MOLLUSCAN TAPHONOMIC PATTERNS BELOW THE SEDIMENT-WATER INTERFACE IN FRESHWATER SHALLOW LAKES FROM THE SOUTHEASTERN PAMPA PLAIN, ARGENTINA

PAULA ANDREA CRISTINI AND CLAUDIO GERMÁN 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
email: paulacristini@mdp.edu.ar*

ABSTRACT: Molluscan taphonomic patterns below the sediment-water interface in three freshwater shallow lakes from the Southeastern Pampa Plain, Argentina (Nahuel Rucá, Las Mostazas, and Los Carpinchos), were analyzed in order to explore the taphonomic alteration suffered by mollusks with depth and determine if this taphonomic alteration varied locally within lakes or between them. Short cores (approximately 30 cm) from littoral environment as well as open water were sampled in each lake. Nine mollusk species were identified: *Heleobia parchappii*, *H. australis*, *Biomphalaria peregrina*, *Uncancylus concentricus*, *Musculium argentinum*, *Drepanotrema kermatoides*, *Succinea meridionalis*, *Antillorbis nordestensis*, and *Pomacea canaliculata*. The highest percentage of moisture, organic matter and carbonates as well as less alkaline pH were recorded at the top of the cores and in littoral environments, indicating less favorable conditions for preservation. Results suggest that the taphonomically active zone occupies the first 10 cm below the sediment-water interface.

INTRODUCTION

Actualistic taphonomy focuses on the study of present-day fossilization patterns and processes in contemporary settings to aid and guide interpretation of the fossil record (Kowalewski and LaBarbera 2004). In the last 40 years there has been considerable progress in the knowledge of taphonomic processes affecting mollusks mainly in marginal marine environments (e.g., Walker and Goldstein 1999; Behrensmeyer et al. 2000; Best and Kidwell 2000; Kidwell et al. 2001, 2005; Best et al. 2007; Krause et al. 2010). From these studies we know that taphonomic loss mainly takes place at and just below (first few centimeters) the sediment-water interface, a zone known as the taphonomically active zone (TAZ; Davies et al. 1989). Destructive processes in the TAZ can be physical (e.g., crushing or boring by organisms, fragmentation and abrasion by waves and currents) or biogeochemical (Cutler et al. 1995; Best and Kidwell 2000; Zuschin et al. 2003; Olszewski 2004; and references therein). Among the latter, dissolution appears to be the main factor affecting preservation, which is governed by the redox state within sediments, which in turn is regulated by microbial activity (Aller 1982; Walker and Goldstein 1999; Best et al. 2007; Cherns et al. 2008). The deepest vertical extension of the TAZ below the sediment-water interface has been estimated at approximately 50 centimeters in coastal environments (Walker 2001). The lower limit of this zone was referred as the depth of final burial (DFB; Olszewski 2004), denoting the deepest point from which shells can be reworked upward in the sediment column. At present, actualistic taphonomy has been mostly conducted above the sediment-water interface with only limited information on the processes occurring below the sediment-water interface (see Walker and Goldstein 1999 for a review on this subject). This clearly biases knowledge on preservation towards the processes acting above the sediment-water interface, which raises questions about what occurs below: Are hard parts differentially affected above and below the sediment-water interface? Is there a taphonomic tiering with depth? Knowledge about the dynamic and intensity of the taphonomic processes acting below the sediment-water interface is of great importance for gaining a more realistic understanding of the preservation of shells in modern habitats as they pass below the DFB and become potential fossils.

Most actualistic taphonomic research has been conducted in marginal marine environments. In contrast, freshwater systems have received less attention; the few taphonomic studies carried out have been mainly conducted in streams and reservoirs from the Northern Hemisphere, Africa, southern Brazil, and the southeastern Pampas of Argentina (Cohen 1989; Briggs et al. 1990; Cummins 1994; Brown et al. 2005; Martello et al. 2006; Kotzian and Simões 2006; Nielsen et al. 2008; Erthal et al. 2011; Tietze and De Francesco 2012, 2014). In particular, studies conducted in freshwater shallow lakes from the southeastern Pampa plain demonstrated that mollusk death assemblages preserved above the sediment-water interface displayed high compositional fidelity, reflecting the taxonomic composition and relative abundance of living species. This suggests that the original biocoenoses do not undergo significant alteration during the transition from life to surficial death assemblages (Tietze and De Francesco 2012). Because of the relatively low energy of shallow lakes, most taphonomic alteration is from dissolution or microbioerosion due to microbial activity (Tietze and De Francesco 2014). The only preliminary study conducted on shell preservation below the sediment-water interface (Cristini and De Francesco 2012) estimated the TAZ to extend below the surface 25 cm. The main taphonomic loss (dissolution) took place within the first 10 centimeters and diminished gradually with depth. Cristini and De Francesco (2012) study provides a first baseline to understand the taphonomic pathway followed by mollusks in freshwater aquatic systems. Yet, their study was exclusively conducted in the littoral environment of one lake and did not address taphonomic processes acting in the open water parts of lakes and if this pattern may be extended over a regional scale.

