted the capability

of diatom taphonomic signatures to capture environmental differences at local scales, these being related to differences in depth, macrophyte coverage, and water composition among sub-environments. For instance, while compositional analysis through PCoA showed a strong overlap between littoral, open waters and planktonic assemblages, littoral assemblages showed a particular taphonomic signature that differentiated them from the assemblages from other sub-environments. This was particularly evident when examining the PROCURUSTES plot, in which sedimentary and planktonic samples appeared clustered when compositional data was used in ordination, while taphonomic attributes led to vector displacements, which separated littoral samples from open waters and planktonic ones. Therefore, even as the differences in diatom assemblages composition between the three sub-environments lead to overlapped ordinations, littoral taphonomic signatures were different enough to separate these assemblages in an ordination space. Under such circumstances, combining taphonomic and compositional analyses would allow to uncover subtle within-lake environmental gradients not identifiable when only compositional analyses are performed. In this case, compositional analyses would allow to discriminate among different microhabitats, leading to paleoenvironmental inferences that would not be possible from taphonomic analyses only.

Epiphytic assemblages, on the other hand, showed the opposite pattern in PROCURUSTES plot, as they were more variable in their assemblage composition than in their taphonomic attributes. This result implies that, even as assemblages from different macrophytes (i.e., free-floating and attached) differed in their dominant taxa (*L. hungarica* and *C. placentula*, respectively), they tended to converge in the taphonomic plot because of similar preservation. Hence, independently of the identity or life-form of the host-macrophyte, epiphytic biofilms constitute microhabitats that facilitate diatom preservation, preventing fragmentation by reworking and sediment resuspension. The low preservation of some epiphytic taxa (such as *L. hungarica*) in surface sediments suggests that these taxa can be easily attacked by taphonomic factors once the biofilms are destroyed. Hence, although the good preservation of diatoms within biofilms encourages the study of epiphytic assemblages in biomonitoring studies of contemporary communities, it does not promote the preservation of epiphytic taxa once incorporated to the lakebed, where they suffer strong taphonomic alteration.

Overall, the results demonstrate that the relative importance of taphonomic and compositional data in unraveling environmental gradients in shallow lakes strongly depends on the ecological and environmental conditions of the habitat under study. Consequently, accompanying paleoenvironmental studies with local and regional analyses on actualistic taphonomy will increase significantly the potential information provided by past taphonomic tendencies, by providing data on the environmental significance of diatom taphonomic signatures under different environmental circumstances. Overall, it becomes clear that diatom-based paleoenvironmental reconstructions should incorporate taphonomic analyses in order to increase the quality of the inferences and provide insights into the past shallow lake dynamics.

Application to the Fossil Record

The joint analysis of compositional and taphonomic fluctuations allowed reconstruction of paleoenvironmental changes during the late Holocene in Nahuel Rucá Lake. In the last ca. 700 cal. years BP, the lake evolved from brackish to freshwater conditions, as shown by changes in both species composition of diatom assemblages and taphonomic signatures. Besides this tendency towards decreasing salinity, diatom zones also showed an alternation between open-waters dominated paleoenvironments characterized by high diatom dissolution and low agreement between modern and fossil assemblages (DZI, DZ III-V), and zones indicating higher littoral development and increased similarity to modern assemblages (D ZII and

DZ VI), characterized by a better preservation of frustules. Dominance of well-preserved planktonic assemblages was recorded in the topmost levels of the core (DZ VII), indicating the establishment of the modern lake conditions.

