DIFFERENTIAL PRESERVATION OF FRESHWATER DIATOMS AND MOLLUSKS IN LATE HOLOCENE SEDIMENTS: PALEOENVIRONMENTAL IMPLICATIONS

GABRIELA S. HASSAN, ELEONOR TIETZE, PAULA A. CRISTINI, AND CLAUDIO G. DE FRANCESCO

Grupo de Ecología y Paleoecología de Ambientes Acuáticos Continentales, Instituto de Investigaciones Marinas y Costeras (IIMyC), CONICET-Universidad Nacional de Mar del Plata, Juan B. Justo 2550, 1 Piso, 7600, Mar del Plata, Argentina

e-mail: ghassan@mdp.edu.ar

ABSTRACT: One of the limitations of paleoenvironmental reconstructions based on multiple bioindicators is a lack of knowledge on the differential preservation of hard parts, which may lead to biases in interpretation. This is particularly important when biological proxies differ in their intrinsic properties, such as skeletal mineralogy or size. We explored and compared the preservational patterns of siliceous (diatoms) and carbonate (mollusks) fossils during the late Holocene (ca. 4000 cal. years B.P.) in two lacustrine sedimentary successions from Argentina (Nahuel Rucá and Hinojales–San Leoncio). Fragmentation and fine-scale surface-alteration indices were calculated on two target species: the diatom *Cyclotella meneghiniana* Kützing and the snail *Heleobia parchappii* (d'Orbigny, 1835). The taphonomic data were smoothed along depth with a locally weighted regression (LOESS) and statistically compared using Spearman correlations. Additionally, past environmental conditions were inferred from the autoecology of the dominant taxa. Diatoms and mollusks displayed similar tendencies in fragmentation, characterized by a gradual decrease of breakage toward the top of the successions. On the other hand, trends in surface preservation were opposite. Diatoms exhibited higher alteration in the oldest sedimentary levels, characterized as saline and less-productive water bodies, while mollusks were more altered at the topmost levels, characterized as freshwater highly productive lakes. This contrasting response of both indicators can be interpreted as a consequence of the differential reaction of carbonate and silica to dissolution agents acting in fresh and saline water. Hence, the accuracy of the paleoenvironmental information provided by both indicators under these contrasting conditions probably would be affected by the taphonomic biases suffered, which highlight the relevance of including taphonomic traits in Quaternary paleoenvironmental or paleoclimatic studies.

INTRODUCTION

It is now widely recognized that multi-proxy approaches are more reliable than single-proxy approaches to reconstruct past environments (e.g., Lotter 2003; Birks and Birks 2006). Different proxies reflect diverse environmental factors at a range of spatial scales and consequently show different strengths and weaknesses. By combining proxies, strengths can be exploited and weaknesses identified (Birks and Birks 2006). The differential preservation and ecological relationships of proxies are among the most commonly overlooked issues in paleoenvironmental reconstructions. As biological proxies are subject to distinct taphonomic biases because of their intrinsic properties (skeletal mineralogy, morphology, strength, size, etc.), a key goal to improve the quality of multi-proxy paleoenvironmental reconstructions is to understand the differences in preservation potential of the organisms that are used as bioindicators (Smol 2009).

Diatoms and mollusks are two widely used paleoenvironmental indicators (see Battarbee et al. 2001; De Francesco 2013, and references therein) that significantly differ in their intrinsic properties. Diatoms are unicellular microorganisms, with a size range of 2 to 500 μm and preservable parts composed of silicon dioxide (SiO_2; Smol and Stoermer 2010). Experimental studies indicate that pH, temperature, salinity, and ionic strength are the most significant factors affecting frustule dissolution (e.g., Lewin 1961; Flower 1993; Barker et al. 1994; Ryves et al. 2006). On the other hand, mollusk shells are macrofossils (~1–1000 mm) composed of calcium carbonate ($CaCO_3$) in the form of aragonite or calcite (Taylor and Reid 1990). In continental settings, their preservation is closely related to pH, calcium (Ca^{+2}), bicarbonate (HCO_3^-), and carbonate (CO_3^{2-}) concentrations (see Kidwell and Bosence 1991, and references therein). Additionally, the preservation of diatoms and mollusks is also related to the physical characteristics of the environment (Walker and Goldstein 1999; Ryves et al. 2003; Zuschin et al. 2003; Olzsewski 2004). In fact, diatom frustules and mollusk shells are subjected to mechanical destruction as consequence of sediment reworking and resuspension (Flower and Nicholson 1987; Olszewski 2004), which are related to water depth, lake fetch, and wind exposure (Wetzel 2001). Studies on comparative taphonomy of mollusks and foraminifera indicate that preservation is scale dependent (Walker and Goldstein 1999). Therefore, it is expected that the preservation of diatoms and mollusks may also vary to a great extent.

In this contribution, we explore the preservational patterns of diatoms and mollusks during the late Holocene in two shallow lakes of the southern Pampas (Argentina). Previous studies of these records indicated the occurrence of wide paleoenvironmental changes, particularly related to fluctuations in salinity, water depth, and nutrient status (Stutz et al. 2010, 2012; De Francesco et al. 2013; Hassan 2013). These environmental changes may have affected diatom and mollusk preservation in different ways. Therefore, the sedimentary successions analyzed here provide an excellent opportunity to study and compare the magnitude of those differences. The results will allow combining taphonomy and community
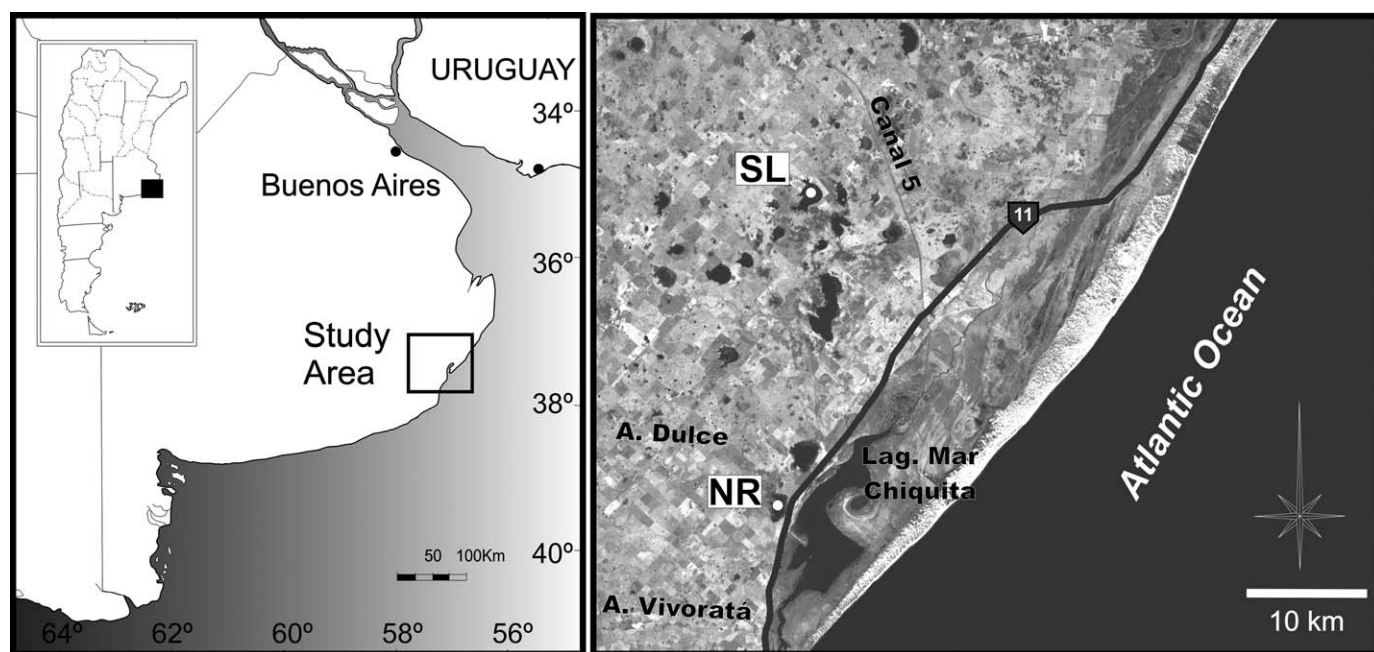
Fig. 1.—Location of study area. SL = Hinojales–San Leoncio, NR = Nahuel Rucá.

paleoecology as a way to improve the accuracy of paleoenvironmental reconstructions based on both indicator taxa.