We hypothesize that: (1) the taphonomic processes acting below the sediment-water interface are the same that act above the sediment-water interface and are mostly related to dissolution and/or microboerosion caused by microorganisms; (2) there is a vertical decrease in taphonomic
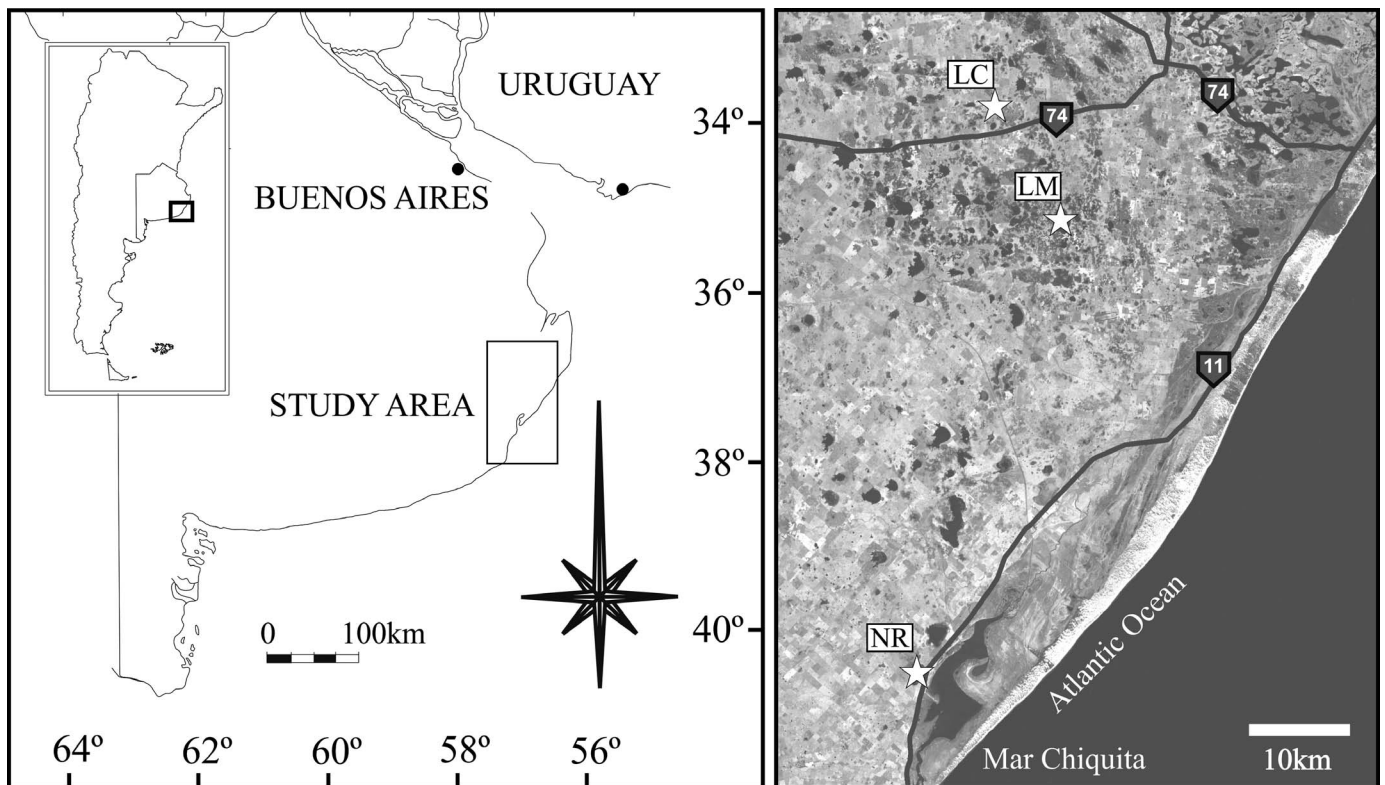
FIG. 1.—Location of study area. Abbreviations: NR = Nahuel Rucá; LM = Las Mostazas; LC = Los Carpinchos.

activity because of the diminution of microorganisms with depth; and (3) taphonomic alteration is higher in the littoral environment of the lakes where most biological activity occurs. Thus, in the present study we: (1) explored the taphonomic alteration suffered by mollusks below the sediment-water interface and (2) analyzed if this taphonomic alteration varied locally (within lake) or regionally (between lake).

STUDY AREA

The study was conducted in three freshwater shallow lakes from the Southeastern Pampa plain, Argentina: Nahuel Rucá (NR) 37°37′21″S, 57°25′42″W; Las Mostazas (LM) 37°9′57″S, 57°14′50″W and Los Carpinchos (LC) 37°3′34″S, 57°19′56″W. The three lakes are located along a north-south gradient and separated from one another by approximately 20 km (Fig. 1). The region is a vast grassy plain that covers the central area of Argentina. From a geological and geomorphological point of view, the study area is a flat plain (Pampas) crossed by a few streams and dominated by shallow lakes (Diovisalvi et al. 2014). The flat geomorphology is responsible for the disparity between the abundance of lentic water bodies and the low density of the drainage net. Local groundwater discharge is the primary source of Pampean lake waters. Infiltration is very important due to the regional lack of slope ($0.3 \mathrm{m\ km^{-1}}$) and the soil characteristics, and thus the water table is near the surface in most places (Fernández Cirelli and Miretzki 2004 and references therein). The soils of the area are generally fertile with a high nutrient content, composed mainly of loess and with a marked capacity for cationic interchange, predominantly involving calcium (Rodrigues Capítulo et al. 2010). The climate is temperate humid or sub-humid with a mean annual temperature of 15°C and a mean annual precipitation of 1100 mm (Feijoó and Lombardo 2007). Precipitation patterns also display large variability, both geographically and inter-annually. This large interannual variability in combination with poorly developed drainage systems results in recurrent

and extensive floods, alternating with drought periods. During flood periods, lakes can exceed their capacity, resulting in very slow surface flows that result in lake interconnections. All these processes affect the lake water residence time, the water content of soils, and the depth of the water table (Diovisalvi et al. 2014).

In general, lakes are very shallow (2 m) and lack thermal stratification except for short periods of time (Quirós and Drago 1999; Fernández Cirelli and Miretzky 2004). The lakes studied in this work contribution are characterized by an extensive and shallow (~ 0.5 m) littoral environment, dominated by the emergent macrophyte *Schoenoplectus californicus* (C.A. Mey) Soják, which forms a complete ring around each lake, and a deeper open water environment (between 0.5 m and 1.5 m approximately), which is generally free of vegetation except for the submerged macrophytes *Myriophyllum elatinoides* and *Ceratophyllum demersum* (Stutz et al. 2010, 2012). The lakes are eutrophic or hypertrophic and turbid due to the large amount of algae (Quirós et al. 2002, 2006). Hypereutrophy is strongly influenced by high loading of phosphorus from agriculture, which is widespread in the area. The water column is almost always thermally homogeneous, saturated with dissolved oxygen, and has a high content of dissolved organic matter (Fernández Cirelli and Miretzky 2004). LC and LM are closed lakes and, therefore, water level is controlled by the balance between precipitation, runoff, and local groundwater while NR is an open lake, fed by a freshwater stream held back by a dam that determines the water level.