Brackish conditions at the base of the core are mainly suggested by the high dissolution of *C. meneghiniana* valves. DDI values inferred for these levels were comparable to those of valves found in brackish Pampean lakes, such as Monte and Cochicó lakes, characterized by salinities of 7.7 and 8.2 ppt, respectively (Hassan and De Francesco in press). However, these higher DDI values can also be related to post-burial conditions, as valve dissolution in saline lakes can also be exacerbated by chemical processes linked to post-depositional circulation of saline and/or alkaline interstitial and groundwaters (Reed 1998). These brackish conditions, however, are only partially suggested when assemblage composition is considered alone. This is because the dominant taxa are mostly euryhaline species adapted to a wide range of salinity conditions (e.g., *C. meneghiniana*, *C. placentula*, *N. amphibia*) with the consequent reduced value for salinity bioindication (Hassan et al. 2011). In fact, only the presence of rare taxa (< 1%), such as *Campylodiscus clypeus*, *Craticula halophila*, *Navicula salinicola*, *Nitzschia vitrea*, and *Synedra platensis*, suggested brackish conditions. Results of constrained ordinations showed that the DDI constitutes a stronger indicator of salinity than species composition in Pampean lakes (Hassan and De Francesco in press). While this environmental variable only explained 11.7% of the variance in diatom composition ($p = 0.07$), it explained 77% of DDI variability ($p < 0.001$). In the case of Nahuel Rucá, the high salinity conditions suggested by high DDI values were coincident with the presence of halophilous taxa. Therefore, the combination of both independent sources of evidence provided reliable data to propose higher salinities in the lake at ca. 700 cal. years BP.

Modern conditions were recorded in the topmost 18 cm of the sedimentary record, as indicated by the specific composition of the assemblages, which showed the lowest Bray-Curtis distances to modern assemblages of the whole succession. These assemblages were very well preserved, being equivalent in terms of dissolution and fragmentation to those of modern planktonic samples. Diatom assemblages were dominated by *Cyclotella meneghiniana*, *Aulacoseira granulata*, and *A. granulata* var. *angustissima*, which were the dominant taxa in modern planktonic and open-waters habitats. Moreover, low proportions of *L. hungarica* in these levels signal the recent development of the duckweed mats in the lake (Emson et al. 2017). This result is consistent with plant macroremains studies, which indicated increased abundances of *Azolla filliculoides* megaspores and *Lemna* seeds in the upper 20 cm of a Nahuel Rucá core (Stutz et al. 2010). According to age-models available for Nahuel Rucá, these levels would represent the last ca. 70 years BP (Stutz et al. 2014), and coincide with the increase of human activity in the region, particularly of agriculture (Rennella and Quirós 2006). In fact, in Nahuel Rucá a dam was built in the 1950s (Rodolfo Castanas personal communication) on the outflow stream of the lake, when agricultural activities intensified in the area. This dam controlled the lake water level, bringing more stable environmental conditions for flora and fauna development than previously recorded. Previous study of late Holocene assemblages from the nearby Lonkoy Lake (Hassan 2013) also showed increased proportions of *L. hungarica* in the topmost 18 cm of the sedimentary record, which were associated with assemblages indicative of increased nutrient loadings in the lake. It has been suggested that increased nutrient inputs from land fertilization lead to rapid increase of *Lemna* productivity in ponds and that duckweed cover is related to eutrophication (Emson 2015). Therefore, the presence of *L. hungarica* can be interpreted as indicator of human-induced eutrophication in Pampean lakes, and the recent environmental conditions that are very different from the natural fluctuations that characterized the Holocene history of these lakes.

CONCLUSION

Results of the present study indicated a strong interaction between the main sub-environments inhabited by diatoms in the shallow Nahuel Rucá Lake. This interaction was mainly mediated by the water column, which served as a vehicle for the transport of resuspended sediments from within-lake sub-environments and its redistribution among them. Even epiphytic assemblages, which were mostly composed of autochthonous valves, incorporated allochthonous diatoms that originated in sedimentary and planktonic assemblages. This effect was noticeable when analyzing compositional similarities between littoral, open waters and planktonic sub-environments, which showed a high overlap in PCoA multivariate space, although the effect was not strong enough to lead to a complete homogenization of assemblages among them.

Compositional similarities were coupled with similarities in the taphonomic signatures of the valves. Both characteristics were significantly correlated in the dataset. This correlation signals the existence of common environmental constraints for diatom assemblages composition and preservation at within-lake local scales, enhancing the usefulness of diatom taphonomic analysis when conducting compositional studies. In the present work, dissolution was lower and fragmentation higher in the shallower littoral areas, whereas planktonic and open waters sediments showed the opposite pattern. The differences among sub-environments were better delineated by taphonomic, rather than compositional differences, with reworking and water chemistry being the main drivers of these differences. Therefore, it becomes clear that including taphonomic analyses in paleoenvironmental studies provides a useful and independent source of information even when short environmental gradients are covered.

