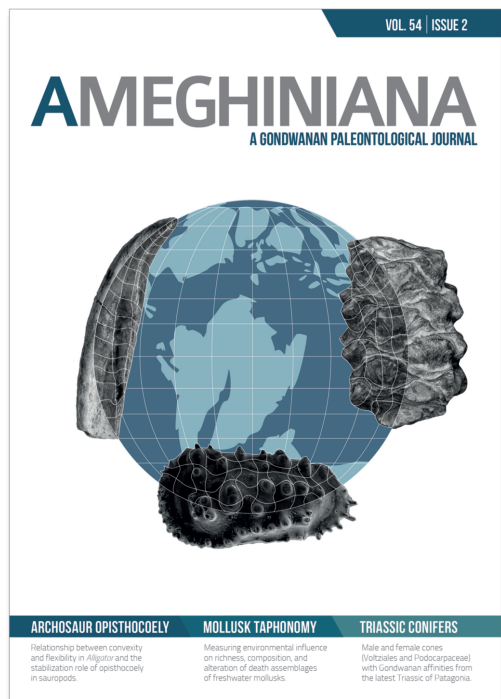




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COMPOSITIONAL FIDELITY AND TAPHONOMY OF FRESHWATER MOLLUSKS FROM THREE PAMPEAN SHALLOW LAKES OF ARGENTINA

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Abstract. Three shallow lakes from the southeastern pampas, which are different in their physicochemical characteristics, were studied with the aim of comparing live/dead fidelity and preservation of mollusk shells. The studied lakes were Las Mostazas, Los Carpinchos and Nahuel Rucá, which proved different in terms of their specific richness, abundance, compositional fidelity and taphonomic alteration. The lake that presented the higher values of conductivity (3.34 ± 0.72), hardness ($286 \pm 83 \text{ mg l}^{-1}$) and carbonates saturation index ($SI_{\text{calcite}} = 1.95 \pm 0.21$) was the one for which lower specific richness in living assemblages was recorded and differences in richness and diversity between the living and the dead assemblages became apparent. It was also the lake where the number of species was higher in death assemblages ($R = 5$) than in living communities ($R = 2$). Such characteristics suggest a higher residence time in the taphonomically active zone. On the other hand, the lakes featuring lower values of the same characteristics (conductivity = 2.2 ± 1.2 ; 0.8 ± 0.5 ; hardness = 157 ± 55 ; $250 \pm 127 \text{ mg l}^{-1}$; saturation index of calcite = 0.35 ± 0.15 ; 0.43 ± 0.36 , for LC and NR respectively) presented a higher species richness, lower numbers of species in death assemblages ($R = 8$) than in living communities ($R = 10$) and taphonomic attributes that suggested recently dead and deposited individuals. All these results indicate that water conditions in these lakes result in the decrease of the preservation of carbonate remains in comparison with the previously mentioned lake. Even though the lakes are located close to each other and are of similar shape and depth, such differences in water characteristics may be affecting shell preservation.

Key words. Freshwater mollusks. Shallow lakes. Compositional fidelity. Taphonomic biases. Paleoenvironments.

Resumen. FIDELIDAD COMPOSICIONAL Y TAFONOMÍA DE MOLUSCOS DULCEACUÍCOLAS EN TRES LAGOS SOMEROS PAMPEANOS DE ARGENTINA. Se estudiaron tres lagos someros del sudeste bonaerense que exhiben diferencias en las características físico-químicas con el objetivo de comparar la fidelidad vivo/muerto y la preservación de las conchas de moluscos. Los lagos estudiados fueron Las Mostazas, Los Carpinchos y Nahuel Rucá los cuales exhibieron diferencias en la riqueza específica, abundancia, fidelidad composicional y alteración tafonómica. El lago que presentó los mayores valores de conductividad (3.34 ± 0.72), dureza ($286 \pm 83 \text{ mg l}^{-1}$) e índice de saturación de carbonatos ($IS_{\text{calcite}} = 1.95 \pm 0.21$) fue el que registró menor riqueza específica en los ensambles de vivos, diferencias en la riqueza y diversidad entre ensambles de vivos y de muertos. También fue el lago con mayor número de especies en el ensamble de moluscos muertos ($R = 5$) que en las comunidades vivientes ($R = 2$), sugiriendo un mayor tiempo de residencia en la zona tafonómicamente activa. Por otro lado, los lagos con menores valores de las mismas características (conductividad = 2.2 ± 1.2 ; 0.8 ± 0.5 ; dureza = 157 ± 55 ; $250 \pm 127 \text{ mg l}^{-1}$; índice de saturación de calcita = 0.35 ± 0.15 ; 0.43 ± 0.36 , para LC y NR respectivamente) mostraron una mayor riqueza de especies, menor número de especies en el ensamble de moluscos muertos ($R = 8$) que en las comunidades vivas ($R = 10$) y atributos tafonómicos que sugerirían individuos recientemente muertos y depositados. Todos estos resultados sugieren que las condiciones del agua de estos lagos disminuye la preservación de restos calcáreos en comparación con el lago mencionado previamente. Aunque estos lagos están localizados próximos entre ellos y tienen similar forma y profundidad, las diferencias que existen en las características del agua estarían afectando la preservación de las conchas.

Palabras clave. Moluscos dulceacuícolas. Lagos someros. Fidelidad composicional. Sesgos tafonómicos. Paleoambientes.

ONE of the main purposes of paleoecological studies is to carry out faithful reconstructions of past environments (Parsons and Brett, 1991). The interpretation of fossil incompleteness, which is a major bias when understanding paleobiological patterns, relies on accurate estimates of the importance of constructive and destructive taphonomic processes that operate during the decay of organisms, the

incorporation of biological remains into death assemblages, the burial, the early diagenesis through the formation of a fossil assemblage (Meldahl and Flessa, 1990; Kowalewski *et al.*, 1994; Puchalski *et al.*, 2008). A first step towards gaining such an understanding is to evaluate which are the taphonomic processes that act during the residence time of deposited remains in the taphonomically active zone; *i.e.*,

the zone at or just below the sediment-water interface (Davies *et al.*, 1989). It is also crucial to explore to which degree the accumulating dead remains in fact preserve the biological signal of their original living communities (Kidwell and Bosence, 1991; Kidwell, 2013; Tomašových and Kidwell, 2013).

In modern environments, the amount of biological remains is high and, hence, quantifying biases and observing patterns which can then be applied to the fossil record proves more feasible (Kowalewski and LaBarbera, 2004; Ritter and Erthal, 2013a; Ritter *et al.*, 2013). Most information regarding taphonomic processes has been obtained from shallow marine environments (see Kidwell and Bosence, 1991 for a review), which exhibit higher abundance and greater diversity of species than freshwater habitats. Studies conducted in freshwater environments indicate that death assemblages may exhibit both high and low compositional fidelity as well as variable preservation (Briggs *et al.*, 1990; Cummins, 1994; Kotzian and Simões, 2006; Martello *et al.*, 2006; Newell *et al.*, 2007; Nielsen *et al.*, 2008; McGlue *et al.*, 2010). In fact, McGlue *et al.* (2010) noticed taphonomic differences between subenvironments within Lake Tanganyika (Africa) while similar results were also observed in rivers of Austria (Briggs *et al.*, 1990) and Brazil (Kotzian and Simões, 2006). These remarks reflect the enormous variability of taphonomic signatures that can be found in freshwater systems and highlight the importance of scale factor in freshwater taphonomy.