The freshwater malacofauna of these lakes is characterized by low taxonomic diversity and dominated by epifaunal gastropods except for the infaunal bivalve *Musculium argentinum* (d'Orbigny 1835), which lives buried within the top few centimeters below the sediment-water interface (for details see Tietze and De Francesco 2012). *Heleobia parchappii* (d'Orbigny 1835), *Biomphalaria peregrina* (d'Orbigny 1835), and *Uncancylus concentricus* (d'Orbigny 1835) are frequently the dominant species in the three lakes studied. In NR, *Pomacea canaliculata* (Lamarck

1822), *Antillorbis nordestensis* (Lucena 1954), *Physa acuta* (Draparnaud 1805), *Musculium argentinum* and O*malonyx* sp. also occur at some times of the year (Tietze and De Francesco 2012). This is mainly because many species have annual life cycles and as a consequence adults are present only in a particular season, generally synchronized with the life cycle of vegetation (Dillon 2000). In LC, life assemblages also included *M. argentinum*, *P. canaliculata*, *Omalonix* sp., *Stenophysa marmorata* (Guildin 1828), *Drepanotrema* spp. and *Succinea meridionalis* (d'Orbigny 1837) in lower frequency (Eleonor Tietze personal communication). In LM, only the three dominant species, *H. parchappii*, *B. peregrina*, and *U. concentricus*, were recorded.

MATERIALS AND METHODS

Fieldwork and Laboratory Analysis

Sampling was designed to allow comparison between the two main habitats represented in each lake: the highly vegetated littoral environment (LIT) and the open water environment (OW). In each lake, five cores (diameter = 6 cm) were randomly collected from both LIT and OW using a piston core manually pushed into the sediment to a depth of approximately 30 cm (core lengths varied depending on hardness and resistance of the substrate). In all cases the same force was applied by the same person. Cores were covered with film and aluminum foil and transported to the laboratory, where they were sub-sampled every 2 cm.

For each sub-sample (approximately 56 cm^3) pH, moisture, organic matter, and carbonates concentration were measured. pH was measured with a Hanna pHep®5 98128 pHmeter. Moisture was calculated by weighing 5 g of wet sediment before and after drying for 24 hours at approximately 105 °C. The organic matter in each sub-sample was estimated using the loss-on-ignition method (LOI) for four hours at 550 °C. Carbonates were estimated by burning sediments at 1000 °C for two hours (Heiri et al. 2001).

The remaining sediments of each sub-sample were sieved (0.5 mm mesh size) to retain mollusks. Shells recovered were identified to the species level (when possible), counted and scaled to a standard volume (100 ml). Any fragment of a shell that included the apex (for gastropods) or the umbo (for bivalves) was considered an individual. 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. In order to evaluate the preservation state of mollusk shells, three taphonomic variables were scored in each sub-sample in a three-grade scale, adopted from the scheme of Kowalewski et al. (1995): (1) degree of fragmentation; (2) fine-scale surface alteration; and (3) presence of periostracum (De Francesco et al. 2013). For each variable, specimens and indeterminable fragments were classified as good (0 = best preservation; < 10% alteration); fair (1 = intermediate; between 10 and 50% alteration); and poor (2 = poorest; > 50 % alteration). Individual taphonomic states were subsequently averaged for each sub-sample.

Data Analysis

Physico-Chemical Variables.—Cores were divided into zones based on physico-chemical variables (pH, moisture, organic matter, and carbonates) using constrained hierarchical clustering based on Euclidean distance (Legendre and Birks 2012), with clusters constrained by stratigraphic order. Physico-chemical variables were standardized by subtracting the mean and dividing by the standard deviation (a "z-transformation") to provide a common scale before ordination (Clarke and Gorley 2006; Legendre and Birks 2012). The statistical significance of the zones was assessed using the 'broken stick' model (Bennett 1996). Hierarchical clustering, 'broken stick' model and graphs were performed in R version 2.12.2 (R Development Core Team 2011), including the package "rioja" version 0.5-6 (Juggins 2009).

In order to assess for differences in physico-chemical variables between LIT and OW environments, permutational multivariate analysis of variance (PERMANOVA, Anderson et al. 2008) with 9999 permutations were performed on Euclidean distances based on standardized but unbalanced physico-chemical datasets. This analysis was chosen because it allows testing of the simultaneous response of one or more variables to one or more factors. Additionally it allows making a posteriori comparisons among levels of factors, including within individual levels of other factors in the case of significant interaction terms. Also, it can accommodate unbalanced data sets (Anderson 2001; Anderson et al. 2008).

The PERMANOVA design consisted of one factor: *lake environment*, with two levels: LIT and OW. Although the PERMANOVA allows making a posteriori comparisons among levels of factors or groups, it does not identify which variables are responsible for the differences found. For that reason, a two-way SIMPER (similarity percentage) analyses was performed. SIMPER is a simple method that allows identification of the contribution of each variable to differences found in the PERMANOVA analysis (Clarke 1993). Additionally, non-metric multidimensional scaling (NMDS) was performed in order to visualize the multivariate pattern. PERMANOVA, SIMPER and NMDS analyses were carried out using the Plymouth Routines in Multivariate Ecological Research (PRIMER-e) package (Clarke and Gorley 2006).

Mollusk Abundances.—Unbalanced mollusk abundance data were square root transformed prior to statistical analyses in order to stabilize their variances (i.e., to compensate the effect of those species very abundant compared to those that are less frequent in these environments). PERMANOVA (9999 permutations) was applied to assess for differences in mollusk assemblage composition among the cores and between LIT and OW (at α = 0.05). Analyses were based on Bray-Curtis distances (Tomašových and Rothfus 2005) and included the factors *lake environment* (with two levels: LIT and OW) and *depth* (with three to five levels depending on the zonation defined by the cluster analysis). Data from each core was analyzed for the two factors including interactions of the model. When main effects or interactions were significant, *a posteriori* comparisons were explored (Anderson 2001). *Pomacea canaliculata* and *Drepanotrema kermatoides* were removed from the analyses because only one specimen of each species was recorded in the dataset. When significant differences were detected, SIMPER analyses were performed in order to identify the contribution of each species to the differences found with the PERMANOVA. NMDS was performed on mollusk abundances of each lake in order to visualize the multivariate pattern among observations. Bar chart plots of abundance data were also constructed to graphically summarize results.