Finally, the application of the contemporary compositional and taphonomic dataset increased the extent of paleoenvironmental inferences made from a core covering the last ca. 700 cal. years BP from Nahuel Rucá history. These analyses allowed us to infer increased salinity conditions towards the base of the core that could be overlooked if only composition of assemblages were addressed. Moreover, the prevalence in modern assemblages of very low percentages of *L. hungarica*, even in littoral sediments adjacent to dense duckweed mats, also demonstrated the importance of considering rare taxa in compositional analyses of paleoenvironments. Overall, we conclude that both taphonomic analyses and a holistic consideration of ecologically meaningful taxa should be considered in order to lead to improved tools for paleoenvironmental reconstructions in environmentally heterogeneous shallow lakes.

ACKNOWLEDGMENTS

Financial support for this study was provided by FONCyT (PICT 2727). We are grateful to Pedro Urrutia for permission to access Estancia Nahuel Rucá, where the lake is located. We also thank Rodolfo Castanas (from Estancia Nahuel Rucá) for providing date on the establishment of the dam in the lake. Two anonymous reviewers made useful comments that improved the manuscript. GS Hassan and CG De Francesco are members of the Scientific Research Career of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

REFERENCES

- ADLER, S. AND HÜBENER, T., 2007, Spatial variability of diatom assemblages in surface lake sediments and its implications for transfer functions: *Journal of Paleolimnology*, v. 37, p. 573–590, doi: 10.1007/s10933-006-9054-1.
- BAE, M.J., LI, F., KWON, Y.S., CHUNG, N., CHOI, H., HWANG, S.J., AND PARK, Y.S., 2014, Concordance of diatom, macroinvertebrate and fish assemblages in streams at nested spatial scales: implications for ecological integrity: *Ecological Indicators*, v. 47, p. 89–101, doi: 10.1016/j.ecolind.2014.07.030.
- BARKER, P., 1992, Differential diatom dissolution in late Quaternary sediments from Lake Manyara, Tanzania: an experimental approach: *Journal of Paleolimnology*, v. 7, p. 235–251, doi: 10.1007/BF00181716.