STUDY AREA

The study was conducted in two shallow lakes located in the southeastern Pampa Plain (Buenos Aires province, Argentina), close to the Atlantic Coast (Fig. 1): (1) Hinojales–San Leoncio (SL, 37°23′24″S; 57°24′17″W) and (2) Nahuel Rucá (NR, 37°37′21″S; 57°25′42″W). These lakes have a surface area of approximately 250 ha and a depth <1.5 m, and are separated by approximately 20 km.

The Pampa Plain is a vast grassy plain characterized by uniform relief. The climate is temperate humid or subhumid with a mean annual temperature of 15 °C and a mean annual precipitation of 1100 mm (Feijoó and Lombardo 2007). Due to the gentle slope of the region, the Pampa Plain is characterized by numerous permanent and temporary shallow lakes, which are small (< 500 ha) and very shallow (< 2 m), and are affected by episodic flooding and drought. Most of them are turbid lakes due to the high amount of algae, while a few are clear macrophyte-dominated lakes (Quirós et al. 2002). These basins and associated paleodunes were probably formed under arid conditions by deflation by the prevailing Westerly Winds (Westerlies) during the late Pleistocene. With the onset of moister Holocene conditions these depressions became areas of groundwater discharge and surface water accumulation, filling gradually with sediment that contains abundant fossils (Stutz et al. 2010).

MATERIAL AND METHODS

Cores for diatom and mollusk analyses were obtained from the deepest point of each lake with a 7-cm-diameter vibracore during 2012. The SL core (113 cm long) has been analyzed for pollen and nonpollen palynomorphs (NPPs) by Peña (2012) and for mollusks by De Francesco et al. (2013). Five AMS ^{14}C dates (from 6401 to 398 cal. years B.P.) were determined on *Heleobia parchappii* (d'Orbigny, 1835) shells. In the present contribution, the study was focused on the late Holocene (last ca. 4000 years BP; uppermost 80 cm). The NR core (140 cm long) was

obtained from the same site where Stutz et al. (2010) extracted a sedimentary core for analysis of pollen, NPPs, calcareous microfossils, plant macrofossils, diatoms, chrysophyte cysts, and opal phytoliths. Based on sedimentology and stratigraphy, the new section was correlated with the previous one, and chronology adjusted with two new dates by De Francesco et al. (2013). Five AMS ^{14}C dates (from 174 to 3788 cal. years B.P.) were determined on *H. parchappii* shells and *Schoenoplectus californicus* (C.A. Meyer) Soják achenes. See De Francesco et al. (2013) for details on lithology and chronology of SL and NR cores.

Samples for diatom analysis were selected at 2 cm intervals and prepared following the procedure of Renberg (1990), which reduces damage to valves compared with more traditional methods (Ryves et al. 2002). After complete homogenization, a subsample was transferred to a coverslip and air dried for 1 h. 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. Light micrographs were taken using a Leica ICC50 digital camera. For scanning electron microscope (SEM) analysis, cleaned material was mounted on 3-μm-pore polytungstate membrane filters, sputter coated with 12 nm gold, and examined using a Jeol JSM-6460LV SEM operating at 15kV. Diatom taxa were identified according to standard floras (see Hassan 2013, for details). Preservation was evaluated under 1000× magnification using the dominant diatom *Cyclotella meneghiniana* Kützing as a target taxon and with a sample size of 50 individuals. 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). The obtained data were used to calculate the F dissolution and breakage 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 to $F = 0$, indicating all valves appear dissolved/broken under LM. To maximize potential information from more dissolved valves, the
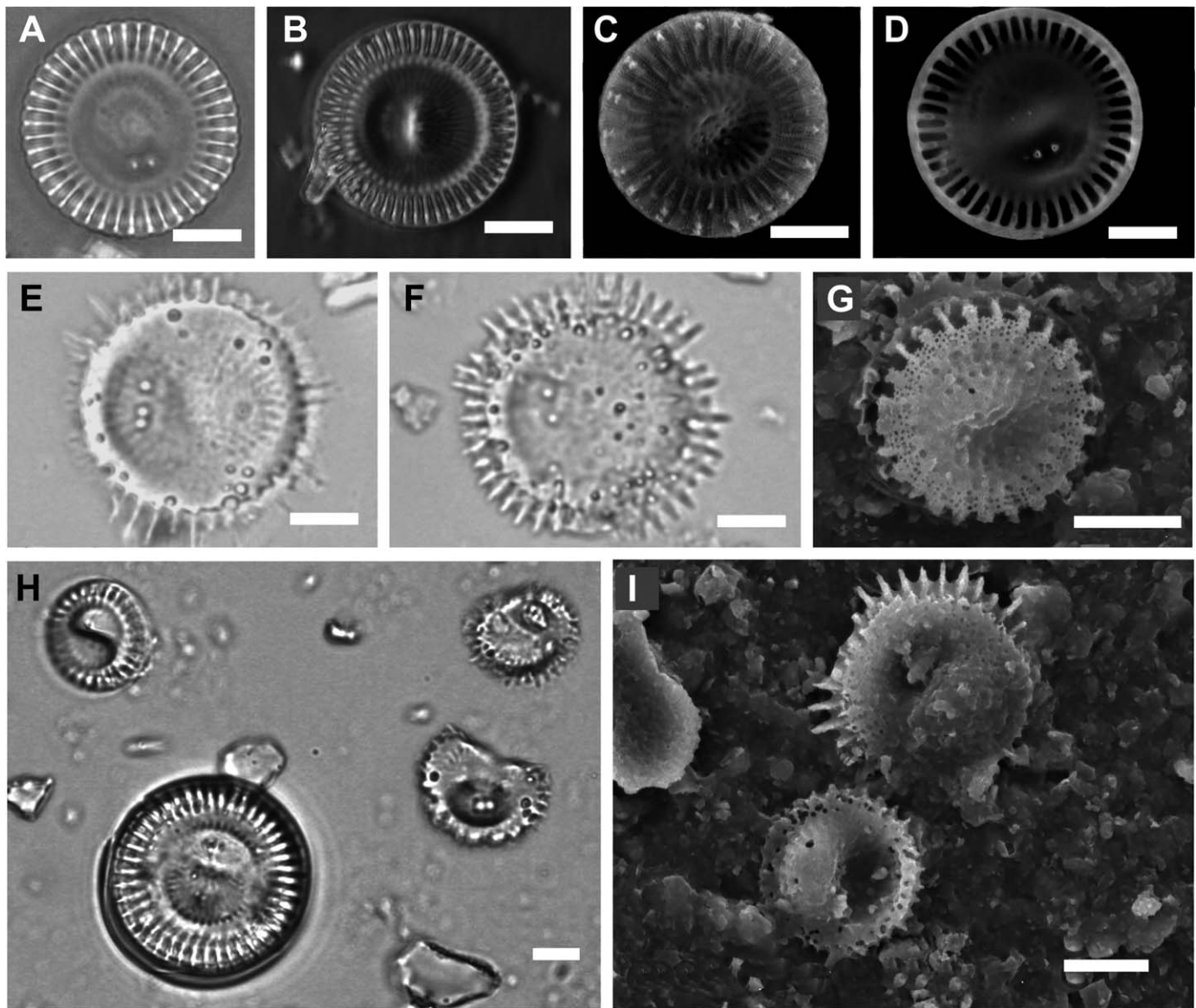
F$_{IG}$. 2.—Scanning electron micrographs (C, D, G, I) and light micrographs (A, B, E, F, H) of A–D) pristine and E–I) dissolved valves of *Cyclotella meneghiniana* preserved in Hinojales–San Leoncio and Nahuel Rucá. Scale bars = 5 µm.

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, a Diatom Fragmentation Index (DFI) was also calculated by applying the same equation to *C. meneghiniana* fragmentation data.