Pampean environments of Argentina are characterized by low beta diversity in mollusk communities (Tietze and De Francesco, 2010). Taphonomic studies recently conducted on mollusk assemblages from these environments indicate that live-dead agreement is expected for within-habitat time-averaged samples, according to results obtained by modeling with neutral communities dynamics in Tomašových and Kidwell (2011), due to the fact that most mollusk species are generalists and spatial mixing may have negligible effects on species along a wide range area. Yet, some differences in diversity of death assemblages among environments possibly due to variations in time-averaging, aspects of preservation or differential turn-over of species, were detected (Tietze and De Francesco, 2012).

In the Pampean plain, the low morphogenetic energy

of the flat landscape combined with their occurrence in humid to sub-humid climates result in a variety of freshwater bodies (ponds, shallow lakes and marshes) (Geraldini *et al.*, 2011). These variations may result in dissimilarities in the preservational processes affecting carbonatic remains in the area. Hence, the understanding of preservational processes in Pampean freshwater environments requires knowledge of the heterogeneity to be expected among and within habitats. In the present contribution, we compared live/dead fidelity and shell preservation of three shallow lakes of the Pampean plain exhibiting differences in water quality and substrate. The aim of such work is to expand the knowledge of preservational processes acting on freshwater mollusks in pampean environments.

GEOLOGICAL SETTING

The study was conducted in three freshwater shallow lakes separated from each other by approximately 20 km: Las Mostazas (**LM**; 37° 9' 57" S; 57° 14' 50" W), Los Carpinchos (**LC**; 37° 3' 34" S; 57° 19' 56" W) and Nahuel Rucá (**NR**; 37° 37' 21" S; 57° 25' 42" W) (Fig. 1). The three lakes are located in the Southeastern Pampa plain, which is part of the depressed Pampa (Tricart, 1973). These lakes are part of the modern geof ormations of the area that originated under the arid or semi-arid conditions and cold temperatures that prevailed during the last glaciation and that were subsequently modified by the increase in temperature and humidity over the last 10,000 years (Zárate and Rabassa, 2005). These shallow lakes are characterized by maximum depths of 3 m and by being naturally eutrophic, with the calcium carbonate fraction of sediments ranging from 1 to 20% and an organic matter content lower than 15% (Fernández Cirelli and Miretzky, 2004; Diovisalvi *et al.*, 2014). The degree of salinity varies between oligohaline (0.5–5 g l⁻¹) and mesohaline (5–15 g l⁻¹). The salt concentration observed is caused by marine ingressions plus the sedimentary and climatic characteristics of Buenos Aires Province. The climate in the region, with warm summers and mild winters and an average annual precipitation of 1100 mm, is temperate humid or subhumid with an average annual temperature of 15 °C (Feijóo and Lombardo, 2007). A large interannual variability in rains, ≈ 200 ml according to Scarpati and Capriolo (2013), in combination with poorly developed drainage systems results in recurrent and extensive floods

alternating with drought periods. These processes affect the lake water-residence time, the water content of soils and the depth of the water table. More recently, human activity has greatly modified the shallow Pampean lakes by emplacing different hydraulic structures (*e.g.*, embankments, dams and floodgates) or by the construction of channels in an attempt to prevent or alleviate floods (Diovisalvi *et al.*, 2014).

MATERIAL AND METHODS

Field methodology

Three pampean shallow lakes, which were sampled between 2010 and 2012, were selected because of their differences in conductivity (as a proxy of salinity). During the summer, LM became very muddy and, given that access to the sampling area was thus inhibited, only three seasons could be sampled in this lake. Data referring to NR were previously published in Tietze and De Francesco (2012, 2014). Five sites from each lake were seasonally sampled for live and dead mollusks, conductivity, pH, temperature, depth and dissolved oxygen. Besides, a water sample of the lake was seasonally secured in order to measure the concentration of major ions and, subsequently, chemically characterize the lake. All samplings were seasonally conducted so as to record annual variations in water charac-

teristics and mollusk assemblages.

Mollusks were collected both manually (picked by hand) and with the aid of sieves (0.5 mm mesh size), using quadrants with sampling areas of 5 m². According to Cummins (1994) and Martello *et al.* (2006), such sampling is adequate for the low abundance of mollusks in freshwater habitats. Living mollusks were searched for among the submerged vegetation, under stones and on the substratum while dead specimens were only sampled from the substratum. Sampling was carried out by time of effort (number of snails caught per hour), following Martín *et al.* (2001), and conducted by the same person to avoid sampling bias.

Conductivity, pH and dissolved oxygen were recorded with field instruments (pH tester Hanna pHep5 HI98108, Conductivity sensor Hanna Dist HI98312, and Portable dissolved oxygen meter Hanna HI 9146). The sample of water utilized for the measurement of the concentration of major ions (CO_3^{2-} , HCO_3^- , PO_4^{3-} , NO_3^- , SO_4^{2-} , Cl^- , Ca^{+2} , Na^+ , Mg^{+2} , SiO_2) and hardness, was collected in polyethylene bottles and stored in ice until transported to the laboratory. Analyses were carried out at the Hydrogeochemistry and Isotope Hydrology Laboratory of the Universidad Nacional de Mar del Plata. Chemical analyses were performed applying standard methods: chloride following the Mhor method,

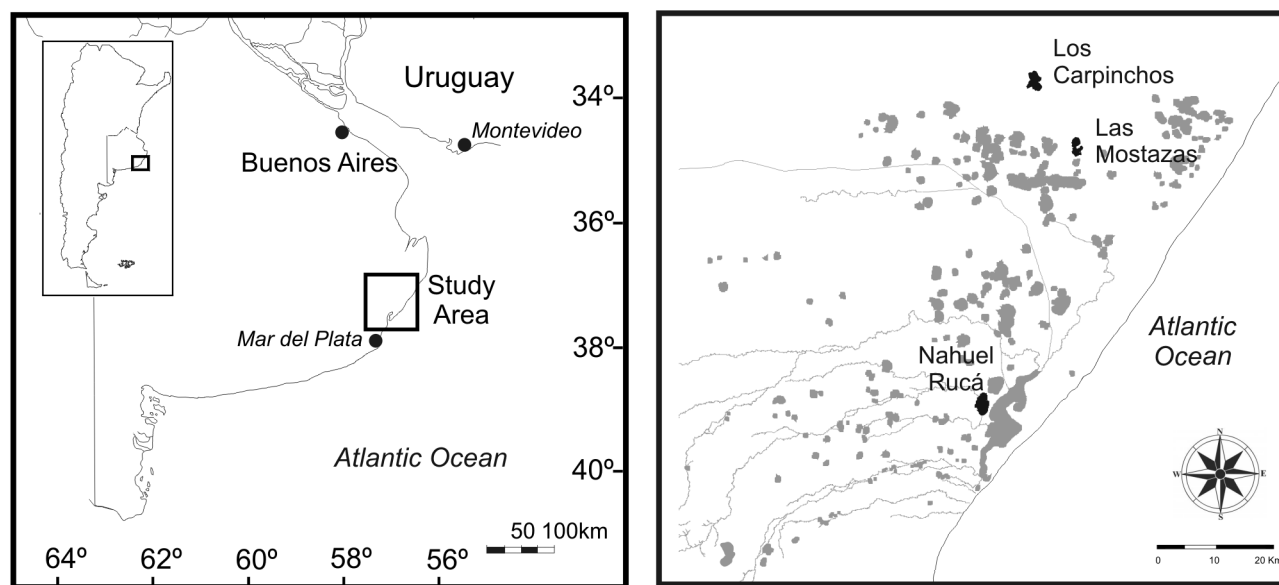


Figure 1. Location of the studied shallow lakes. Las Mostazas (LM); Los Carpinchos (LC); Nahuel Rucá (NR).