- BARKER, P., FONTES, J.C., GASSE, F., AND DRUART, J.-C., 1994, Experimental dissolution of diatom silica in concentrated salt solutions and implications for paleoenvironmental reconstruction: *Limnology and Oceanography*, v. 39, p. 99–110, doi: 10.4319/lo.1994.39.1.0099.
- BATTARBEE, R.W., 2000, Palaeolimnological approaches to climate change, with special regard to the biological record: *Quaternary Science Reviews*, v. 19, p. 107–124, doi: 10.1016/S0277-3791(99)00057-8.
- BAUER, D.E., GÓMEZ, N., AND HUALDE, P.R., 2007, Biofilms coating *Schoenoplectus californicus* as indicators of water quality in the Río de la Plata Estuary (Argentina): *Environmental Monitoring and Assessment*, v. 133, p. 309–320, doi: 10.1007/s10661-006-9586-x.
- BEHRENSMEYER, A.K. AND KIDWELL, S.M., 1985, Taphonomy's contributions to Paleobiology: *Paleobiology*, v. 11, p. 105–119.
- BEHRENSMEYER, A.K., KIDWELL, S.M., AND GASTALDO, R.A., 2000, Taphonomy and paleobiology: *Paleobiology*, v. 26, p. 103–147, doi: 10.1666/0094-8373(2000)26[103:TAP]2.0.CO;2.
- BENNETT, K.D., 1996, Determination of the number of zones in a biostratigraphical sequence: *New Phytologist*, v. 132, p. 155–170, doi: 10.1111/j.1469-8137.1996.tb04521.x.
- BENNION, H., SAYER, C.D., TIBBY, J., AND CARRICK, H.J., 2010, Diatoms as indicators of environmental change in shallow lakes, in J.P. Smol and E.F. Stoermer (eds.), *The Diatoms: Applications for the Environmental and Earth Sciences*, second edition, chapter 8: Cambridge University Press, Cambridge, p. 152–173.
- BIRKS, H.J.B., 1998, Numerical tools in palaeolimnology—progress, potentialities, and problems: *Journal of Paleolimnology*, v. 20, p. 307–332, doi: 10.1023/A:1008038808690.
- BIRKS, H.J.B., 2012, Overview of numerical methods in palaeolimnology, in H.J.B. Birks, A.F. Lotter, S. Juggins, and J.P. Smol (eds.), *Tracking Environmental Change Using Lake Sediments*: Springer, Netherlands, p. 19–92.
- BRADBURY, J.P., 1975, Diatom stratigraphy and human settlement in Minnesota: *Geological Society of America, Special Paper*, v. 171, p. 1–74.
- CHARLES, D., DIXIT, S., CUMMING, B., AND SMOL, J.P., 1991, Variability in diatom and chrysophyte assemblages and inferred pH: paleolimnological studies of Big Moose Lake, New York, USA: *Journal of Paleolimnology*, v. 5, 267–284, doi: 10.1007/bf00200350.
- CRISTINI, P.A., TIETZE, E., DE FRANCESCO, C.G., AND MARTÍNEZ, D.E., 2017, Water geochemistry of shallow lakes from the southeastern Pampa plain, Argentina and their implications on mollusk shells preservation: *Science of the Total Environment*, v. 603, p. 155–166, doi: 10.1016/j.scitotenv.2017.06.043.
- DE FRANCESCO, C.G., TIETZE, E., AND CRISTINI, P.A., 2013, Mollusk successions of Holocene shallow-lake deposits from the southeastern Pampa plain, Argentina: *PALAIOS*, v. 28, p. 851–862, doi: 10.2110/palo.2013.100.
- DE NICOLA, D.M., 1986, The representation of living diatom communities in deep-water sedimentary diatom assemblages in two Maine (U.S.A.) lakes, in J.P. Smol, R.W. Battarbee, R.B. Davis, and J. Meriläinen (eds.), *Diatoms and Lake Acidity*, chapter 7: Dr. W. Junk Publishers, Dordrecht, p. 73–85.
- DIOVISALVI, N., BOHN, V.Y., PICCOLO, M.C., PERILLO, G.M.E., BAIGÚN, C., AND ZAGARESE, H.E., 2015, Shallow lakes from the Central Plains of Argentina: an overview and worldwide comparative analysis of their basic limnological features: *Hydrobiologia*, v. 752, p. 5–20, doi: 10.1007/s10750-014-1946-x.
- DONG, X., BENNION, H., BATTARBEE, R., YANG, X., YANG, H., AND LIU, E., 2008, Tracking eutrophication in Taihu Lake using the diatom record: potential and problems: *Journal of Paleolimnology*, v. 40, p. 413–429, doi: 10.1007/s10933-007-9170-6.