Taphonomy.—PERMANOVA (9999 permutations) was also applied to untransformed and unbalanced taphonomic data in order to assess for differences in mollusk preservation among cores and between LIT and OW. Analyses were based on Manhattan distances (Tomašových and Rothfus 2005) and included the factors *lake environment* and *depth* previously described. In contrast to Euclidean distances, effects of outliers are diminished because between-sample differences in taphonomic variables are not squared. PERMANOVA decomposes among- and within-group sum of squared dissimilarities (Anderson 2001). Only samples with n > 10 were included. NMDS was performed on taphonomic variables from each lake in order to visualize the multivariate pattern among observations. Additionally, taphonomic data were summarized as taphograms, in order to identify those variables responsible for the differences obtained with the PERMANOVA analyses. Taphograms constitute a simple graphic technique that retains information not found in calculated average taphonomic scores and permits a rapid comparison of the taphonomic characteristics among samples (Kowalewski et al. 1995). Taphograms were produced with the computer program PAST v 1.81 (Hammer et al. 2001).

TABLE 1.—*Cores from Nahuel Rucá (NR), Las Mostazas (LM) and Los Carpinchos (LC) showing the number of zones as well as the depth of each zone. Values are expressed in centimeters and indicate the depth of each zone's base. Abbreviations: C1–C5 = cores 1–5, respectively; LIT = littoral; OW = open water; Z1–Z5 = zones 1–5, respectively.*

	Nahuel Rucá (NR)									
	LIT					OW				
	C1	C2	C3	C4	C5	C1	C2	C3	C4	C5
Z1	2	6	8	10	8	6	8	4	6	4
Z2	12	20	32	24	32	18	22	16	18	22
Z3	28	42	38		48	22	32	26		24
Z4	44	54				26	36			
Z5		56								

	Las Mostazas (LM)									
	LIT					OW				
	C1	C2	C3	C4	C5	C1	C2	C3	C4	C5
Z1	2	6	6	12	6	2	6	2	2	4
Z2	8	16	20	28	26	16	12	6	10	18
Z3	22	22				22	20	22	16	

	Los Carpinchos (LC)									
	LIT					OW				
	C1	C2	C3	C4	C5	C1	C2	C3	C4	C5
Z1	2	12	10	8	6	6	8	8	8	6
Z2	10	22	16	16	24	12	26	24	16	12
Z3	16	28	22	24		20		30	30	24
Z4	24		30			24				28

RESULTS

Physico-Chemical Variables

Cores from the three lakes had lengths that varied between 16 and 56 cm (average 27 cm) (Table 1). pH varied between 6.46 and 8.64, moisture between 22.15 and 89%, organic matter between 1.4 and 61.86%, and carbonate between 0.58 and 8.24% (Fig. 2).

The number of zones defined by cluster analysis varied among cores and lakes. In NR, two to five zones were defined in LIT and two to four zones in OW. Zones 1 and 2 included the first 24 cm and the first 19.2 cm in LIT and OW, respectively. The remaining levels included three to five zones (Table 1). Cores from LM were divided into two to three zones in both lake environments. Zones 1 and 2 covered the first 19.6 cm in LIT and 12.4 cm in OW, while the lowest part of the cores was grouped in zone 3 (Table 1). Finally, LC cores were divided into two to four zones: Zones 1 and 2 grouped the topmost 18 cm in both lake environments, while zones 3 and 4 included the lowermost sediments of the cores (Table 1).

The highest percentage of moisture, organic matter, and carbonate were recorded at the top of the cores (Z1) and diminished gradually downward except in NR where they increased towards the bottom of the succession in some cases. Furthermore, pH showed the opposite trend increasing when the other physico-chemical variables decreased and vice versa, except in LM, where it showed a similar trend to other physico-chemical variables (Fig. 2A–2C).

Physico-chemical variables were significantly different between LIT and OW (NR: Pseudo-F = 16.252, p = 0.0001; LM: Pseudo-F = 5.4832, p = 0.0058; LC: Pseudo-F = 8.6282, p = 0.0005) in the three lakes (Tables 2, 3, Fig. 3A–3C). The highest percentage of moisture, organic matter, and carbonates as well as the lowest pH (low alkalinity), were recorded in the littoral environment. The only exception was LC, which exhibited higher moisture, organic matter and carbonates at depth Z1 in OW (Fig. 2A–2C). Although SIMPER analysis showed that all variables contributed with similar percentages to the differences found, pH and carbonate showed percentages slightly higher in NR and LC and moisture in LM (Table 4).

Mollusk Abundances

Nine mollusk species were identified: *Heleobia parchappii*, *H. australis*, *Biomphalaria peregrina*, *Uncancylus concentricus*, *Musculium argentinum*, *Drepanotrema kermatoides*, *Succinea meridionalis*, *Antillorbis nordestensis*, and *Pomacea canaliculata* (Fig. 4).

All nine species were present in NR. The most abundant species were *H. parchappii*, *B. peregrina*, and *U. concentricus* (Fig. 5A). Species abundances varied between LIT and OW (pseudo-F = 3.6353; p = 0.0141) but not in depth. The factors *depth* and *lake environment* (littoral versus open water) were significantly related (Table 2, Fig. 6A). *A posteriori* comparisons showed higher abundance in OW than LIT only at depth Z2 (t = 3.5788; p = 0.0002) and there was only a significant difference between Z1 and Z2 in LIT (t = 2.4010, p = 0.0032), not in OW (Fig. 5B).

LM and LC included by *H. parchappii*, *B. peregrina*, and *U. concentricus* at even lower abundances than in NR. In LM, *B. peregrina* was the most abundant species (Fig. 5C). Mollusk abundances were significantly different among depths (pseudo-F = 7.4654, p = 0.0022) but not between LIT and OW (Table 3A, Fig. 6B) with higher abundance in Z1 (Table 3A, Fig. 5D). In LC, the LIT and Z1 of OW were sterile. *Heleobia parchappii* was the most abundant species at all depths (Fig. 5E). Mollusk abundances were not significantly different among depths (Table 3B, Fig. 6C).