sulfate by turbidimetry, calcium and magnesium by complexometric titrations with EDTA, sodium by flame spectrometry, silica by means of the silicomolibdate method and nitrate by the brucine method (APHA, 1992). The carbonate saturation index was calculated using the PHREEQC program on the basis of ionic composition, temperature and pH of water (Parkhurst and Appelo, 1999).

Laboratory study

All live specimens, whole shells and fragments >2 mm in length were recovered, counted and identified, when possible to the species level, under stereoscopic microscope (10X). Mollusk identification was based on Ageitos de Castellanos and Fernández (1976), Gaillard and Ageitos de Castellanos (1976), Ageitos de Castellanos and Gaillard (1981), Fernández (1981a, b), Rumi (1991) and Ageitos de Castellanos and Landoni (1995). The counting of the number of specimens in each sample was calculated taking into consideration whole shells and any fragment of the shell that included the apex. For bivalves, each disarticulated valve was classified as left or right. The total number of bivalves per sample corresponded to that of the most abundant valve.

For all specimens, taphonomic damage was examined under a stereoscopic microscope at 10X magnification. Seven taphonomic variables were scored: (1) fragmentation, (2) edge rounding of commissure and hinge line (for bivalves) and aperture (for gastropods), (3) loss of proteinaceous parts (periostracum, ligament and operculum), (4) fine-scale surface alteration (damage to shell surface resulting from some combination of dissolution, abrasion and microbioerosion), (5) articulation (only for bivalves), (6) encrustation (presence of periphyton and/or egg capsules) and (7) presence of deposits of ferruginous material. Each variable was represented by a proportional value that was defined by the sum of altered specimens relative to the total sum of specimens at a given site. Fragmentation was measured as the number of fragments divided by the sum of fragments and whole specimens. Complete shells were defined as those that preserved more than 95% of the original entire skeleton while fragmented shells comprised any piece of mollusk shell that had lost more than 5%. Edge rounding is referred to the smoothness of shell edges such as the commissures of bivalves and the apertures of gastropods: rounded or chipped. Given that dissolution, abra-

sion and microbioerosion contribute to produce the same alteration, the three processes were combined under a single variable referred to as "fine-scale surface alteration" (Best and Kidwell, 2000) and observed under low (10X) magnification. Fine-scale surface alteration was quantified in terms of the proportion of shells with 20% of their surface affected by this condition. Encrustation was computed as the proportion of shells covered with periphyton or eggs.

Data analysis

Fidelity analyses focused on composition and diversity (*i.e.*, presence/absence of species and proportional abundances) between life (**LAs**) and death (**DAs**) assemblages at site (1 to 5) and environmental scales (lakes NR, LM and LC). The following measurements were calculated based on absolute counts at each sampling site: (1) total number of shells (**n**), (2) relative abundance of species, (3) richness (**S**) and (4) two alpha-diversity indices; that is, Shannon-Wiener index (**H'**; Magurran, 1988) and Simpson index (1-D; Simpson, 1949). Diversity indices were based on rarefied samples (standardized samples on the basis of sample size) because species richness and the diversity indices are highly sensitive to sample size (Gotelli and Colwell, 2010; Chao *et al.*, 2014). Differences between LAs and DAs at environmental scale in each diversity index were evaluated with two-sample permutation tests by means of Monte Carlo. The accuracy to which DAs reflect the taxonomic composition of LAs was tested using the Jaccard-Chao index of taxonomic similarity (Chao *et al.*, 2005). Since modern communities contain fewer individuals than death assemblages, the Jaccard-Chao index, which consists of the proportion of shared species between LAs and DAs with a correction for unseen shared species, was used in order to correct discrepancies in sample sizes. The correlation between the rank abundance of LAs and DAs was tested using Spearman's rho (Kidwell, 2001), which measures whether the most (or least) abundant species in LA are also the most (or least) abundant species in DA. Thus, while rho measures the correlation between the rank abundance of each species in LAs and their rank abundance in DAs, the Jaccard-Chao index measures the taxonomic similarity between both assemblages.

Uni- and multivariate methods were applied so as to evaluate taphonomic differences between lakes. Samples

with less than 10 individuals were excluded from subsequent analyses. Univariate analyses focused on the mean proportions of taphonomic variables using two sample permutation tests based on Monte Carlo and Spearman rank order correlations between variables. In order to explore the relationship of the samples in terms of taphonomic variables, an ordination of the samples in the low-dimensional space using non-metric multidimensional scaling (NMDS) and a permutational analysis of variance (NPMANOVA; Anderson, 2001) was performed. NMDS and NPMANOVA were based on the Manhattan distance.

All statistical analyses were performed using R (R Development Core Team, 2009). The packages “vegan” (Oksanen *et al.*, 2011), “perm” (Fay and Shaw, 2010), “graphics” (Murrell, 2005) and “fossil” (Vavrek, 2011) were used.

RESULTS

Environmental variables

The lakes were characterized by an alkaline pH (varying between 7.4 and 10.32), low conductivity (mean conductivity between 0.3 and 4.3 mS cm⁻¹) and moderate to hard hardness (mean hardness between 104.03 and 438.04 mg l⁻¹ of CaCO₃). The three lakes exhibited differences in pH, conductivity and hardness. LM showed the highest values for the three variables. The lowest values of pH and conductivity were recorded in NR while LC presented the lowest value of mean hardness (Tab. 1). The carbonate saturation index yielded low values for LC (mean SI_{aragonite}= 0.21; mean SI_{calcite}= 0.35), intermediate values for NR (mean SI_{aragonite}= 0.29; mean SI_{calcite}= 0.43) and high values for LM (mean SI_{aragonite}= 1.81; mean SI_{calcite}= 1.95) (Tab. 1). Vege-

TABLE 1 – Summary of environmental information. Values are mean±SD; minimum and maximum values.