- EARLE, J.C., DUTHIE, H., GLOOSCHENKO, W.A., AND HAMILTON, P.B., 1988, Factors affecting the spatial distribution of diatoms on the surface sediments of three Precambrian shield lakes: *Canadian Journal of Fisheries and Aquatic Sciences*, v. 45, p. 469–478, doi: 10.1139/f88-056.
- EMSON, D., 2015, Ecology and palaeoecology of diatom duckweed relationships: Unpublished Ph.D. thesis, University College London, departments of Geography and Botany: Natural History Museum, London, 346 p.
- EMSON, D., SAYER, C.D., BENNION, H., PATMORE, I.R., AND RIOUAL, P., 2017, Mission possible: diatoms can be used to infer past duckweed (lemnoid Araceae) dominance in ponds: *Journal of Paleolimnology*, published online 15 November 2017, doi: 10.1007/s10933-017-0008-6.
- FLOWER, R.J. AND NICHOLSON, A.J., 1987, Relationships between bathymetry, water quality and diatoms in some Hebridean lochs: *Freshwater Biology*, v. 18, p. 71–85, doi: 10.1111/j.1365-2427.1987.tb01296.x.
- FREY, D., 1988, Littoral and offshore communities of diatoms, cladocerans and dipterous larvae, and their interpretation in paleolimnology: *Journal of Paleolimnology*, v. 1, p. 179–191, doi: 10.1007/bf00177764.
- GONZÁLEZ SAGRARIO, M.A. AND FERRERO, L., 2013, The trophic role of *Cyphocharax voga* (Hensel 1869) according to foraging area and diet analysis in turbid shallow lakes: *Fundamental and Applied Limnology*, v. 183, p. 75–88, doi: 10.1127/1863-9135/2013/0385.
- GONZÁLEZ SAGRARIO, M.A., RODRÍGUEZ GOLPE, D., LA SALA, L., SANCHEZ VUICHARD, G., MINOTTI, P., AND PANARELLO, H.O., 2018, Lake size, macrophytes, and omnivory contribute to food web linkage in temperate shallow eutrophic lakes: *Hydrobiologia*, v. 818, p. 87–103, doi: 10.1007/s10750-018-3594-z.
- HABERYAN, K., 1985, The role of copepod fecal pellets in the deposition of diatoms in Lake Tanganyika: *Limnology and Oceanography*, v. 30, p. 1010–1023, doi: 10.4319/lo.1985.30.5.1010.
- HAMM, C.E., MERKEL, R., SPRINGER, O., JURKOIC, P., MAIER, C., PRECHTEL, K., AND SMETACEK, V., 2003, Architecture and material properties of diatom shells provide effective mechanical protection: *Nature*, v. 421, p. 841–843, doi: 10.1038/nature01416.
- HAMMER, Ø., HARPER, D.A.T., AND RYAN, P.D., 2001, PAST: Paleontological Statistics Software Package for Education and Data Analysis: *Palaeontologia Electronica*, v. 4, p. 184.
- HASSAN, G.S., 2013, Diatom-based reconstruction of middle to late Holocene paleoenvironments in Lake Lonkoy, southern Pampas, Argentina: *Diatom Research*, v. 28, p. 473–486, doi: 10.1080/0269249X.2013.851118.
- HASSAN, G.S., 2015a, Variabilidad en la composición de los ensambles de muerte de diatomeas en lagos someros pampeanos y sus implicancias para la construcción de funciones de transferencia: *Ameghiniana*, v. 53, supplement, p. 26.
- HASSAN, G.S., 2015b, On the benefits of being redundant: low compositional fidelity of diatom death assemblages does not hamper the preservation of environmental gradients in shallow lakes: *Paleobiology*, v. 41, p. 154–173, doi: 10.1017/pab.2014.10.
- HASSAN, G.S. AND DE FRANCESCO, C.G., in press, Preservation of *Cyclotella meneghiniana* Kützing (Bacillariophyceae) along a continental salinity gradient: implications for diatom-based paleoenvironmental reconstruction: *Ameghiniana*, preprint doi: 10.5710/AMGH.20.11.2017.3144.
- HASSAN, G.S., TIETZE, E., CRISTINI, P.A., AND DE FRANCESCO, C.G., 2014, Differential preservation of freshwater diatoms and mollusks in late Holocene sediments: paleoenvironmental implications: *PALAIOS*, v. 29, p. 612–623, doi: 10.2110/palo.2014.016.