Raw data on mollusk abundance and preservation were taken from De Francesco et al. (2013). In that work, samples were collected at 1 cm intervals, the volume of each sample measured, and then sieved (1 φ), carefully washed (avoiding breakage of shells), and dried at room temperature. All mollusks recovered were counted and sorted at the species level under stereoscopic microscope (10×). In order to avoid influence by species-dependent preservational factors, in the present contribution the dominant taxon *H. parchappii* was selected as a target taxon for taphonomic analyses. The taphonomic signature of shells and shell fragments was examined under stereoscopic microscope. Two taphonomic variables: (1) degree of fragmentation and (2) fine-scale surface alteration (*sensu* Best and Kidwell 2000; i.e., the taphonomic alteration produced by abrasion, dissolution and/or bioerosion on the shell surface) were scored on each sample in a three-grade scale: good (0 = best preservation; < 10% of alteration), fair (1 = intermediate, between 10% and 50% of alteration), and poor (2 = poorest; > 50% of alteration). The magnitude of each taphonomic variable was subsequently averaged for each sample. Correlations between dissolution and fragmentation for each bioindicator taxon were evaluated for each core using Spearman correlation coefficients.
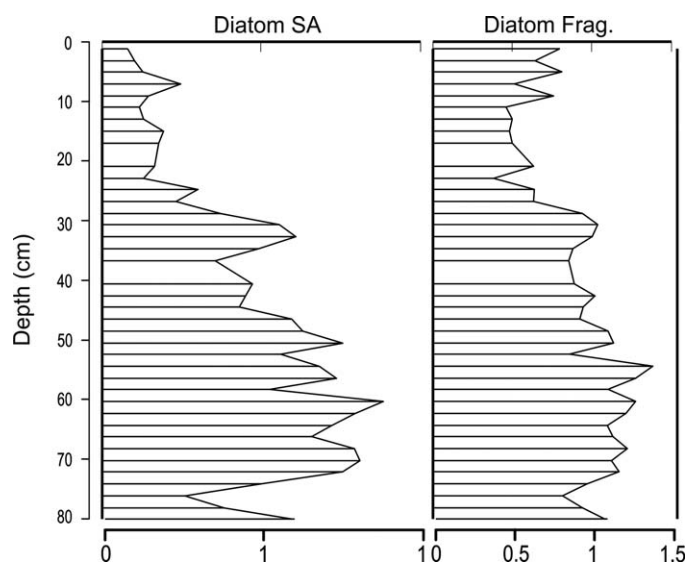
FIG. 3.—Surface alteration (SA) and fragmentation (Frag.) of diatom valves from Lake Hinojales–San Leoncio.

FIG. 4.—Surface alteration (SA) and fragmentation (Frag.) of diatom valves from Lake Nahuel Rucá.

In order to allow a direct comparison between diatom and mollusk data, the taphonomic variables were smoothed along depth with a locally weighted regression (LOESS; Cleveland et al. 1993) in order to standardize the resolution of both records. LOESS smoothers are nonparametric local regressions that use a parametric regression within a span defined by the user that subsequently combines all these parametric regressions into one regression. The smoothing process is considered local because each smoothed value is determined by neighboring data points (subset) defined within a span. LOESS is nonparametric in the sense that the fitting technique does not require an *a priori* specification of the relationship between the dependent and independent variables (Jacoby 2000). A span of 0.33 was used; this span defines the subset of data points included in each local regression and must be defined by the user. From this regression an estimate of the taphonomic variables was interpolated for the midpoint of each depth. These values were used for a tendency comparison which was evaluated using Spearman correlation coefficients. All statistical analyses and graphs were performed in R version 2.14.0 (R Development Core Team 2009), including the package "rioja" version 0.5–6 (Juggins 2009).

RESULTS

Taphonomy

Diatom Preservation.—The preservation of valves of *C. meneghiniana* was highly variable, with both pristine and highly damaged individuals represented (Fig. 2). DDI ranged between 0.20 and 1.80 in SL and between 0.10 and 1.36 in NR. The DFI values showed a smaller variation, ranging between 0.38 and 1.40 in SL and between 0.40 and 1.30 in NR (Figs. 3–4). DDI was significantly correlated to DFI both in SL ($r = 0.34$; $p < 0.01$) and NR ($r = 0.70$; $p < 0.001$).

At the base of the SL core (between 80 and 75 cm), diatom preservation was characterized by dissolution and fragmentation mean values smaller than 1 (DDI = 0.87 ± 0.29; DFI = 0.95 ± 0.11, Fig. 3). Values increased between 75 and 45 cm, reaching values higher than 1 (DDI = 1.41 ± 0.20; DFI = 1.14 ± 0.14, Fig. 3). Between 45 and 27 cm both indices decreased (DDI = 0.93 ± 0.17; DFI = 0.95 ± 0.07, Fig. 3) until they reached the best preservation of the sequence toward the top or the core (between 27 and 0 cm; DDI = 0.33 ± 0.13; DFI = 0.60 ± 0.14, Fig. 3).
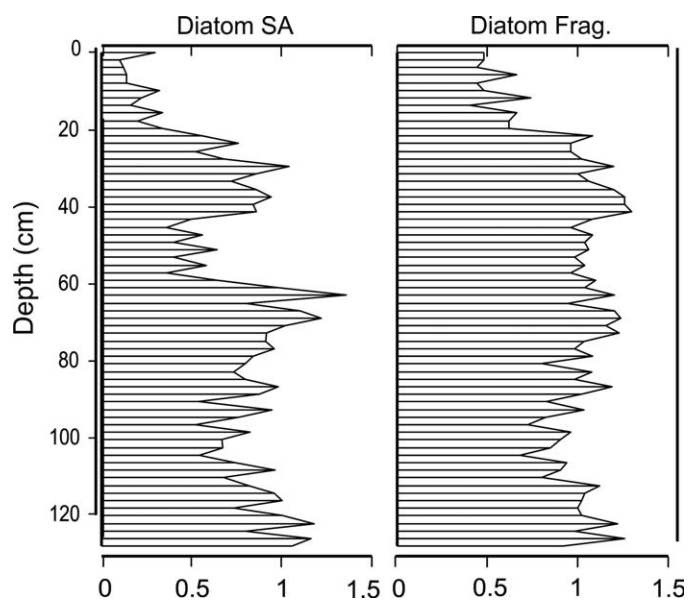
Diatom preservation from the base of the NR core (between 130 and 113 cm) was characterized by dissolution and fragmentation mean values ranging around 1 (DDI = 0.97 ± 0.15; DFI = 1.06 ± 0.11, Fig. 4). These values slightly decreased to values smaller than 1 between 113 and 91 cm (DDI = 0.71 ± 0.15; DFI = 0.86 ± 0.10, Fig. 4). A further increase in the values of taphonomic indices was registered between 91 and 61 cm, reaching values similar to the base of core (DDI = 0.95 ± 0.17; DFI = 1.07 ± 0.12, Fig. 4). Between 61 and 43 cm the dissolution state of *C. meneghiniana* significantly improved, while fragmentation remained constant (DDI = 0.40 ± 0.11; DFI = 1.03 ± 0.05, Fig. 4). Between 43 and 21 cm, fragmentation remained constant and dissolution showed a further increase (DDI = 0.78 ± 0.15; DFI = 1.12 ± 0.13, Fig. 4), followed by a significant diminution toward the top of the sequence (between 21 and 0 cm), where valves showed the lowest values of both indices (DDI = 0.22 ± 0.10; DFI = 0.55 ± 0.11, Fig. 4).

Mollusk Preservation.—Both records registered fluctuations in the taphonomic attributes of *H. parchappii* shells. Valves were very scarce at the topmost section of the cores, and were too few in number to perform reliable taphonomic analyses. Overall, most shells showed signs of fragmentation, whereas surface alteration ranged from shells without any sign of alteration to highly altered shells (Fig. 5). Surface alteration values ranged between 0.008 and 0.3 in SL and between 0.03 and 0.97 in NR. Fragmentation reached higher values, ranging between 0.25 and 1.26 in SL and between 1 and 2 in NR (Figs. 6–7). Surface alteration was negatively correlated to fragmentation in SL ($r = -0.29$; $p < 0.05$) and positively in NR ($r = 0.34$; $p < 0.01$).