Variable	Las Mostazas		Los Carpinchos		Nahuel Rucá	
	Mean ± SD	Min-Max	Mean ± SD	Min-Max	Mean ± SD	Min-Max
Temperature (°C)	18.2±4.14	14.30-24.5	18.5±7.9	10.2-32.5	16.3±7.3	7.2-25.5
pH	9.71±0.42	9.09-10.32	8.7±0.8	7.7-10	8±0.3	7.4-8.5
Conductivity (mS/cm)	3.34±0.72	2.48-4.28	2.2±1.2	1.3-4.3	0.8±0.5	0.3-1.6
Oxygen saturation (%)	101.47±51.51	31.1-177.8	56.2±40	1.6-90	78.8±22.9	25.2-100
Littoral depth (cm)	73.33±13.83	50-100	57.4±22.9	20-90	40±14	15-65
Carbonates (mg L ⁻¹)	173.73±144.76	51.3-333.5	45.8±91.7	0-183.3	0±0	0-0
Bicarbonates (mg L ⁻¹)	664.27±87.49	568.5-740	743.3±135.4	583.6-894.4	528.6±230	303.2-849
Chloride (mg L ⁻¹)	822.80±119.99	750.1-961.3	877.2±1053.2	269.7-2451.0	144±81.8	91.1-266
Hardness (mg L ⁻¹ of CaCO ₃)	285.97±83.11	190-334.4	156.93±54.51	104.03-229	249.8-126.7	172.5-438.4
Calcium (mg L ⁻¹)	60.43±10.88	54.10-73	16.3±11.6	1-27.4	30.7±16.5	18.1-53.2
Magnesium (mg L ⁻¹)	32.33±17.56	13.10-47.5	20.9±16.9	2.4-38.5	41.7±29.7	18.8-85.4
Sulfate (mg L ⁻¹)	188.33±33.65	153-220	90.2±83.9	1.2-188	108.9±61.4	27.4-169
Nitrate (mg L ⁻¹)	40.7±8.94	35-51	18.1±3.3	15.8-20.4	161.3±88.7	98.6-224
Phosphates (mg L ⁻¹)	146.5±30.41	125-168	45.4±8.4	40-55.1	67±0	67
Silica (mg L ⁻¹)	18.73±11-96	9.7-32.3	52.1±48.3	9.4-111	17.7±1.3	16.8-18.6
Calcite Saturation Index	1.95±0.21	1.82-2.2	0.35±0.15	0.19-0.54	0.43±0.36	-0.08-0.73
Aragonite Saturation Index	1.81±0.21	1.68-2.05	0.21±0.15	0.05-0.39	0.29±0.37	-0.24-0.59

tation in the form of an emergent macrophyte ring of *Schoenoplectus californicus* (C.A. Mey) Soják and small patches of submerged (e.g., *Ceratophyllum* sp. and *Miriophyllum* sp.) and/or free floating (*Azolla* sp., *Ricciocarpus* sp., *Lemna* sp.) macrophytes located near the littoral zone was observed in all the three lakes.

Compositional similarities between life and death assemblages

LM recorded lower species richness (5) than LC (10) and NR (10). The three lakes were dominated by different gastropod species: LM was dominated by *Biomphalaria peregrina* in LAs and DAs while LC proved most abundant in *Uncancylus concentricus* in LAs and DAs, and NR was dominated by *Heleobia parchappii* in LAs and by *B. peregrina* in DAs (Tab. 2). LM presented five species of mollusks of which two, *H. parchappii* and *B. peregrina*, were present both in LAs and DAs while the remaining three species, *U. concentricus*, *Pomacea canaliculata* and *Omalonyx* sp., were only found in DAs (Fig. 2; Tab. 2). In LC and NR, nine gastropods and one bivalve were recorded. Most species, *H. parchappii*, *B. peregrina*, *U. concentricus*, *P. canaliculata*, *Omalonyx* sp. and the bivalve *Musculium argentinum*, were recorded from both LAs and DAs (Fig. 2; Tab. 2). Two species, *Stenophysa marmorata* and *Drepanotrema lucidum*, were recorded only in LAs while there was one gastropod species, *Antillorbis nordestensis*, which was found only in DAs of LC and another one, *D. heloicum*, in DAs of NR. Additionally, specimens of *Succinea meridionalis*, both alive and dead, were found exclusively in LC while the same was observed for the occurrence of *Physa acuta* in NR.

Richness varied between 2 and 6 species for LM, in which differences between LAs and DAs were detected ($p = 0.01$; 0.81; 0.21 for LM, LC and NR, respectively), as well as for LC while, in NR, its value was of 4–9 species (Fig. 3). Differences in diversity (Shannon–Weiner index) between LAs and DAs were also observed in LM ($p = 0.03$; 0.32, 0.14 for LM, LC and NR, respectively) (Fig. 3). No differences in dominance between LAs and DAs were perceived ($p \leq 0.05$ in all cases).

The compositional similarity was good at site scale in all environments (Jaccard–Chao index varied between 0.75 and 0.97 for LM, between 0.66 and 0.99 for LC and between 0.98 and 1 for NR) (Fig. 4; Tab. 3). Conversely, the rank correlation between LAs and DAs proved high for all sites

from LM (varying between 0.89 and 0.91), three of the sites from NR (rho between 0.87 and 0.75) and only one LC site (rho = 0.84). On the other hand, it was poorly to non-correlated at site scale in four sites of LC (rho values between 0.11 and 0.47) and two sites of NR (rho between 0.43 and 0.55) (Fig. 4; Tab. 3).

Taphonomy

Only one sample from LC was excluded from the analysis because it had less than 10 individuals. Shells were mainly affected by the loss of proteinaceous parts, fine-scale surface alterations, fragmentation and roundness. Taphonomic attributes proved greatly variable, higher between-lake than within-lake (NPMANOVA $F = 15.36$; $p \leq 0.01$; Fig. 6, NMDS stress = 0.07), among lakes and sites (Fig. 5; Tab. 4). Besides, all pair-wise comparisons between lakes in the NPMANOVA analysis were significant at the 0.05 alpha level (Bonferroni-corrected p values = 0.02 in LM–NR, 0.02 in NR–LC, 0.04 in LM–LC). When taphonomic variables were compared, LC featured the best states of preservation while NR displayed the worst ones. The presence of incrustations and deposits was also recorded in shells from LM but proved absent in the other two lakes. The presence of proteinaceous parts was notably higher in LC than in LM and NR ($p = 0.01$ and 0.02, respectively). The proportion of rounded and fragmented shells proved significantly higher in NR, which was significantly different from LC and LM ($p = 0.02$ and $p < 0.01$, respectively, for both attributes).

DISCUSSION

Environmental variability

The three lakes exhibited subtle differences in some physico-chemical conditions, such as pH, conductivity, hardness and carbonate saturation index, which remained constant seasonally. When considering carbonate preservation, the carbonate saturation index is the more important variable and yielded its higher values for LM and its lower values for LC. Although the three lakes presented saturated to supersaturated waters, carbonate saturation indices were calculated on the basis of chemical analyses of column water. However, a recent study performed on the same three lakes (LM, LC and NR) yielded, when comparing both subenvironments, different water conditions between