- HASSAN, G.S., TIETZE, E., DE FRANCESCO, C.G., AND CRISTINI, P.A., 2011, Problems and potentialities of using diatoms as paleoclimatic indicators in central Argentina, in J.C. Compton (ed.), *Diatoms: Ecology and Life Cycle*, chapter 8: Nova Science Publishers, New York, p. 185–216.
- HEGGEN, M., BIRKS, H., HEIRI, O., GRYTNES, J.-A., AND BIRKS, H.J., 2012, Are fossil assemblages in a single sediment core from a small lake representative of total deposition of mite, chironomid, and plant macrofossil remains?: *Journal of Paleolimnology*, v. 48, p. 669–691, doi: 10.1007/s10933-012-9637-y.
- HOAGLAND, K.D., ROSOWSKI, J.R., GRETZ, M.R., AND ROEMER, S.C., 1993, Diatom extracellular polymeric substances: function, fine structure, chemistry, and physiology: *Journal of Phycology*, v. 29, p. 537–566, doi: 10.1111/j.0022-3646.1993.00537.x.
- JACKSON, D.A., 1995, PROTEST: a PROcrustean randomization TEST of community environment concordance: *Ecoscience (Sainte-Foy)*, v. 2, p. 297–303.
- JACKSON, S.T., 2012, Representation of flora and vegetation in Quaternary fossil assemblages: known and unknown knowns and unknowns: *Quaternary Science Reviews*, v. 49, p. 1–15, doi: 10.1016/j.quascirev.2012.05.020.
- JUGGINS, S., 2016, Rioja: analysis of quaternary science data: R package version 0.9-9, available from: <https://cran.r-project.org/package=rioja>.
- KIDWELL, S.M., 2002, Time-averaged molluscan death assemblages: palimpsests of richness, snapshots of abundance: *Geology*, v. 30, p. 803–806, doi: 10.1130/0091-7613(2002)030<0803:TAMDAP>2.0.CO;2.
- KIDWELL, S.M. AND FLESSA, K.W., 1995, The quality of the fossil record: populations, species, and communities: *Annual Review of Ecology and Systematics*, v. 26, p. 269–299, doi: 10.1146/annurev.es.26.110195.001413.
- KINDT, R., 2017, BiodiversityR: GUI for biodiversity, suitability and community ecology analysis. R package version 2.8-0, available from: <https://cran.r-project.org/package=BiodiversityR>.
- KRAMMER, K. AND LANGE-BERTALOT, H., 1997, Bacillariophyceae 2, Teil: Bacillariophyceae, Epithemiaceae, Surirellaceae, in H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer (eds.), *Süßwasserflora von Mitteleuropa* Vol. 2/2: Spektrum Akademischer Verlag, Stuttgart, 610 p.
- KRAMMER, K. AND LANGE-BERTALOT, H., 1999, Bacillariophyceae 1, Teil: Naviculaceae, in H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer (eds.), *Süßwasserflora von Mitteleuropa*, vol. 2/1: Spektrum Akademischer Verlag, Stuttgart, 876 p.
- KRAMMER, K. AND LANGE-BERTALOT, H., 2004a, Bacillariophyceae 3, Teil: Centrales; Fragilariaceae, Eunotiaceae, in H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer (eds.), *Süßwasserflora von Mitteleuropa*, vol. 2/3: Spektrum Akademischer Verlag, Stuttgart, 596 p.
- KRAMMER, K. AND LANGE-BERTALOT, H., 2004b, Bacillariophyceae 4, Teil: Bacillariophyceae, Epithemiaceae, Surirellaceae, in H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer (eds.), *Süßwasserflora von Mitteleuropa*, vol. 2/4: Spektrum Akademischer Verlag, Stuttgart, 468 p.
- LANGE-BERTALOT, H., KÜLBS, K., LAUSER, T., NÖRPEL-SCHEMP, M., AND WILLMANN, M., 1996, Diatom taxa introduced by Georg Krasske documentation and revision: *Iconographia Diatomologica*, v. 3, p. 1–358.
- LARSEN, C.P.S. AND MACDONALD, G.M., 1993, Lake morphometry, sediment mixing and the selection of sites for fine resolution palaeoecological studies: *Quaternary Science Reviews*, v. 12, p. 781–792, doi: 10.1016/0277-3791(93)90017-G.
- LEPŠ, J. AND ŠMILAUER, P., 2003, Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge, 269 p.