Taphonomy

Recovered mollusks were dominated by fragments. Most shells lost more than 50% of their periostracum both in LIT and OW as well as in different depths (Fig. 7). In NR, taphonomic variables were significantly different between LIT and OW (pseudo F = 10.428; p = 0.0006), but they did not differ with depth (Table 2, Fig. 8A), where mollusks recovered from OW were better preserved. Fine-scale surface alteration was mainly responsible for the differences observed (Fig. 7A). In LM and LC, preservation was intermediate to good (Fig. 7B, 7C) without significant differences in depth and between LIT and OW (Table 3, Fig. 8B, 8C).

DISCUSSION

Factors Affecting Mollusk Preservation Below the Sediment-Water Interface

The three lakes exhibited differences in physico-chemical variables, mollusk abundances, and preservation. Most differences may be responding to local variations. Yet, some common patterns can be recognized in all three lakes. For instance, the littoral environment had less alkaline conditions and higher percentages of moisture, organic matter, and carbonate than the open water environment, which was expected due to the abundant vegetation present in the littoral environment. It is known that acidic conditions can result from the bacterial decomposition of organic matter (Aller 1982; Best et al. 2007). In fact, recent studies demonstrate that littoral environments from these lakes are expected to have the worst conditions for preservation due to the higher concentration of macrophytes, which constitutes a greater source of organic matter available for decomposition (Cristini et al. 2017). In most cores roots were also observed. In general, higher abundance was recorded at the top of the
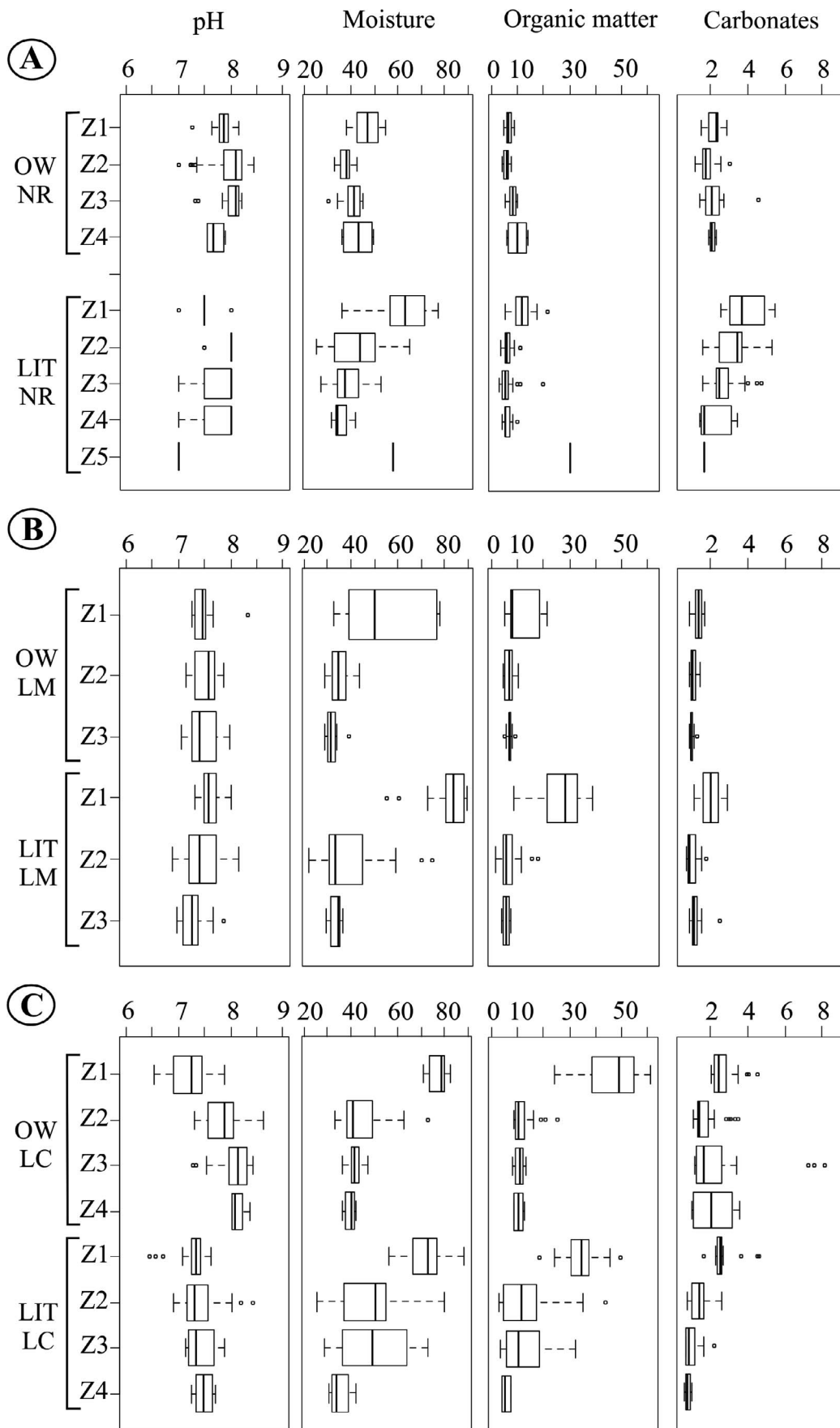
Fig. 2.—Box plot showing physico-chemical variables. **A)** Nahuel Rucá (NR). **B)** Las Mostazas (LM). **C)** Los Carpinchos (LC). Abbreviations: LIT = littoral; OW = open water; Z1–Z5 = depths 1–5, respectively.