In the basal levels of the SL core (between 80 and 70 cm), the preservation of mollusk shells was characterized by very low surface alteration and fragmentation values smaller than 1 (SA = 0.07 ± 0.07; F = 0.74 ± 0.11, Fig. 6). Between 70 and 50 cm a slight decrease in surface alteration values, accompanied by a small increase in fragmentation values, was recorded (SA = 0.05 ± 0.02; F = 1.10 ± 0.10, Fig. 6). Between 50 and 29 cm a further decrease in both indices was recorded, although it was very small in the case of surface alteration (SA = 0.04 ± 0.04; F = 0.85 ± 0.13, Fig. 6). Finally, shells from the top of the core (between 29 and 18 cm) showed the highest surface alteration and lowest

FIG. 5.—Fossil shells of *Heleobia parchappii* showing different degrees of surface alteration. Left to right: good, fair, and poor shell conditions. Scale bar = 2 mm.
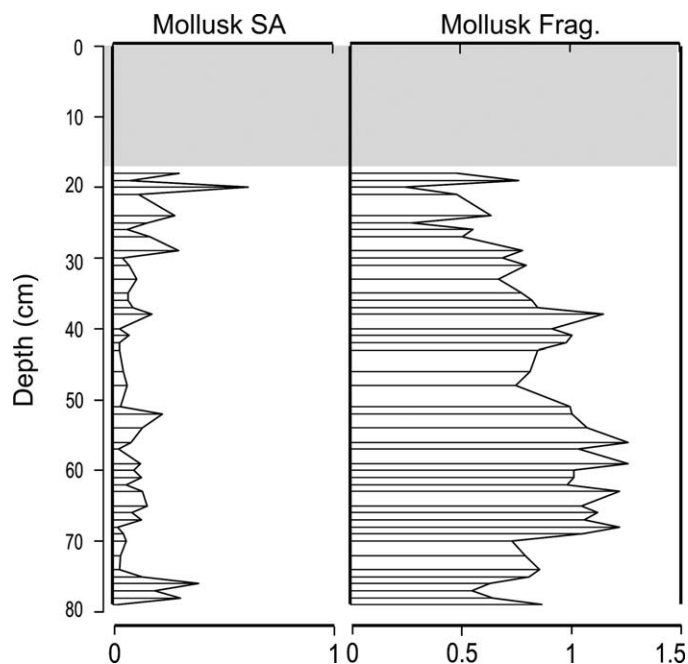
fragmentation of the whole sequence (SA = 0.11 ± 0.10; F = 0.49 ± 0.17, Fig. 6).

Mollusk shells from the basal levels of the NR core (between 126 and 103 cm) were characterized by low surface alteration and very high fragmentation values (SA = 0.21 ± 0.10; F = 1.80 ± 0.12, Fig. 7). Between 103 and 65 cm a slight decrease in both taphonomic attributes

FIG. 6.—Surface alteration (SA) and fragmentation (Frag.) of mollusk shells from Lake Hinojales–San Leoncio. Shaded zones indicate sedimentary levels with no data.
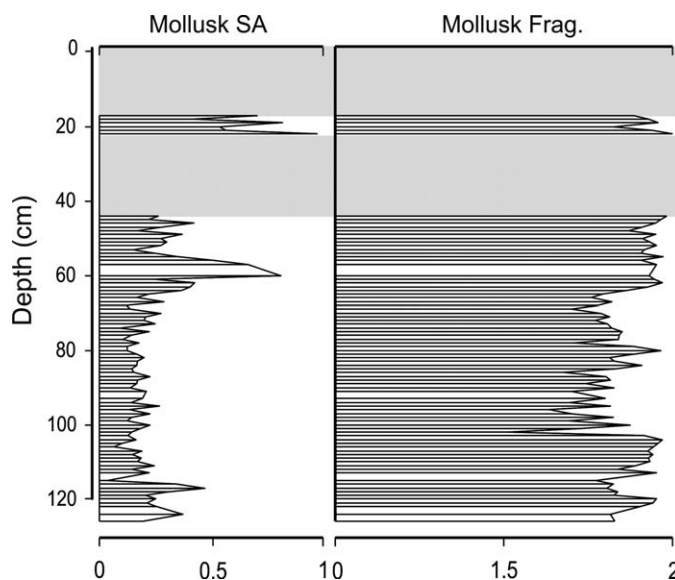

FIG. 7.—Surface alteration (SA) and fragmentation (Frag.) of mollusk shells from Lake Nahuel Rucá. Shaded zones indicate sedimentary levels with no data.

was recorded (SA = 0.17 ± 0.05; F = 1.57 ± 0.17, Fig. 7). Between 65 and 44 cm a further increase in both indices was recorded, reaching values closer to those of the base of the sequence (SA = 0.35 ± 0.16; F = 1.86 ± 0.06, Fig. 7). Finally, shells from the top of the sequence (between 22 and 17 cm) showed the highest surface alteration of the whole core, while fragmentation values remained high (SA = 0.66 ± 0.20; F = 1.84 ± 0.12, Fig. 7).

Diatom-Mollusk Comparative Taphonomy.—Both mollusks and diatoms showed similar tendencies of skeletal breakage, with an overall tendency for less fragmentation toward the top of the sequences (Fig. 8). The only exceptions were the mollusks from NR, which did not show decreased fragmentation at the top. There were significant positive correlations between the LOESS smoothers of both variables for NR (r = 0.31; p < 0.001) and SL (r = 0.87; p < 0.001).

On the other hand, comparison between DDI and mollusk surface alteration provided strong evidences of a negative relationship between these variables in both lacustrine records (Fig. 9). In fact, levels containing well-preserved diatoms also contained the worst-preserved mollusks, while levels with better preserved mollusks also contained the worst-preserved diatom frustules. There were significant negative correlations between the LOESS smoothers of both variables for NR (r = −0.34; p < 0.001) and SL (r = −0.42; p < 0.01).

Paleoecology

SL.—A total of 136 diatom and five mollusk taxa were preserved in this section (Fig. 10). Between the base and 70 cm, diatom assemblages were dominated by a mixture of brackish to hypersaline taxa, such as *Cocconeis placentula* Ehrenberg, *Navicula salinicola* Hustedt, *Cyclotella choctawhatcheeana* Prasad, *Cyclotella meneghiniana*, *Navicula cincta* (Ehrenberg) Ralfs, *Nitzschia hustedtiana* Salah, and *Staurosirella pinnata* (Ehrenberg) Williams and Round. Mollusk assemblages were dominated by the brackish/freshwater mudsnail *Heleobia parchappii* (which was in fact the dominant mollusk species all along the core; see De Francesco et al. 2013), accompanied by low proportions of *Biomphalaria peregrina* (d'Orbigny, 1835).

Between 70 and 65 cm, diatom assemblages were characterized by an increase in the relative abundance of *N. hustedtiana.* This zone was also characterized by the appearance of the estuarine gastropod *Heleobia australis* (d'Orbigny, 1835) and a few specimens of the hygrophilous land snail *Succinea meridionalis* d'Orbigny, 1846.

Between 65 and 25 cm, there was a decrease in the frequency of *N. hustedtiana,* while *N. cincta* and *S. pinnata* remained stable. The section was characterized by the appearance of freshwater diatoms such as *Pseudostaurosira brevistriata* (Grunow) Williams and Round, *Aulacoseira granulata* (Ehrenberg) Simonsen, and *Hippodonta hungarica* (Grunow) Lange-Bertalot, Metzeltin and Witkowski. Mollusk assemblages were characterized by a gradual increase in the abundance of the freshwater pulmonate *B. peregrina*. Low abundance of the freshwater limpet *Uncancylus concentricus* (d'Orbigny, 1835) was also present in this zone. The proportions of *H. parchappii* and *H. australis* remained relatively constant.

In the topmost 25 cm, diatom assemblages were composed of the freshwater taxa *P. brevistriata, A. granulata, A. granulata* var. *angustissima* (Müller) Simonsen, *H. hungarica, C. placentula, C. meneghiniana, Achnanthes delicatissima* Simonsen, and *Navicula* sp. 3. Only the mollusks *H. parchappii* and *B. peregrina* were recorded in this section.

NR.—A total of 117 diatom and 5 mollusk taxa were identified in the NR core (Fig. 11). From the base to 70 cm, diatom assemblages were dominated by the freshwater planktonic *A. granulata* and the brackish/ freshwater *C. meneghiniana,* accompanied by low percentages of benthic and epiphytic taxa, such as *H. hungarica, Aulacoseira muzzanensis* (Meister) Krammer, *Epithemia adnata* (Kützing) Brébisson, and the brackish *N. cincta* and *Pseudostaurosira subsalina* (Hustedt) Morales. Some levels containing high proportions of the aerophilous *Denticula elegans* Kützing were also registered at nearly 100 cm. Mollusk assemblages were composed of *H. parchappii, B. peregrina, S. meridionalis*, and *H. australis*.

Between 70 and 40 cm, diatom assemblages were characterized by increases in the percentages of freshwater/brackish benthic and periphytic taxa, such as *Nitzschia amphibia* Grunow, *P. subsalina, C. placentula,* and *E. adnata*. Mollusks showed a decrease in the relative abundance of *H. parchappii*, an increase in the frequency of *B. peregrina*, and small proportions of *U. concentricus* and *S. meridionalis.*

Between 40 and 22 cm, diatom assemblages were characterized by the presence of large proportions of the freshwater taxa *Staurosira longirostris* (Frenguelli) Metzeltin, Lange-Bertalot, and García-Rodríguez and *Aulacoseira granulata* var. *angustissima*, while mollusks were absent from those levels.