- LEVKOV, Z., 2009, *Amphora* sensu lato, in H. Lange-Bertalot (ed.), Diatoms of Europe: Diatoms of European inland waters and comparable habitats, vol. 5: A.R.G. GantnerVerlag KG, Ruggell, 916 p.
- LINK, W.A., BARKER, R.J., SAUER, J.R., AND DROEGE, S., 1994, Within-site variability in surveys of wildlife populations: *Ecology*, v. 75, p. 1097–1108, doi: 10.2307/1939433.
- METZELTIN, D. AND LANGE-BERTALOT, H., 1998, Tropical diatoms of South America I, about 700 predominantly rarely known or new taxa representative of the neotropical flora: *Iconographia Diatomologica*, v. 5, p. 1–695.
- METZELTIN, D. AND LANGE-BERTALOT, H., 2007, Tropical diatoms of South America II, special remarks on biogeographic disjunction: *Iconographia Diatomologica*, v. 18, p. 1–876.
- METZELTIN, D., LANGE-BERTALOT, H., AND GARCÍA-RODRÍGUEZ F., 2005, Diatoms of Uruguay compared with other taxa from South America and elsewhere: *Iconographia Diatomologica*, v. 15, p. 1–736.
- MITCHELL, E.D., PAYNE, R., AND LAMENTOWICZ, M., 2008, Potential implications of differential preservation of testate amoeba shells for paleoenvironmental reconstruction in peatlands: *Journal of Paleolimnology*, v. 40, p. 603–618, doi: 10.1007/s10933-007-9185-z.
- OKSANEN, J., BLANCHET, F.G., FRIENDLY, M., KINDT, R., LEGENDRE, P., MCGILLEN, D., MINCHIN, P.R., O'HARA, R.B., SIMPSON, G.L., SOLYMO, P., HENRY, M., STEVENS, H., SZOEC, E., AND WAGNER, H., 2017, Vegan: community ecology package: R package version 2.4-2, <https://CRAN.R-project.org/package=vegan>.
- PARSONS, K.M. AND BRETT, C.E., 1991, Taphonomic processes and biases in modern marine environments: an actualistic perspective on fossil assemblage preservation, in S.K. Donovan (ed.), *The Processes of Fossilization*: Columbia University Press, New York, p. 22–65.
- PERES-NETO, P.R. AND JACKSON, D.A., 2001, How well do multivariate datasets match? The advantages of a procrustean superimposition approach over the mantel test: *Oecologia*, v. 129, p. 169–178, doi: 10.1007/s004420100720.
- R DEVELOPMENT CORE TEAM, 2016, R: a language and environment for statistical computing: R Foundation for Statistical Computing, Vienna, www.R-project.org.
- REED, J.M., 1998, A diatom-conductivity transfer function for Spanish salt lakes: *Journal of Paleolimnology*, v. 19, p. 399–416, doi: 10.1023/A:1007934627134.
- RENNELLA, A.M. AND QUIRÓS, R., 2006, The effects of hydrology on plankton biomass in shallow lakes of the Pampa Plain: *Hydrobiologia*, v. 556, p. 181–191, doi: 10.1007/s10750-005-0318-y.
- RODRÍGUEZ, P., TELL, G., AND PIZARRO, H., 2011, Epiphytic algal biodiversity in humic shallow lakes from the Lower Paraná River Basin (Argentina): *Wetlands*, v. 31, p. 53–63, doi: 10.1007/s13157-010-0128-5.
- ROJAS, L.A., 2016, Distribución de diatomeas epífitas y su representación en sedimentos en la laguna Nahuel Rucá (Buenos Aires, Argentina): Unpublished M.S. thesis, Universidad Nacional de Mar del Plata, Mar del Plata, 50 p.
- ROJAS, L.A. AND HASSAN, G.S., 2017, Distribution of epiphytic diatoms on five macrophytes from a Pampean shallow lake: host-specificity and implications for paleoenvironmental reconstructions: *Diatom Research*, v. 32, p. 263–275, doi: 10.1080/0269249X.2017.1378128.
- ROUBEIX, V., BECQUEVORT, S., AND LANCELOT, C., 2008, Influence of bacteria and salinity on diatom biogenic silica dissolution in estuarine systems: *Biogeochemistry*, v. 88, p. 47–62, doi: 10.1007/s10533-008-9193-8.
- ROUND, F.E., 1964, The diatom sequence in lake deposits, some problems of interpretation: *Verhandlungen Internationale Vereinigung für Theoretische und angewandte Limnologie*, v. 15, p. 1012–1020.
- RUMRICH, U., LANGE-BERTALOT, H., AND RUMRICH, M., 2000, Diatoms of the Andes from Venezuela to Patagonia/Tierra del Fuego: *Iconographia Diatomologica*, v. 9, p. 1–673.