TABLE 2.—*PERMANOVA on Euclidean distances for physico-chemical variables, on Bray-Curtis distances for species abundance variables, on Manhattan distances for taphonomic variables: at different depths (Z1, Z2, Z3, Z4, Z5) and different environments of the Nahuel Rucá (NR): littoral (LIT) and open water (OW). *Pair-wise test comparison of interaction "Lake environment × Depth" for factor "Lake environment". **Pair-wise test comparison of "Lake environment × Depth" for factor "depth". Values in bold indicate significant p values (α = 0.05).*

Source	Physico-chemical		Species abundance		Taphonomic	
	Pseudo-F	*p*	*Pseudo-F*	*p*	*Pseudo-F*	*p*
Lake environment	16.252	**0.0001**	3.6353	**0.0141**	10.428	**0.0006**
Depth	-	-	1.5864	0.1101	1.5255	0.2055
Lake environment×depth	-	-	2.2948	**0.0195**	1.7927	0.1401

Comparison*			Comparison**			
LIT vs OW				LIT		OW	
Groups	t	p	Groups	t	p	t	p
Z1	0.9295	0.4116	Z1 vs. Z2	2.4010	**0.0032**	1.5027	0.0707
			Z1 vs. Z3	1.6019	0.0631	1.2742	0.1537
Z2	3.5788	**0.0002**	Z1 vs. Z4	1.4563	0.1673	0.5841	1
			Z1 vs. Z5	0.8634	0.7069		
Z3	1.4263	0.1012	Z2 vs. Z3	1.4459	0.1116	1.1909	0.2421
			Z2 vs. Z4	0.7855	0.3829	0.6489	0.7511
Z4	2.6430	0.2498	Z2 vs. Z5	2.1976	0.1366		
			Z3 vs. Z4	0.9977	0.3275	2.2887	1
			Z3 vs. Z5	1.3478	0.2441		
			Z4 vs. Z5	3.7043	0.2529		

successions and gradually diminished downward. These roots could explain the less alkaline conditions in the littoral environment and at the top of the successions as they would provide a source of organic matter to decompose, which would produce corrosive pore waters and lower the pH.

These results are in agreement with previous work (see Cristini et al. 2017). In some cores from NR, higher abundance of roots was also observed towards the bottom of the cores, which explains the higher percentage of organic matter and less alkaline conditions present at those

TABLE 3.—*PERMANOVA on Euclidean distances for physico-chemical variables, on Bray-Curtis distances for species abundance variables, on Mahattan distances for taphonomic variables: at different depths (Z1, Z2, Z3, Z4) and different environments in the lake A: Las Mostazas (LM) and B: Los Carpinchos (LC): littoral (LIT) and open water environments (OW). *Pair-wise test comparison for factor "depth". Values in bold indicate significant p values.*

	A. Las Mostazas					
	Physico-chemical		Species abundance		Taphonomic	
Source	*Pseudo-F*	*p*	*Pseudo-F*	*p*	*Pseudo-F*	*p*
Lake environment	5.4832	**0.0058**	0.4259	0.6006	1.4253	0.2328
Depth	-	-	7.4654	**0.0022**	1.0933	0.3501
Lake environment×Depth	-	-	1.1656	0.3225	0.3771	0.7794

	Groups of depth		
Comparison*	Z1 vs. Z2	Z1 vs. Z3	Z2 vs. Z3
t	2.5775	4.4698	1.4963
p	**0.0140**	**0.0010**	0.1468

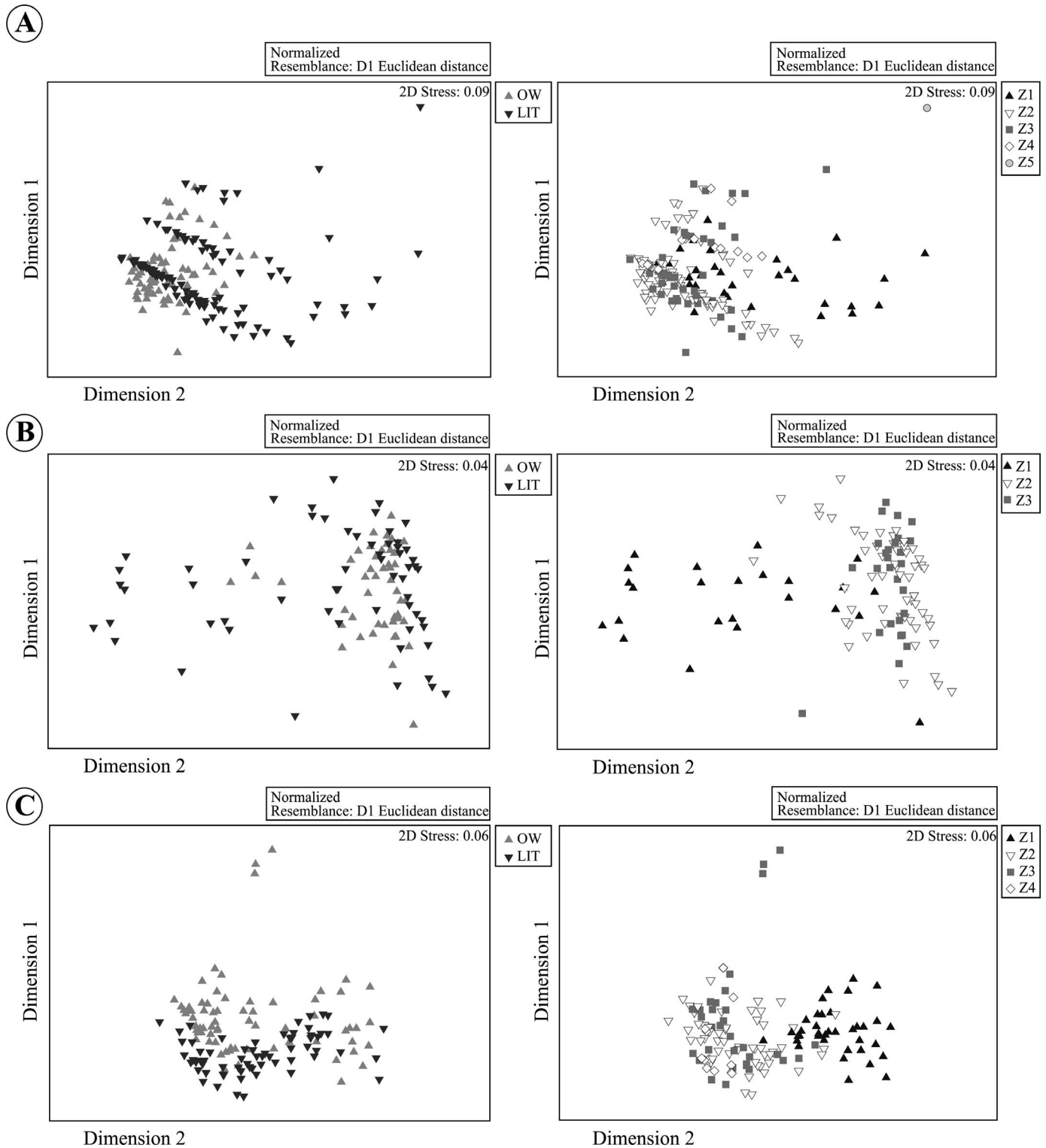|	**B**. Los Carpinchos					
	Physico-chemical		Species abundance		Taphonomic	
Source	*Pseudo-F*	*p*	*Pseudo-F*	*p*	*Pseudo-F*	*p*
Lake environment	8.6282	**0.0005**	-		-	
Depth	-	-	1.0408	0.3820	2.4687	0.093
Lake environment×Depth	-	-	-		-	