TABLE 2 – Table of life (LAs) and death assemblages (DAs) composition of Las Mostazas (LM), Los Carpinchos (LC) and Nahuel Rucá (NR).																															
	Life assemblages (LAs)													Death assemblages (DAs)																	
	Las Mostazas (LM)					Los Carpinchos (LC)					Nahuel Rucá (NR)			Las Mostazas (LM)					Los Carpinchos (LC)					Nahuel Rucá (NR)							
Site	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5						
Heleobia parchappii	3	20	15	10	18	1	0	2	0	6	60	32	251	219	348	20	6	7	13	15	0	2	1	1	3	38	1	33	38	28	
Biomphalaria peregrina	12	45	41	25	33	0	5	4	27	14	50	16	9	8	34	31	17	41	92	52	0	1	0	2	0	37	36	45	19	27	
Uncancylus concentricus	0	0	0	0	0	26	71	85	52	60	2	1	1	16	10	12	1	1	10	0	3	8	8	5	16	34	4	43	9	11	
Antillorbis nordestensis	0	0	0	0	0	0	0	0	0	0	30	5	0	5	1	0	0	0	0	0	0	7	0	0	1	6	3	5	6	2	
Drepanotrema heloicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Drepanotrema lucidum	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Pomacea canaliculata	0	0	0	0	0	0	0	1	0	0	2	1	3	1	1	3	0	1	6	1	0	1	0	4	0	0	2	1	0	1	0
Omalonyx sp.	0	0	0	0	0	2	2	2	0	3	2	2	0	0	1	2	0	0	1	2	0	0	0	0	0	1	1	0	0	0	0
Succinea meridionalis	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Musculium argentinum	0	0	0	0	0	1	1	0	0	1	15	16	10	24	2	0	0	0	0	0	1	0	0	0	0	2	12	1	4	1	1
‘Stenophysa marmorata’	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	3	3
‘Physa acuta’	0	0	0	0	0	0	0	0	0	0	8	5	4	6	29	0	0	0	0	0	0	0	0	0	0	7	1	3	2	7	7
Total	15	65	56	35	51	31	66	88	81	107	169	78	278	279	426	68	24	50	121	69	6	20	9	12	20	127	60	133	78	80	80

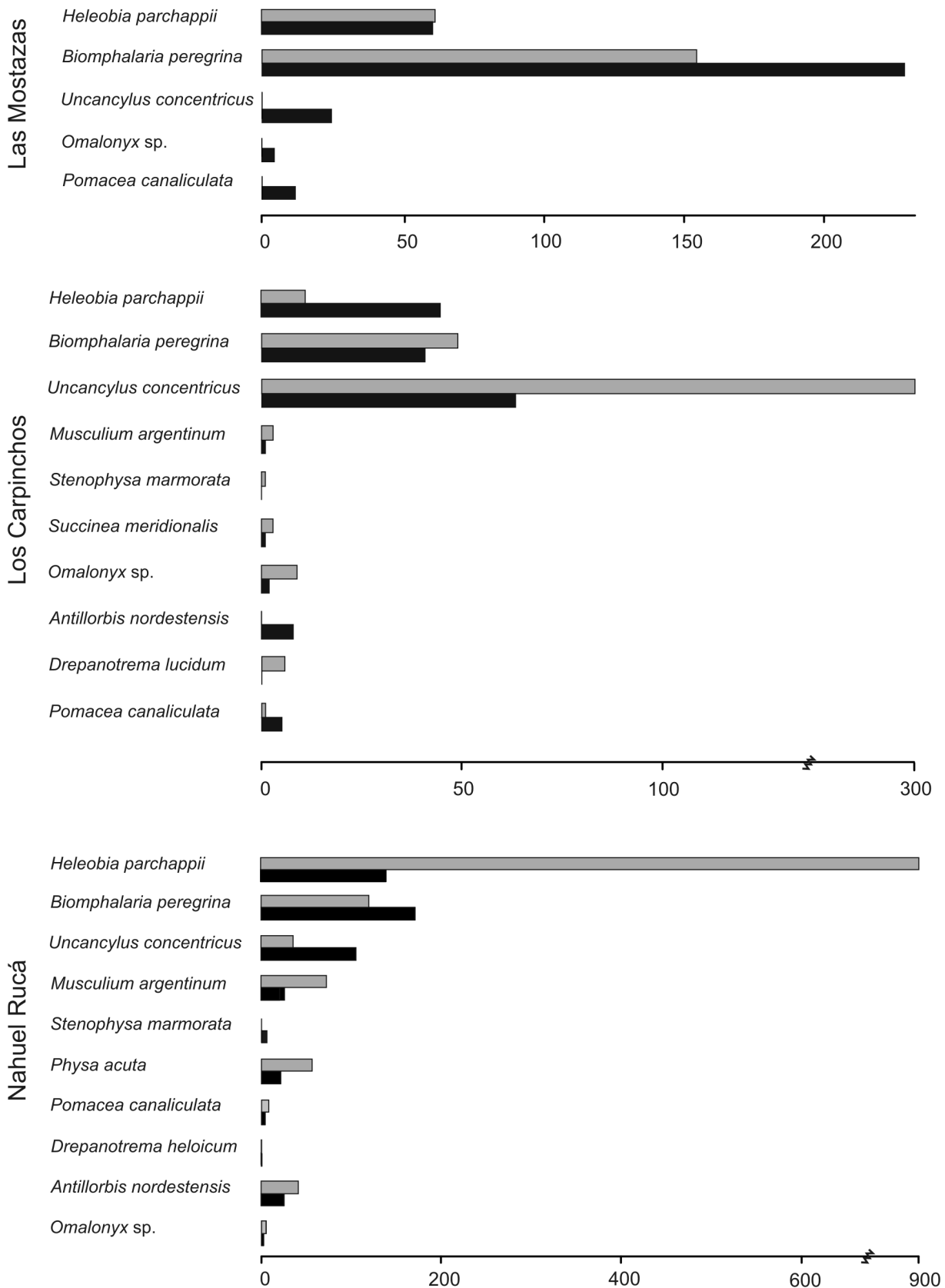


Figure 2. Mollusk abundance of life assemblages (LAs) in light gray, and death assemblages (DAs) in black, in Las Mostazas (LM), Los Carpinchos (LC) and Nahuel Rucá (NR) lakes.

TABLE 3 – Table of Richness, Shannon-Wiener and Simpson indices at site scale and LAs/DAs comparison using Jaccard-Chao index and Spearman's rho correlation.

			Richness	Shannon-Wiener index	Simpson index	LAs/DAs Jaccard-Chao index	LAs/DAs Spearman's rho
Las Mostazas	1	LAs	2	0.41	0.24	0.75	0.89
		DAs	5	1.39	0.71		
	2	LAs	2	0.45	0.28	0.95	0.91
		DAs	3	0.72	0.43		
	3	LAs	2	0.57	0.38	0.96	0.91
		DAs	4	0.60	0.31		
	4	LAs	2	0.55	0.37	0.87	0.89
		DAs	4	0.87	0.44		
	5	LAs	2	0.63	0.44	0.97	0.92
		DAs	3	0.60	0.36		
Los Carpinchos	1	LAs	2	0.45	0.28	0.99	0.84
		DAs	3	1.01	0.61		
	2	LAs	4	0.59	0.27	0.70	0.11
		DAs	6	1.41	0.70		
	3	LAs	2	0.35	0.20	0.83	0.31
		DAs	2	0.35	0.19		
	4	LAs	4	1.20	0.65	0.66	0.45
		DAs	4	1.24	0.68		
	5	LAs	4	0.71	0.34	0.80	0.47
		DAs	3	0.61	0.33		
Nahuel Rucá	1	LAs	8	1.51	0.73	0.98	0.75
		DAs	9	1.56	0.75		
	2	LAs	8	1.57	0.73	1	0.55
		DAs	8	1.28	0.59		
	3	LAs	5	0.42	0.17	0.99	0.43
		DAs	8	1.42	0.72		
	4	LAs	6	1.01	0.48	0.99	0.87
		DAs	6	1.39	0.68		
	5	LAs	4	0.74	0.38	0.99	0.78
		DAs	8	1.54	0.73		

column and interstitial water. Such analyses resulted in the observation that the carbonate saturation index was near equilibrium or slightly subsaturated in interstitial water, associated to more acidic pHs, while column water was marked by more alkaline and highly supersaturated as regards CaCO_3 (Cristini, 2016). These results explain the reason why there is dissolution of carbonate remains deposited in the sediment-water interface when carbonate saturation indices in column water are saturated or supersaturated

with respect to CaCO_3 .