Between 22 and 18 cm, a further increase in the proportions of benthic and periphytic taxa, such as *N. amphibia*, *C. placentula*, *Epithemia adnata*, and *Epithemia sorex* Kützing was registered. A mollusk assemblage dominated by *B. peregrina* and low proportions of *H. parchappii* reappeared in this section of the core.

In the topmost 18 cm, diatom assemblages were dominated by *C. meneghiniana, A. granulata, A. granulata* var. *angustissima, C. placentula,* and *H. hungarica*. Mollusks were absent here.

DISCUSSION

Diatom Preservation

Results from both sedimentary records showed significant correlations of diatom dissolution and fragmentation, which is in agreement with previous studies carried out in other continental settings (Ryves et al. 2006). High-energy environments may promote valve dissolution through breakage, which is intimately linked to wind speed, fetch, and water depth. Moreover, continuous resuspension of valves may enhance dissolution in Si-undersaturated waters (Ryves et al. 2006). Given the low water levels that would have characterized the San Leoncio and Nahuel Rucá lakes during the late Holocene, it is expected that reworking and resuspension would have played a key role in diatom preservation.

Paleoenvironmental changes, particularly related to variations in salinity, explain the observed taphonomic changes in diatom assemblages. The worst preservation was coincident with assemblages indicative of brackish to hypersaline conditions, in some cases associated with subaerial exposure. Saline shallow lakes are prone to periodic desiccation, which can lead to severely damaged diatom records as a consequence of aerial exposure or breakage caused by the growth of salt crystals inside diatom frustules (Flower 1993). Moreover, dissolution weakens the valves and makes them more susceptible to breakage (Ryves et al. 2013). Hence, the high salinities and low lake levels inferred at the base of both sequences could have significantly altered diatom remains.

Two factors may be related to the improvement in the preservation of diatoms recorded toward the top of the successions. First, the development of highly vegetated freshwater lakes during the last ca. 400 years BP, as indicated by diatom and mollusk assemblages, could be linked to the decrease in the salinity in both lakes, and therefore, better diatom preservation. It is known that silica dissolution is positively correlated to salinity (Ryves et al. 2006 and references therein), but the chemical causes of this interaction are not clearly known (Roubeix et al. 2008). Second, increase in sedimentation rates over the last ca. 500 years BP could have influenced diatom preservation by increasing burial rates and reducing the exposure of valves to taphonomic processes. Well-

Diatom DFI (—●—)

Mollusk fragmentation (- - - ○ - - -)
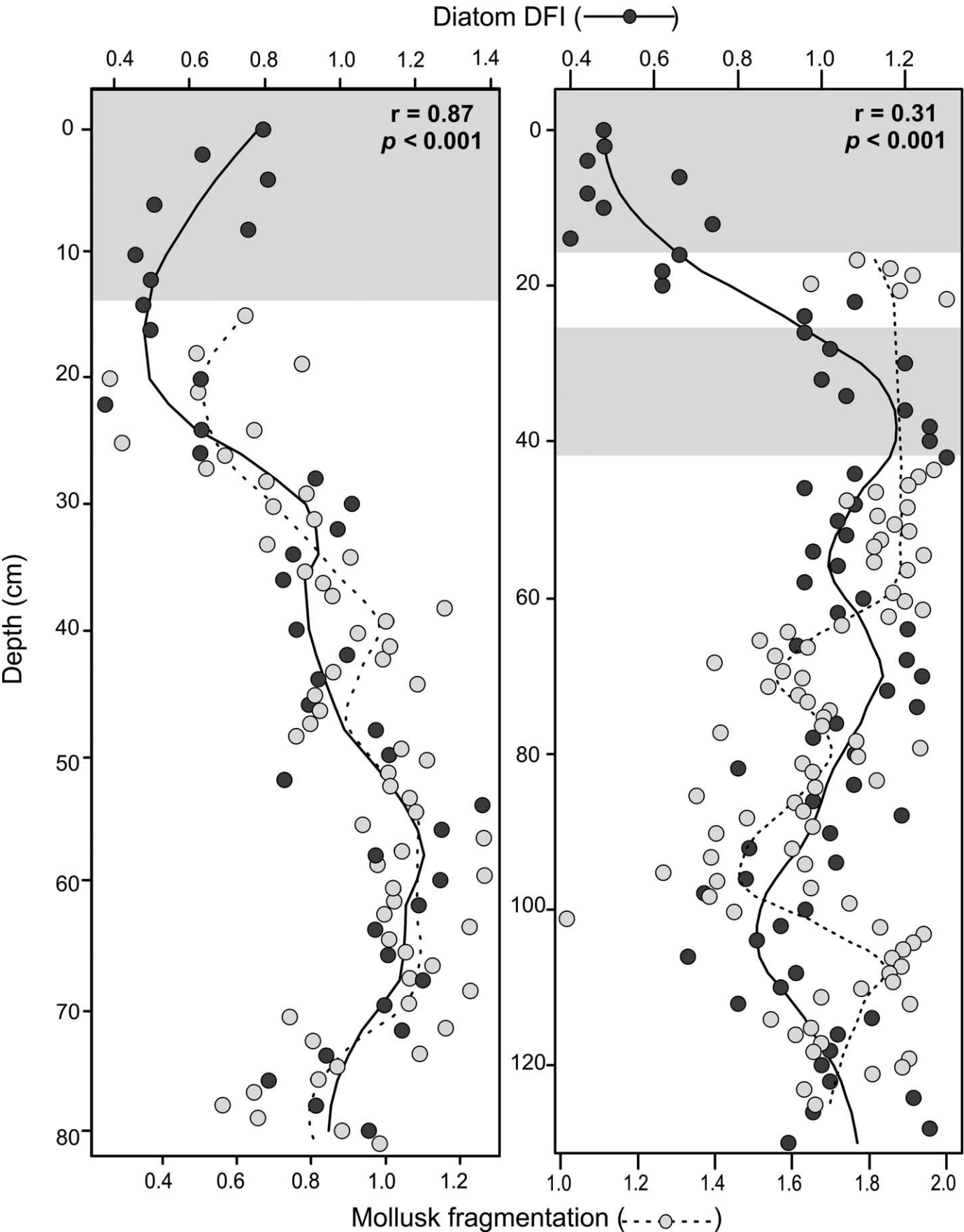
preserved fossil assemblages generally reflect accumulation over short time spans (Brandt 1989). Hence, recent diatom assemblages preserved in SL and NR would have spent less time in the sediment-water interface than older assemblages, allowing a rapid deposition of pristine valves that suffered very little dissolution and breakage as lakes became less saline during the late Holocene.

The strong taphonomic alterations exhibited by diatom assemblages preserved in SL and NR highlight the importance of incorporating preservational aspects in paleolimnological interpretation of diatoms. Results indicate that taphonomic processes have played a critical role by altering and probably biasing fossil assemblages. Stratigraphic intervals strongly affected by dissolution may have, in fact, lost part of the diatom assemblage, leading to the preservation of the most resistant frustules. Although the target taxon, *Cyclotella meneghiniana*, has experimentally proven to be very sensitive to dissolution, it is also more resistant than many other less silicified taxa (Ryves et al. 2001), which could have been completely lost during fossilization. Overall, paleoenvironmental inferences derived from these taphonomically altered levels are prone to uncertain errors.

Mollusk Preservation

Mollusks showed an inverse pattern of variation between fragmentation and surface alteration in SL but a similar trend in NR. Physical abrasion, dissolution, and bioerosion would be among the main taphonomic processes responsible for shell surface alteration and fragmentation. Mollusk fragmentation is difficult to interpret because it can be broadly caused by ecological, biostratinomic, or diagenetic processes, and also depends on shell strength. Breakage resulting from these mechanisms generally cannot be distinguished from that caused by most crushing predation. Similarly, abrasion can produce fractures and fragmentation, but fragments are an unreliable measure of this environmental variable (Zuschin et al. 2003). On the other hand, surface alteration may be responding to dissolution (chemical or biological in origin) according to results obtained in actualistic taphonomic studies conducted in these Pampean lakes (Cristini and De Francesco 2012; Tietze and De Francesco 2014). Therefore, those levels characterized by high surface alteration and low fragmentation would have been subjected to higher influence of biogeochemical dissolution than levels characterized by lower surface alteration.