FIG. 3.—Two-dimensional Non metric MDS plot of physico-chemical variables. **A**) Nahuel Rucá (NR). **B**) Las Mostazas (LM). **C**) Los Carpinchos (LC). Abbreviations: LIT = littoral; OW = open water; Z1–Z5 = depths 1–5, respectively.

levels. In LC the successions showed the same pattern observed in the other two lakes except for Z1 in OW, which showed the highest percentages of moisture, organic matter, and carbonate and the lowest pH, probably due to the high abundance of roots recorded at that level.

Mollusk Abundances and Preservation Below the Sediment-Water Interface

Most living mollusks from the Pampas prefer microhabitats located in shallow parts of water bodies associated with dense vegetation (Tietze et al.

TABLE 4.—*SIMPER analysis on Euclidean distances for physico-chemical variables showing contribution (%) to the differences found between LIT and OW in NR, LM, and LC lakes. Abbreviations: Mois. = moisture; OM = organic matter; carb. = carbonates.*

	Nahuel Rucá				Las Mostazas				Los Carpinchos			
Groups	pH	Mois.	OM	carb.	pH	Mois	OM	carb.	pH	Mois.	OM	carb.
LIT vs. OW	26.2	22.4	21.7	29.7	24.6	26.1	24.7	24.6	27.7	23.8	23.7	24.9

2011 and references therein). In the present study, shells were recovered both in LIT and OW. The lack of ecological information on molluscan spatial distribution within these lakes prevents determining if the remains found in OW represent autochthonous death assemblages (at present all modern surveys were carried out only in LIT) or allochthonous assemblages resulting from shell transport caused by mixing processes such as waves produced by wind. Resuspension occurs continually above wave base in shallow lakes and deposition is random as a function of water depth (Evans 1994). It is also possible that death assemblages represent autochthonous dead remains deposited in past LITs (i.e., palimpsest assemblages), when the lake was smaller. It is known that shallow lakes from the region experience changes in area, depth and salinity due to drought- flood cycles (Quiros et al. 2006).

Of the eight species represented in life and death assemblages above the sediment-water interface (Tietze and De Francesco 2012), six (75%) were recorded below the sediment-water interface in this study, and four (50%) were also recorded as fossils in the lake (see De Francesco et al. 2013). This pattern suggests a taphonomic tiering below the sediment-water interface, which may be acting as a destructive agent for shell preservation. In fact, the two species not preserved in death assemblages below the sediment-water interface are *Physa acuta* and *Omalonyx* sp., both species that occur in low numbers in modern communities and have thin shells. The former is an exotic species that only recently invaded the area (which also explain its absence in fossil deposits). It is known that the actual occurrence of a taxon in a fossil assemblage depends not only on its per capita preservation probability (resulting from all durability factors), but also the supply side of original biological populations (their abundance and turnover rates) (Beherensmeyer et al. 2005). Therefore, the great abundances of *U. concentricus* in modern populations of the lakes would explain its robust representation in the fossil record despite having small and thin shell. It is important to highlight that in LC, of the nine mollusk species recorded in life assemblages, only three were recovered in death
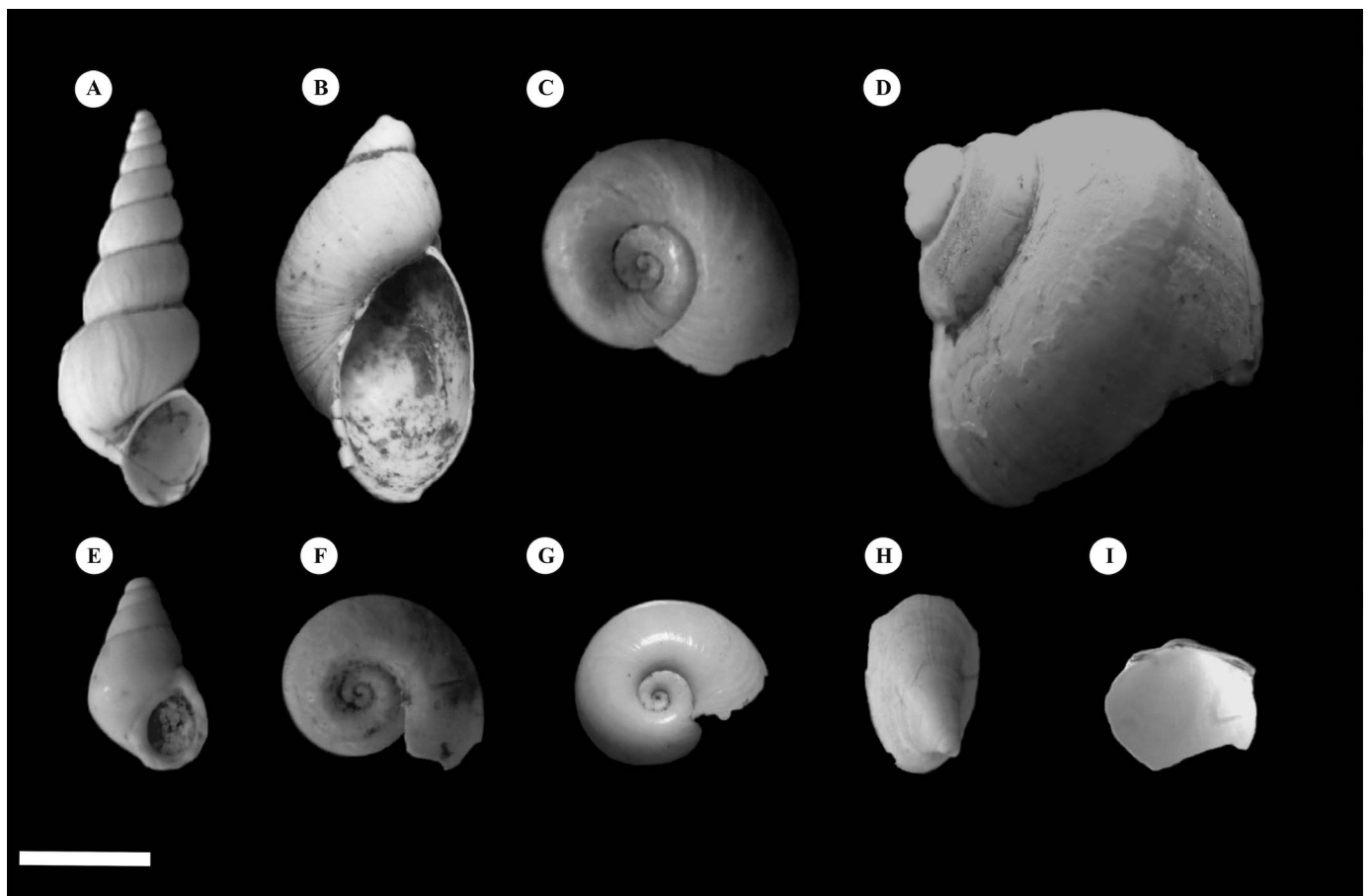