The mollusks recorded in this study represent species commonly found in other Pampean environments (Tietze and De Francesco, 2010; Tietze *et al.*, 2011). Even though *Heleobia parchappii* is the dominant species of the entire aquatic malacofauna of the region (Tietze and De Francesco, 2010, 2012), in the present study, the species was only dominant in NR. On the other hand, *Biomphalaria peregrina*, a pulmonate species strongly related with an aquatic vege-

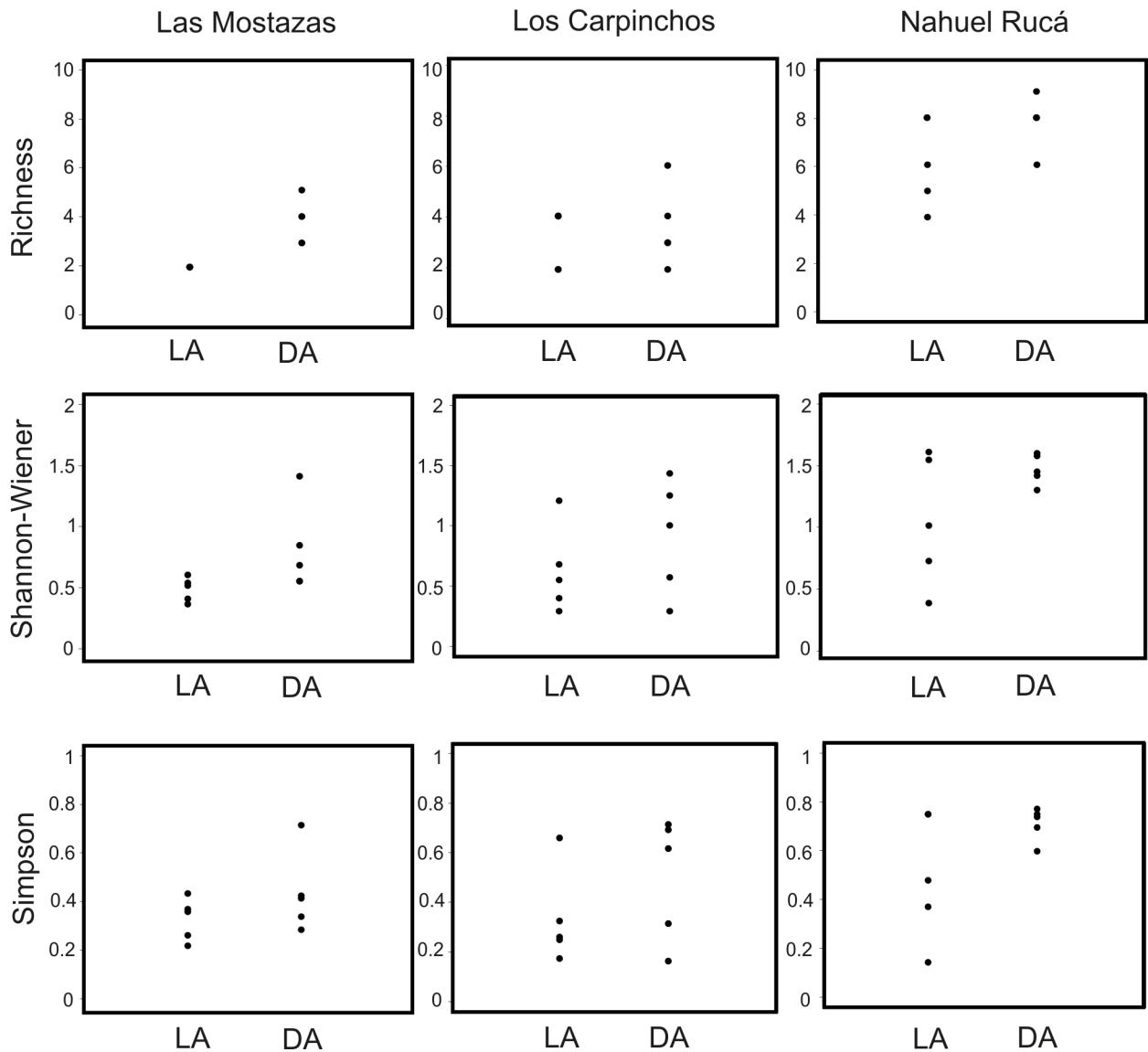


Figure 3. Jitter plot of diversity indices: Richness (S), Shannon-Wiener and Simpson indexes of Las Mostazas (LM), Los Carpinchos (LC) and Nahuel Rucá (NR) lakes.

tation cover (Rumi, 1991; Tietze and De Francesco, 2010), was dominant in nearly all sites from LM, which can be explained by the higher abundance of submerged macrophytes present in this lake. The dominance of the freshwater limpet *Uncancylus concentricus* in LC is difficult to explain because basic ecological information regarding this snail species is limited. However, seeing that a high abundance of this species was recorded in a dam with calcium content below what is considered as limiting for most freshwater gastropods (Ca^{+2} content $1\text{--}4\text{ mg l}^{-1}$) (Martín, 1998),

a possible explanation relies on its tolerance to poorly mineralized waters such as that of LC, for which the lower values of calcium content were recorded (Min–Max values of Ca^{+2} content: LM $54.1\text{--}73$; LC $1\text{--}27.4$; NR $18.1\text{--}53.2\text{ mg l}^{-1}$).

Compositional fidelity of life and death assemblages

The low richness recorded in communities of LM may be related to the rather higher values of conductivity, pH and hardness detected for the area. Although average values are