- RYVES, D.B., BATTARBEE, R., JUGGINS, S., FRITZ, S.C., AND ANDERSON, N.J., 2006, Physical and chemical predictors of diatom dissolution in freshwater and saline lake sediments in North America and West Greenland: *Limnology and Oceanography*, v. 51, p. 1355–1368, doi: 10.4319/lo.2006.51.3.1355.
- RYVES, D.B., BATTARBEE, R.W., AND FRITZ, S.C., 2009, The dilemma of disappearing diatoms: incorporating diatom dissolution data into palaeoenvironmental modelling and reconstruction: *Quaternary Science Reviews*, v. 28, p. 120–136, doi: 10.1016/j.quascirev.2008.08.021.
- RYVES, D.B.R., ANDERSON, N.J., FLOWER, R., AND RIPPEY, B., 2013, Diatom taphonomy and silica cycling in two freshwater lakes and their implications for inferring past lake productivity: *Journal of Paleolimnology*, v. 49, p. 411–430, doi: 10.1007/s10933-013-9694-x.
- SAR, E.A., SALA, S.E., SUNESEN, I., HENNINGER, S., AND MONTASTRUT, M., 2009, Catálogo de los géneros, especies y taxa intraespecíficos erigidos por J. Frenguelli, in A. Witkowski (ed.), *Diatom Monographs*, vol. 10: Koeltz Scientific Books, Koenigstein, 419 p.
- SAWAI, Y., 2001, Distribution of living and dead diatoms in tidal wetlands of northern Japan: relations to taphonomy: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 173, p. 125–141, doi: 10.1016/S0031-0182(01)00313-3.
- SMOL, J.P., 1981, Problems associated with the use of “Species Diversity” in paleolimnological studies: *Quaternary Research*, v. 15, p. 209–212, doi: 10.1016/0033-5894(81)90105-8.
- SMOL, J.P., 1992, Paleolimnology: an important tool for effective ecosystem management: *Journal of Aquatic Ecosystem Health*, v. 1, p. 49–58, doi: 10.1007/BF00044408.
- SMOL, J.P. AND STOERMER, E.F., 2010, *The Diatoms: Applications for the Environmental and Earth Sciences*: Cambridge University Press, Cambridge, 667 p.
- SPEYER, S.E. AND BRETT, C.E., 1986, Trilobite taphonomy and Middle Devonian Taphofacies: *PALAIOS*, v. 1, p. 312–327, doi: 10.2307/3514694.
- STAFF, G.M. AND POWELL, E.N., 1990, Local variability of taphonomic attributes in a parautochthonous assemblage: can taphonomic signature distinguish a heterogeneous environment?: *Journal of Paleontology*, v. 64, p. 648–658, doi: 10.1017/S0022336000042682.
- STUTZ, S.M., BOREL, M., FONTANA, S.L., DEL PUERTO, L., INDA, H., GARCÍA-RODRÍGUEZ, F., AND TONELLO, M.S., 2010, Late Holocene climate and environment of the SE Pampa grasslands, Argentina, inferred from biological indicators in shallow, freshwater Lake Nahuel Rucá: *Journal of Paleolimnology*, v. 44, p. 761–775, doi: 10.1007/s10933-010-9450-4.
- STUTZ, S.M., TONELLO, M.S., GONZÁLEZ-SAGRARIO, M.A., NAVARRO, D., AND FONTANA, S., 2014, Historia ambiental de los lagos someros de la llanura Pampeana (Argentina) desde el Holoceno medio: Inferencias paleoclimáticas: *Latin American Journal of Sedimentology and Basin Analysis*, v. 21, p. 119–138.
- TIETZE, E. AND DE FRANCESCO, C.G., 2017, Compositional fidelity and taphonomy of freshwater mollusks in three pampean shallow lakes of Argentina: *Ameghiniana*, v. 54, p. 208–223, doi: 10.5710/AMGH.18.10.2016.3022.
- TOMAŠOVÝCH, A. AND KIDWELL, S.M., 2009, Fidelity of variation in species composition and diversity partitioning by death assemblages: time-averaging transfers diversity from beta to alpha levels: *Paleobiology*, v. 35, p. 94–118, doi: 10.1666/08024.1.
- TOMAŠOVÝCH, A. AND ZUSCHIN, M., 2009, Variation in brachiopod preservation along a carbonate shelf-basin transect (Red Sea and Gulf of Aden): Environmental sensitivity of taphofacies: *PALAIOS*, v. 24, p. 697–716, doi: 10.2110/palo.2009.p09-018r.
- VAN CAPPELLEN, P., DIXIT, S., AND VAN BEUSEKOM, J., 2002, Biogenic silica dissolution in the oceans: reconciling experimental and field-based dissolution rates: *Global Biogeochemical Cycles*, v. 16, p. 1075, doi:10.1029/2001GB001431.
- WETZEL, R., 2001, *Limnology: Lake and River Ecosystems*: Academic Press, San Diego, 1006 p.
- ZAR, J.H., 2010, *Biostatistical Analysis*, fifth edition: Prentice Hall, Englewood Cliffs, 945 p.

Received 28 December 2017; accepted 23 May 2018.