The variations in these preservational traits along the cores may provide important clues for recognizing the influence of different environments on preservation. In fact, taphonomic changes agree well with environmental changes (see De Francesco et al. 2013). For example, surface alteration was lower in levels where brackish to saline water conditions were inferred. This was particularly clear in the lower-middle section of the cores, characterized by the excellent preservation of *H. parchappii* in correspondence with the presence of *H. australis* and *S. meridionalis*. The preservation potential of mollusks in hard water is higher than in fresh water, mainly because the former is saturated with respect to calcium carbonate (Hagan et al. 1998), and because biological activity that may result in bioturbation is lower. In addition, it is expectable that shells have also grown heavier in brackish habitats because of the higher concentration of calcium and bicarbonates (see Zalizniak et al. 2006 and references therein). Moreover, the subaerial exposure suggested by the presence of *S. meridionalis* and aerophilous diatoms may have been responsible for the higher shell fragmentation recorded at the base.

On the other hand, in the younger levels characterized by freshwater conditions (middle-top section of the cores) surface alteration was higher,

indicating poorer preservation. Moreover, in the topmost levels mollusks were very scarce, probably as consequence of a combination of poor preservation and increased sedimentation rates. The poorer preservation of mollusk shells in freshwater may be explained by the lower concentrations of carbonate and bicarbonates in the water as well as by increased biological activity as a consequence of higher nutrient levels. Fungi, algae, and bacteria have been mentioned as responsible for the dissolution of shells in freshwater settings (Hagan 1998). Also, dissolution or etching by roots and rhizoids of lacustrine plants may be significant. Root penetration was evident in many short cores taken from Lake Nahuel Rucá (Cristini and De Francesco 2012). These Pampean lakes increased their nutrient levels during the late Holocene (Stutz et al. 2012; Hassan 2013) and, consequently, their biological activity. At ca. 700 cal. years B.P., belts of diverse emergent macrophytes and carpets of free-floating plant species developed, representing the onset of the modern lake conditions (Stutz et al. 2010, 2012). Therefore, the influence of bioinduced dissolution on mollusk shells may have become more intense during the last centuries.

Diatom-Mollusk Comparative Taphonomy

Diatoms and mollusks displayed opposite trends of surface preservation in both lacustrine records. Overall, mollusks showed less surface alteration in the most ancient sedimentary levels, and tended to deteriorate toward the top of both sequences. Diatoms, on the other hand, were strongly dissolved in the basal levels and improved considerably toward the youngest sediments. This contrasting response of both indicators can be interpreted as a consequence of the differential reaction of carbonate and siliceous remains to dissolution agents. The high salinities inferred at the basal levels of both sequences would have differentially affected diatom and mollusks shells: while the higher carbonate and calcium concentrations would have favored the development of thicker and stronger mollusk shells, it would have inhibited diatom preservation by increasing silica solubility. This tendency would have become reversed toward the top of both cores: as shallow lakes evolved to less saline and more productive conditions, the preservation of diatoms became favored; while an increase in bioturbation activity (by an augmentation in vegetation cover) together with higher carbonate dissolution (because of low carbonate and calcium concentrations in freshwater) would have favored mollusk destruction.

Trends in diatom and mollusk shell fragmentation were very similar, particularly in the SL core. Both indicators showed a general tendency to better preservation at the top of the sequences, except for the mollusks of NR, which were heavily fragmented and showed no trend all along the core. The similar tendency of shell breakage is suggesting that fragmentation may have been related to physical and mechanical environmental processes rather than biogeochemical factors. The most heavily fragmented shells would have been exposed to higher reworking and subaerial exposure as a consequence of lower sedimentation rates, resulting in intense destruction of both diatoms and mollusks. Overall, physical processes seem to have produced similar biases in diatom and mollusk records; whereas biogeochemical processes causing surface alteration and dissolution generated opposite taphonomic signatures.

CONCLUSIONS

The differential preservation exhibited by diatoms and mollusks highlights the potential bias that taphonomic processes can produce on the fossil record. Although Quaternary paleoenvironmental studies are usually based on a high number of biological proxies (i.e., pollen, plant

---

←

FIG. 8.—Plots of diatom fragmentation index (black circles) and mollusk fragmentation (gray circles) and corresponding LOESS smoothers against depth in Nahuel Rucá (left) and Hinojales–San Leoncio (right). Values of correlation (r) among diatom and mollusk LOESS curves and its significance (p) are given.
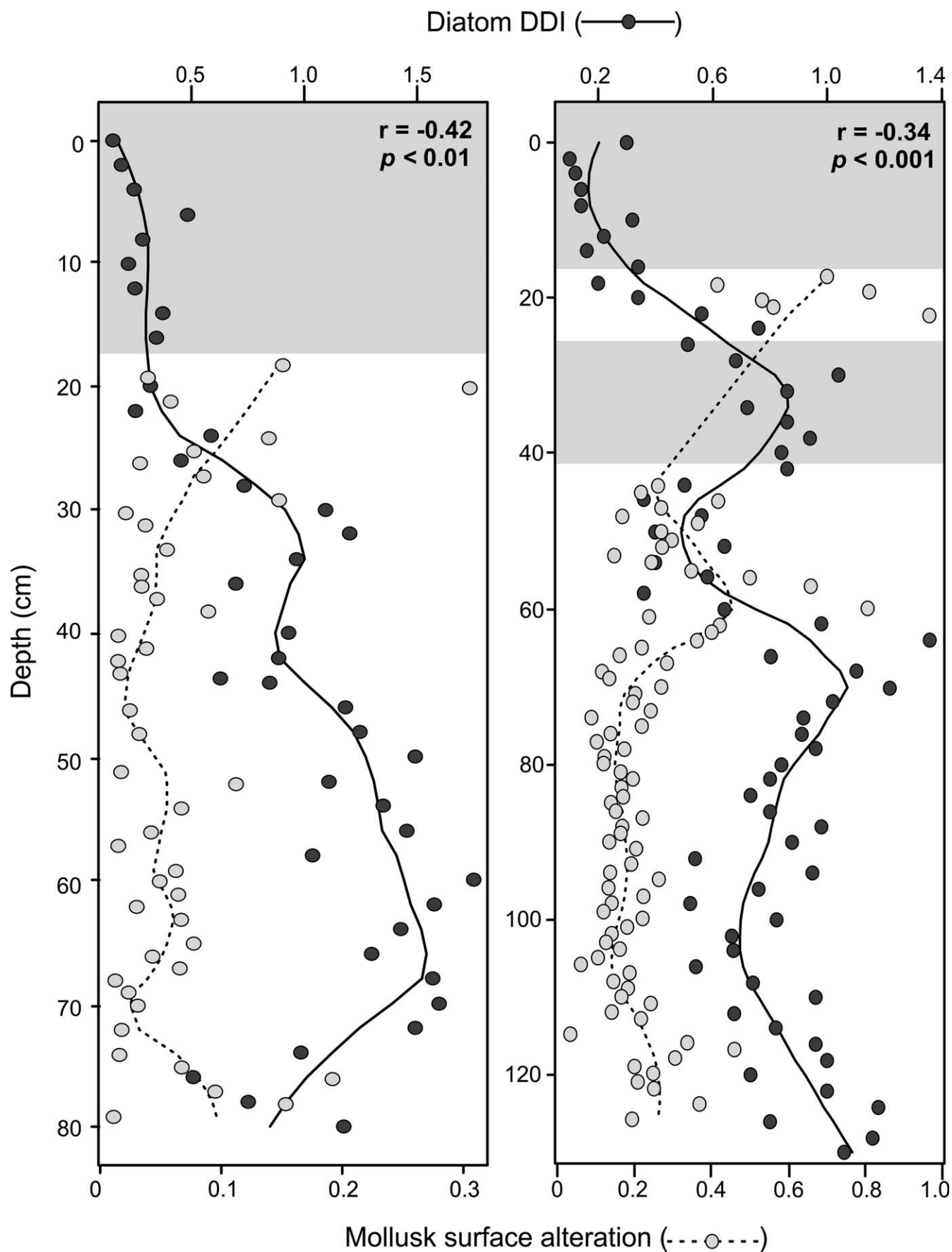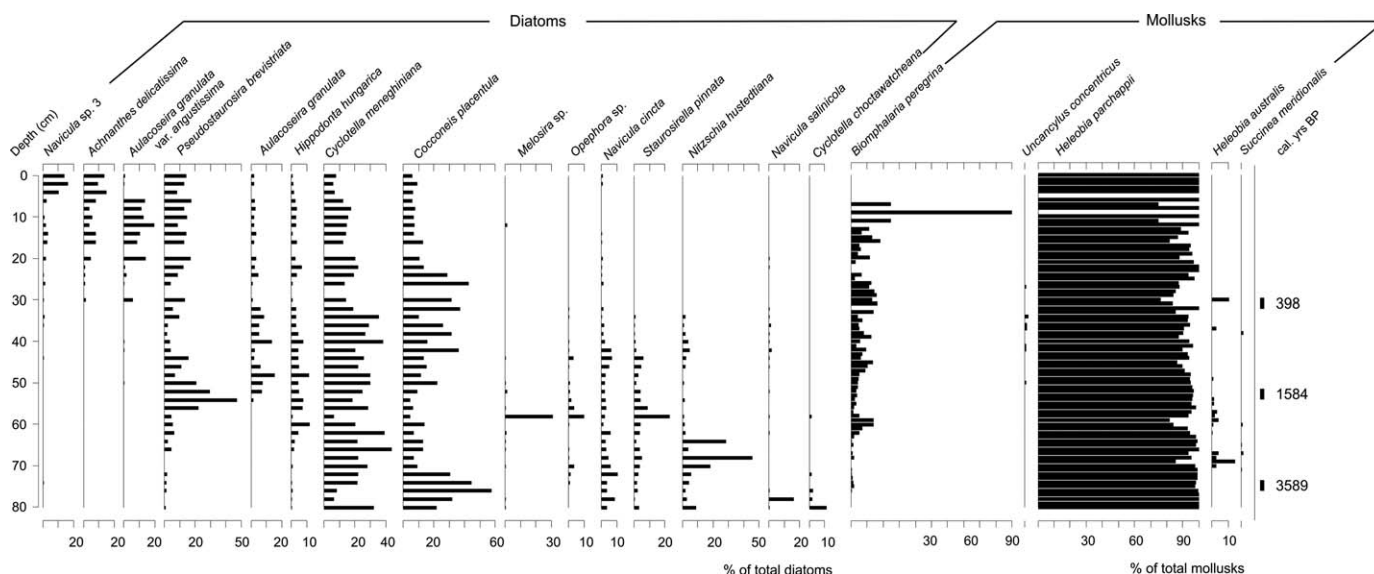
FIG. 10.—Relative abundance (%) of diatom and mollusk species along the sedimentary succession of Hinojales–San Leoncio.