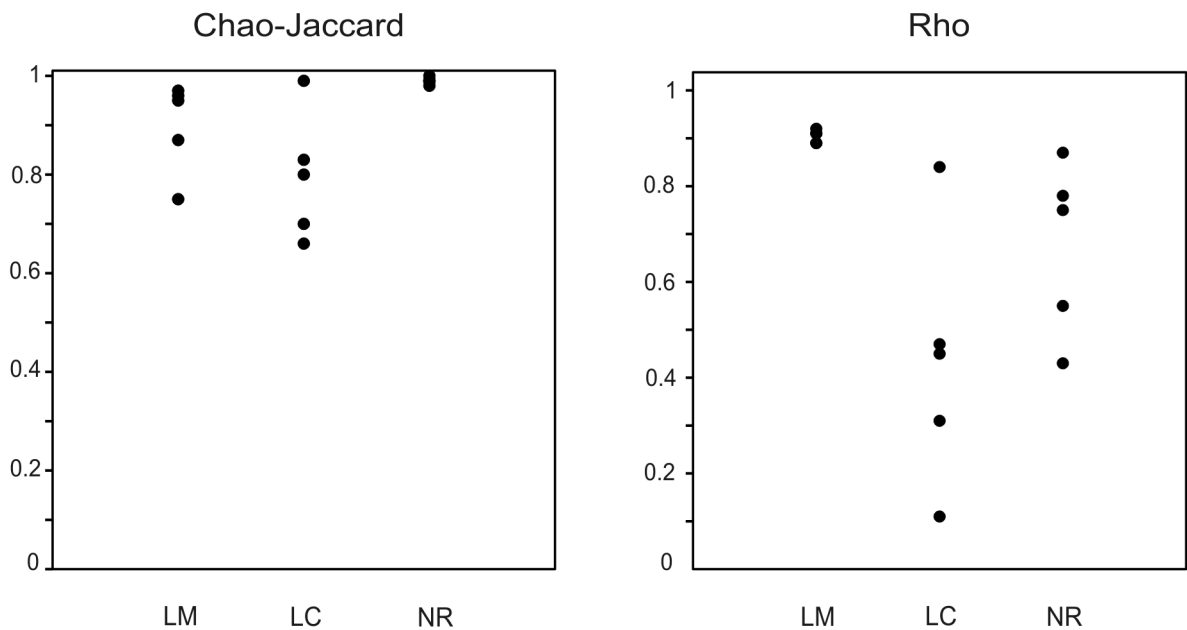


Figure 4. Jitter plot of Chao-Jaccard and Spearman’s Rho of LAs-DAs assemblage comparisons in Las Mostazas (LM), Los Carpinchos (LC) and Nahuel Rucá (NR) lakes.

TABLE 4 – Proportions of taphonomic attributes.															
	Las Mostazas					Los Carpinchos					Nahuel Rucá				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Loss of proteinaceous parts	0.41	0.22	0.51	0.42	0.51	0.04	0	0.06	0.13	--	0.57	0.14	0.56	0.55	0.50
Fine-scale surface alteration	0.19	0.44	0.20	0.14	0.15	0.13	0.30	0.07	0.00	--	0.43	0.12	0.42	0.51	0.29
Encrustation	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	--	0.00	0.00	0.00	0.00	0.00
Presence of deposits	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	--	0.00	0.00	0.00	0.00	0.00
Roundness	0.29	0.07	0.33	0.17	0.13	0.17	0.20	0.13	0.04	--	0.60	0.57	0.63	0.56	0.53
Fragmentation	0.26	0.44	0.42	0.18	0.12	0.13	0.20	0.26	0.09	--	0.58	0.53	0.61	0.66	0.45

relatively similar among the three lakes, subtle differences become crucial in periods of drought (these lakes are naturally exposed to episodes of drought and flooding over seasons and years). In fact, during drought periods, lakes are subject to strong evaporation and the consequent substantial increase of ionic concentration that, in the case of values

above 5 mS cm⁻¹, surpasses the tolerance of many fresh-water mollusks. Therefore, the species composition of such environments may be variable, with colonization and local disappearances of stenohaline species highly depending on oscillating water characteristics. In other words, the particular hydrochemical characteristics of LM may behave as

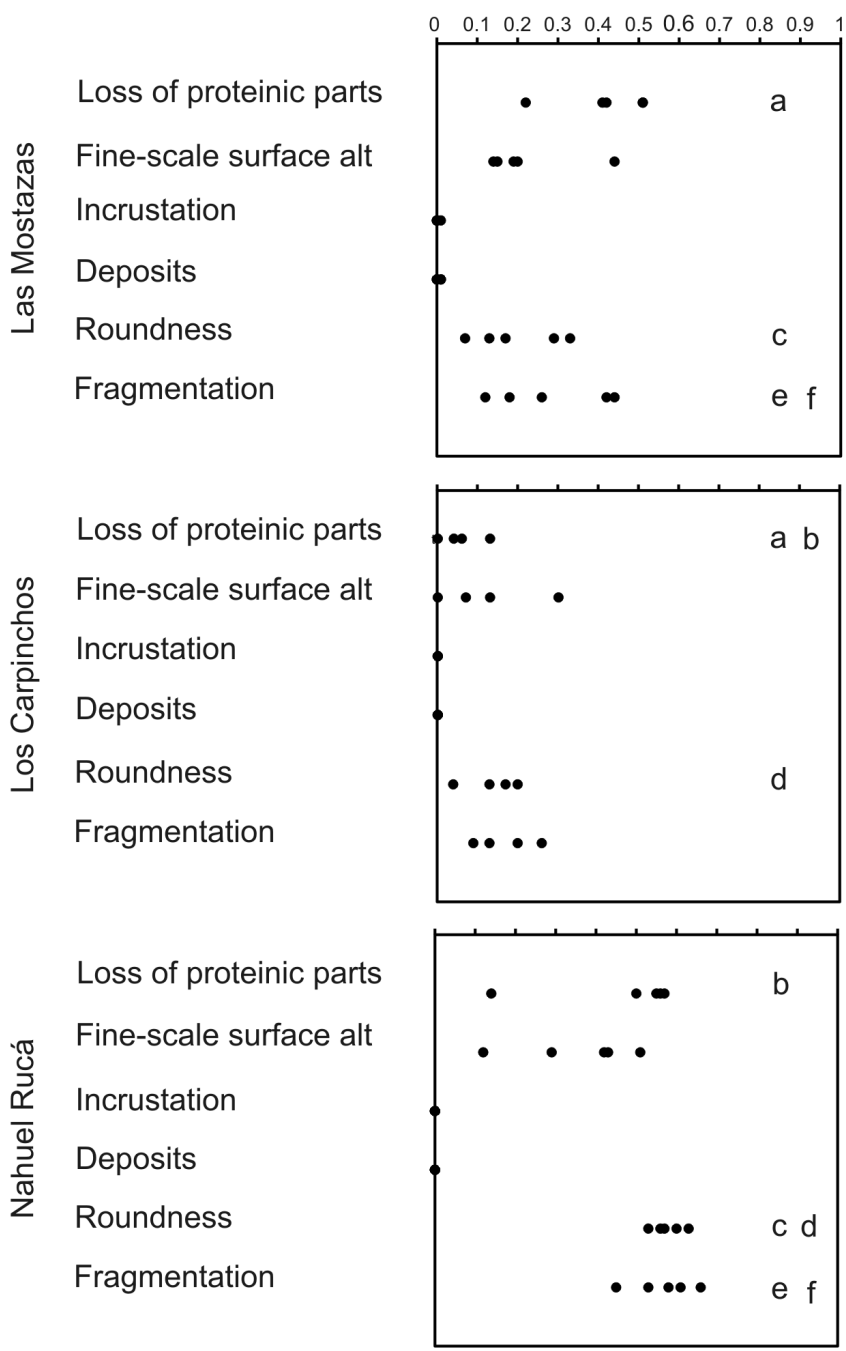


Figure 5. Jitter plot of taphonomic variables: Loss of proteinic parts, Fine-scale surface alteration, Incrustation, Presence of Deposits, Edge-Roundness and Fragmentation. Significant differences in pairwise comparisons are identified with letters.

a natural barrier for the establishment of stenohaline species. Hassan *et al.* (2012) noted that the same two snail species that inhabited this lake (*Heleobia parchappii* and *Biomphalaria peregrina*) were also recorded from brackish lakes characterized by highly alkaline (pH 9.5–10.5) and very

hard (120–1874 mg l⁻¹ CaCO₃) waters from the semiarid Pampean region of Argentina. Such observation reinforces the hypothesis that these two species are more tolerant to high ionic concentrations than other freshwater mollusks.