macrofossils, charophytes, ostracoda, cladocera, chironomidae, chrisophyte, phytoliths, diatoms, mollusks, etc.), taphonomic biases are rarely considered. Hence, variations in the relative abundances of species through time are generally interpreted in terms of changing environments, with the assumption that fossil assemblages faithfully reflect the original composition of the living communities and reflect species-environment relationships of the living assemblages. This assumption has proven to be erroneous in many situations, not only by our own results, but also by several taphonomic studies that reported preservational biases both on organic (e.g., Campbell and Campbell 1994; Campbell 1999; Wilmshurst and McGlone 2005; Zonneveld et al. 2008; Tweddle and Edwards 2010) and inorganic-walled (e.g., Danielopol et al. 1987; Piperno 1993; Flower and Ryves 2009) bioindicators. As the strength and direction of these biases would differ among the different proxies, it can constitute a key overlooked factor that could lead to significant and unpredictable errors on multi-proxy paleoenvironmental reconstructions. Hence, detailed consideration of taphonomic data in these studies should be imperative in order to improve the interpretation of community data by identifying parts of the record that may have been biased or altered in some way, and to select the best indicator for each circumstance.

REFERENCES

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.

BATTARBEE, R.W, JONES, V.J., FLOWER, R.J., CAMERON, N.G., BENNION, H., CARVALHO, L., AND JUGGINS, S., 2001, Diatoms, in Smol, J.P., Birks, H.J.B., and Last, W.M., eds., Tracking Environmental Change Using Lake Sediments, vol. 3: Terrestrial, Algal, and Siliceous Indicators: Dordrecht, Kluwer Academic Publishers, p. 155–202.

BEST, M.M.R., AND KIDWELL, S.M., 2000, Bivalve taphonomy in tropical mixed siliciclastic-carbonate settings. I. Environmental variation in shell condition: Paleobiology, v. 26, p. 80–102, doi: 10.1666/0094-8373(2000)026<0080:BTITMS>2.0.CO;2.

BIRKS, H.H., AND BIRKS, H.J.B., 2006, Multi-proxy studies in palaeolimnology: Vegetation History and Archaeobotany, v. 15, p. 235–251, doi: 10.1007/s00334-006-0066-6.

BRANDT, D.S., 1989, Taphonomic grades as a classification for fossiliferous assemblages and implications for paleoecology: PALAIOS, v. 4, p. 303–309, doi: 10.2307/3514554.

CLEVELAND, W.S., GROSSE, E., AND SHYU, W.M., 1993, Local regression models, in Chambers, J.M, and Hastie, T.J., eds., Statistical Models in S: London, Chapman and Hall, p. 309–376.

CAMPBELL, I.D., 1999, Quaternary pollen taphonomy: examples of differential redeposition and differential preservation: Palaeogeography, Palaeoclimatology, Palaeoecology, vol. 149, p. 245–256, doi: 10.1016/S0031-0182(98)00204-1.

CAMPBELL, I.D, AND CAMPBELL, C., 1994, Pollen preservation: experimental wet-dry cycles in saline and desalinated sediments: Palynology, vol. 18, p. 5–10.

CRISTINI, P.A., AND DE FRANCESCO, C.G., 2012, Análisis tafonómico de moluscos por debajo de la interfase agua-sedimento en la laguna Nahuel Rucá (provincia de Buenos Aires, Argentina): Ameghiniana, v. 49, p. 594–605, doi: 10.5710/AMGh.1.12.2012.352.

DANIELOPOL, D.L., CASALE, L.M., AND OLTEANU, R., 1987, On the preservation of carapaces of some limnic ostracods: an exercise in actuopalaeontology, in Löffler, H., ed., Paleolimnology IV: Amsterdam, Springer Netherlands, p. 143–157.

DE FRANCESCO, C.G., 2013, Freshwater molluscs, in Elias, S., ed., The Encyclopedia of Quaternary Science, vol. 3: Amsterdam, Elsevier, p. 281–291.

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.

FEIJOÓ, C.S., AND LOMBARDO, R.J., 2007, Baseline water quality and macrophyte assemblages in Pampean streams: a regional approach: Water Research, v. 41, p. 1399–1410, doi: 10.1016/j.watres.2006.08.026.

FLOWER, R.J., 1993, Diatom preservation: experiments and observations on dissolution and breakage in modern and fossil material: Hydrobiologia, v. 269–270, p. 473–484, doi: 10.1007/BF00028045.

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.

FLOWER, R.J., AND RYVES, D.B., 2009, Diatom preservation: differential preservation of sedimentary diatoms in two saline lakes: Acta Botanica Croatica, v. 68, p. 381–399.

HAGAN, T.H., CONIGLIO, M., AND EDWARDS, T.W.D., 1998, Subfossil bioerosion of mollusc shells from a freshwater lake, Ontario, Canada: Ichnos, v. 6, p. 117–127, doi: 10.1080/10420949809386442.

←

FIG. 9.—Plots of diatom dissolution index (black circles) and mollusk surface alteration (gray circles) and corresponding LOESS smoothers against depth in Nahuel Rucá (left) and Hinojales–San Leoncio (right). Values of correlation (r) among diatom and mollusk LOESS curves and its significance (p) are given.
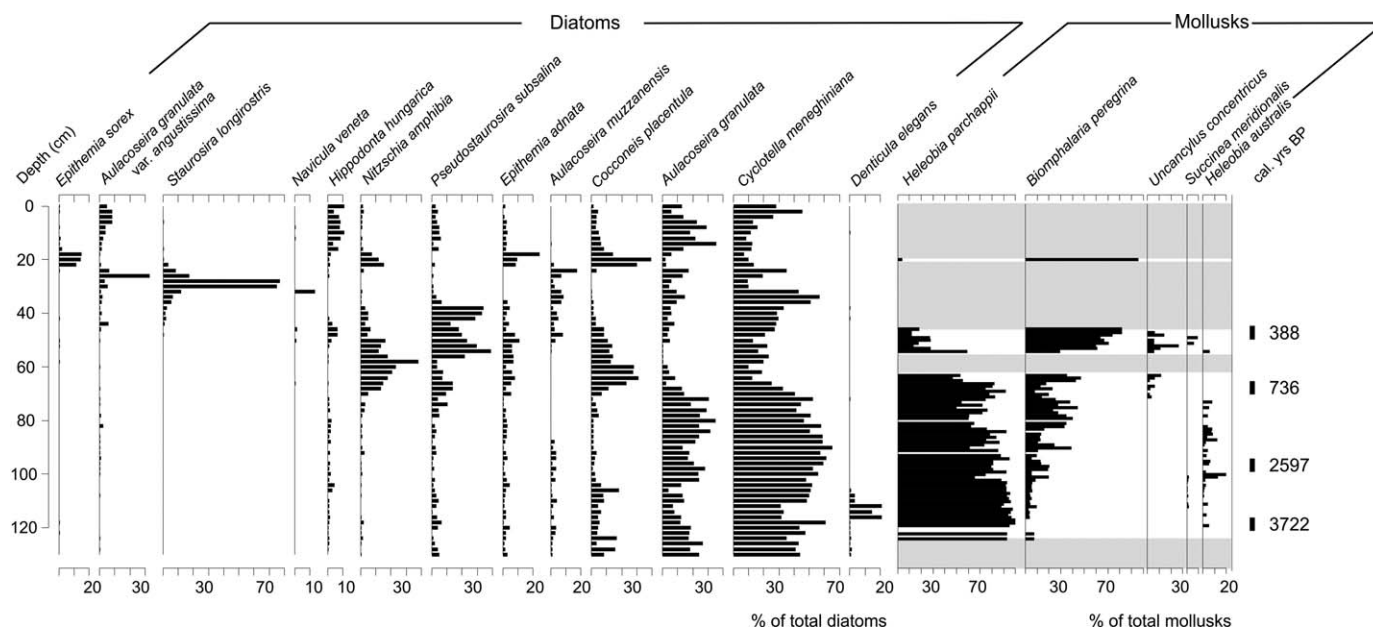
FIG. 11.—Relative abundance (%) of diatom and mollusk species along the sedimentary succession of Nahuel Rucá.

HAGAN, T.H., CONIGLIO, M., AND EDWARDS, T.W.D., 1998, Subfossil bioerosion of mollusc shells from a freshwater lake, Ontario, Canada: Ichnos, v. 6, p. 117–127, doi: 10.1080/10420949809386442.

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.

JACOBY, W.G., 2000, Loess: a nonparametric, graphical tool for depicting relationships between variables: Electoral Studies, v. 19, p. 577–613, doi: 10.1016/S0261-3794(99)00028-1.

JUGGINS, S., 2009, Rioja: analysis of quaternary science data, R package version 0.5–6, http://cran.r-project.org/package=rioja, October 2009.

KIDWELL, S.M., AND BOSENCE, D.W.J., 1991, Taphonomy and time-averaging of marine shelly faunas, in Allison, P.A., and Briggs, D.E.G., eds. Taphonomy: Releasing the Data Locked in the Fossil Record: New York, Plenum Press, p. 115–209.

LEWIN, J.C., 1961, The dissolution of silica from diatom walls: Geochimica et Cosmochimica Acta, v. 21, p. 182–198, doi: 10.1016/S0016-7037(61)80054-9.

LOTTER, A.F., 2003, Multi-proxy climatic reconstructions, in Battarbee, R., Mackay, A., Birks, H.J.B., and Oldfield, F., eds., Global Change in the Holocene: London, Arnold, p. 373–383.

OLSZEWSKI, T.D., 2004, Modeling the influence of taphonomic destruction, reworking, and burial on time-averaging in fossil accumulations: PALAIOS, v. 19, p. 39–50, doi: 10.1669/0883-1351(2004)019<0039:MTIOTD>2.0.CO;2.

PEÑA, L., 2012, Reconstrucción de la historia reciente de los lagos someros del SE de la llanura Pampeana a partir del análisis de múltiples indicadores: Unpublished M.S. thesis, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina, 47 p.

PIPERNO, D.R., 1993, The nature and status of phytolith analysis, in Pearsall, D.M., and Piperno, D.R., eds., Current Research in Phytolith Analysis: Applications in Archaeology and Paleoecology: University of Pennsylvania, Philadelphia, Pennsylvania, p. 9–18.

QUIRÓS, R., RENELLA, A.M., BOVERI, M.B., ROSSO, J.J., AND SOSNOVSKY, A., 2002, Factores que afectan la estructura y el funcionamiento de las lagunas pampeanas: Ecología Austral, v. 12, p. 175–185.

R DEVELOPMENT CORE TEAM, 2009, R: a language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, http://www.R-project.org, October 2009.

RENBERG, I., 1990, A procedure for preparing large sets of diatom slides from sediment cores: Journal of Paleolimnology, v. 4, p. 87–90, doi: 10.1007/BF00208301.

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.

RYVES, D.B., JUGGINS, S., FRITZ, S.C., AND BATTARBEE, R.W., 2001, Experimental diatom dissolution and the quantification of microfossil preservation in sediments: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 172, p. 99–113, doi: 10.1016/S0031-0182(01)00273-5.

RYVES, D.B., MCGOWAN, S., AND ANDERSON, N.J., 2002, Development and evaluation of a diatom-conductivity model from lakes in West Greenland: Freshwater Biology, v. 47, p. 995–1014, doi: 10.1046/j.1365-2427.2002.00832.x.

RYVES, D.B., JEWSON, D.H., STURM, M., BATTARBEE, R.W., FLOWER, R.J., MACKAY, A.W., AND GRANIN, N.G., 2003, Quantitative and qualitative relationships between planktonic diatom communities and diatom assemblages in sedimenting material and surface sediments in Lake Baikal, Siberia: Limnology and Oceanography, v. 48, p. 1643–1661, doi: 10.4319/lo.2003.48.4.1643.

RYVES, D.B., BATTARBEE, R.W., 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., ANDERSON, N.J., FLOWER, R.J., 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.

SMOL, J.P., 2009, Pollution of Lakes and Rivers. A Paleoenvironmental Perspective: New York, Oxford University Press Inc.

SMOL, J.P., AND STOERMER, E.F., 2010, The Diatoms: Applications for the Environmental and Earth Sciences: Cambridge, UK, Cambridge University Press, 396 p.

STUTZ, S.M., BOREL, C.M., FONTANA, S., 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., BOREL, C.M., FONTANA, S., AND TONELLO, M.S., 2012, Holocene changes in trophic states of shallow lakes from the Pampa plain of Argentina: The Holocene, v. 22, p. 1263–1270, doi: 10.1177/0959683612446667.

TAYLOR, J.D., AND REID, D.G., 1990, Shell microstructure and mineralogy of the Littorinidae: ecological and evolutionary significance: Hydrobiologia, v. 193, p. 199–215, doi: 10.1007/BF00028077.

TIETZE, E., AND DE FRANCESCO, C.G., 2014, Taphonomic differences in molluscan shell preservation in freshwater environments from southeastern Pampas, Argentina: PALAIOS, v. 29, p. 501–511, doi: 10.2110/palo.2014.019.

TWEDDLE, J.C., AND EDWARDS, K.J., 2010, Pollen preservation zones as an interpretative tool in Holocene palynology: Review of Palaeobotany and Palynology, v. 161, p. 59–76, doi: 10.1016/j.revpalbo.2010.03.004.

WALKER, S.E., AND GOLDSTEIN, S.T., 1999, Taphonomic tiering: experimental field taphonomy of molluscs and foraminifera above and below the sediment–water interface: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 149, p. 227–244, doi: 10.1016/S0031-0182(98)00203-X.

WETZEL, R., 2001, Limnology: Lake and River Ecosystems: San Diego, Academic Press, 1006 p.

WILMSHURST, J.M., AND MCGLONE, M.S., 2005, Origin of pollen and spores in surface lake sediments: comparison of modern palynomorph assemblages in moss cushions, surface soils and surface lake sediments: Review of Palaeobotany and Palynology, v. 136, p. 1–15, doi: 10.1016/j.revpalbo.2005.03.007.

ZALIZNIAK, L., KEFFORD, B.J., AND NUGEGODA, D., 2006, Is all salinity the same? I. The effect of ionic compositions on the salinity tolerance of five species of freshwater invertebrates: Marine and Freshwater Research, v. 57, p. 75–82, doi: 10.1071/MF05103.

ZONNEVELD, K.A.F., VERSTEEGH, G., AND KODRANS-NSIAH, M., 2008, Preservation and organic chemistry of late Cenozoic organic-walled dinoflagellate cysts: A review: Marine Micropaleontology, v. 68, p. 179–197, doi: 10.1016/j.marmicro.2008.01.015.

ZUSCHIN, M., STACHOWITSCH, M., AND STANTON, R.J., JR., 2003, Patterns and processes of shell fragmentation in modern and ancient marine environments: Earth-Science Reviews, v. 63, p. 33–82, doi: 10.1016/S0012-8252(03)00014-X.