The adverse conditions of LM for the development of

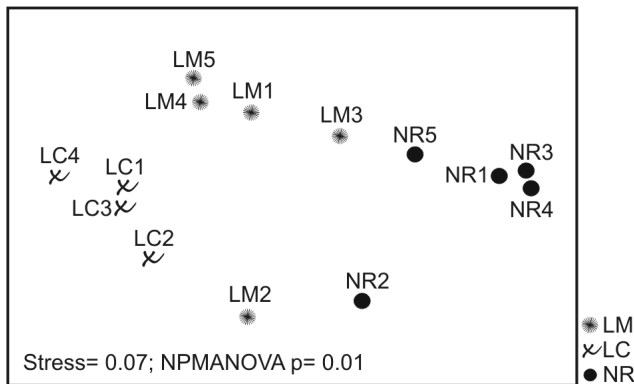


Figure 6. NMDS scatterplot of taphonomic variables at site scale. LM, Las Mostazas; LC, Los Carpinchos; NR, Nahuel Rucá.

mollusk communities and the better conditions for carbonate remains preservation may explain the higher richness and diversity recorded in DAs. DAs reflect input from past generations of organisms that lived in the lake, either temporally or permanently. In the present case, the higher richness and diversity of DAs (compared to LAs) may be given by the occurrence of species that would have inhabited the lake in moments when the environment was suitable for them but cannot live under the present conditions. Because of time averaging, these species may still be recorded as included in the DAs. The major directionality of shell preservation and time averaging appears to be deeply related with the sediment type (*e.g.*, Kidwell *et al.*, 2005; Korpanty and Kelley, 2014) but also depend on geochemical features (Canfield and Raiswell, 1991; Best and Kidwell, 2000; Parsons-Hubbard, 2005; Best *et al.*, 2007; Cherns *et al.*, 2008, 2011) and time of exposure within the Taphonomically Active Zone (TAZ) (Olszewski, 2004; Ritter and Erthal, 2013b). It is a fact that the preservation potential of mollusks in hard water is higher than in freshwater mainly because the former is saturated with respect to calcium carbonate (Hagan *et al.*, 1998). Therefore, the higher values of hardness and carbonates saturation index recorded for LM may favor time averaging and, therefore, explain the occurrence in DAs of species that lived in different time intervals.

Contrariwise, LC and NR recorded more live than dead species (10 species in LAs, 8 in DAs) and less faithful DAs when abundances were compared (Spearman rank correla-

tion poorly to non-correlated in two and four sites of NR and LC, respectively). The rapid disappearance of carbonate shells via carbonate dissolution represents the most likely explanation for the observed live-dead disagreement and proves consistent with the chemical characteristics of lake water. 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 the increased biological activity given by higher nutrient levels. Fungi, algae and bacteria have been proposed as responsible for the dissolution of shells in freshwater settings (Hagan *et al.*, 1998). A higher destruction rate in LC and NR, limiting shell accumulation and time averaging, may be expected. Kidwell (2002) pointed out that a given DA is dominated by recent input because, after death, shells “decay” randomly at a constant albeit exponential rate while dead mollusk shells are usually far more abundant than living individuals. Thus, the fluctuation in number of shells in sediments from NR and LC throughout the years can be best described as a balance between the rate of production and the rate of death and subsequent loss.

Taphonomy

Shell preservation varied among lakes. Between-lake variability was higher than within-lake variability, which may be consequence of the different species dominating DAs. In fact, the best state of preservation, especially the low rates of loss of proteinaceous parts, was recorded in LC, a lake dominated by *Uncancylus concentricus*, a species that is more prone to be destroyed due to its thin shell. The presence of well-preserved *U. concentricus* shells in DAs may be explained in terms of the fact that they constitute recently dead remains; *i.e.*, shells that span very low residence time in the TAZ. Such explanation is consistent with previous findings regarding fidelity (discussed in the previous paragraph) that suggest this lake (and NR) is subject to high destruction rate and might thus be marked by a lower time averaging than that of LM. These results also support preliminary conclusions drawn in other studies conducted in Argentinean and Brazilian freshwater systems in which significant differences in preservation between thin- and thick-shelled species were recorded (Erthal *et al.*, 2011; Tietze and De Francesco, 2014). In fact, intrinsic factors related to shell thickness are probably more important for the preservation

of freshwater mollusks than for that of marine shells (Erthal *et al.*, 2011; Kosnik *et al.*, 2011), even at a local scale (Tietze and De Francesco, 2014).

NR shells presented poor preservation, evidenced by higher values of roundness and fragmentation, akin to that of LC. Fragmentation is an attribute of difficult interpretation for it may be caused by chemical (*e.g.*, dissolution), physical (*e.g.*, wind effect, currents) and/or biological (*e.g.*, predation) processes (Zuschin *et al.*, 2003). It should be noted that, in the freshwater systems herein discussed, this variable also responds to dissolution turning shells into fragile bioclasts. In a previous taphonomic study conducted along the Touro Passo River (Brazil), some unionid bivalve shells were recovered completely disintegrated, and the integrity of shells only kept by the periostracum (Kotzian and Simões, 2006). All in all, the more destructive sedimentary environment of NR may be responsible for the poor preservation of shells in DAs. The difference with the preservation of shells in the DAs from LC may respond to the fact that, in NR, DAs are dominated by *H. parchappii*, a more robust species than *U. concentricus*, which may remain for a longer period in the TAZ during decay.

LM shells proved well preserved when compared with shells from LC and NR. Indeed, the fact that only the shells collected from LM exhibited incrustations, a taphonomic variable associated with time of exposure at the sediment-water interface, is consistent with the previous interpretations based on LA/DA comparisons that indicate a better preservation in this lake. Additionally, the relatively greater thickness of shells recovered from this lake may contribute to such pattern. In previous studies (Tietze and De Francesco, 2012, 2014), the presence of incrustations was linked to a higher frequency of thick-shelled species that also suggested a dependence of these attributes on the time of exposure of a shell at the sediment-water interface.

CONCLUSIONS

The three lakes studied in the present contribution presented differences in shell richness, compositional fidelity and taphonomic alteration. The lowest richness was recorded in the lake with the highest values of conductivity, hardness and saturation index of carbonates. Moreover, this lake was proved the only one in which the number of

species was higher in DAs than in LAs, therefore indicating a higher residence time in the taphonomically active zone and consequently suggesting better preservation conditions. On the other hand, the lakes with lower values of conductivity, hardness and saturation index of carbonates displayed a lower number of species in DAs than in LAs. Furthermore, the few shells recorded in DAs corresponded to recently dead specimens. These results suggest that shell preservation is more affected herein than in the aforementioned lake. Even though the lakes are close to each other and of similar shape and depth, the differences in the water characteristics that mark them may affect shell preservation and thus give rise to diverse fossil assemblages.

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