FIG. 4.—Mollusks recovered from cores in Nahuel Rucá (NR), Las Mostazas (LM), and Los Carpinchos (LC). **A**) *Heleobia parchappii*. **B**) *Succinea meridionalis*. **C**) *Biomphalaria peregrina*. **D**) *Pomacea canaliculata*. **E**) *Heleobia australis*. **F**) *Drepanotrema kermatoides*. **G**) *Antillorbis nordestensis*. **H**) *Uncancylus concentricus*. **I**) *Musculium argentinum*. Scale = 2 mm.
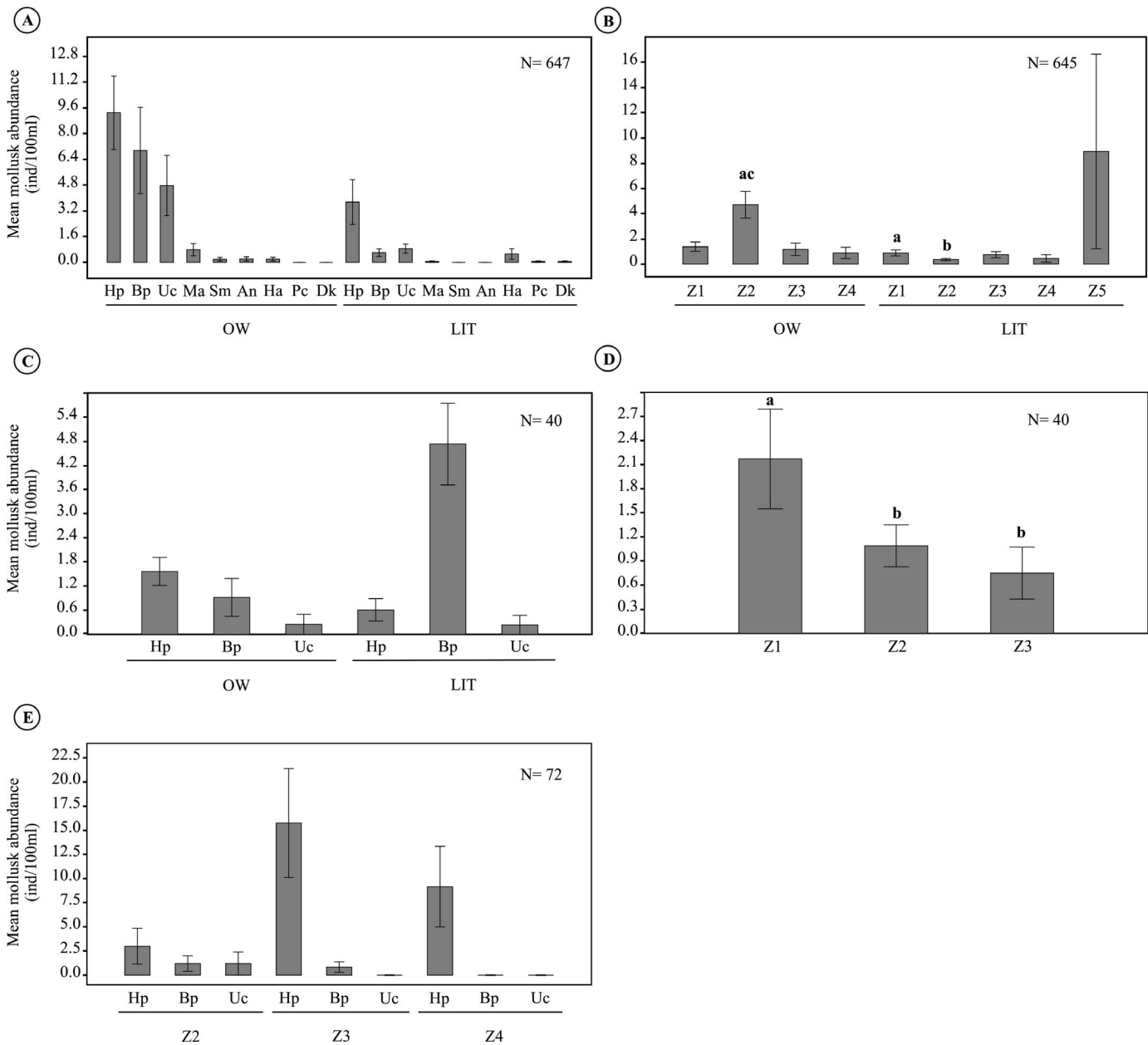
FIG. 5.—Bar chart plot showing species abundance. **A**) Nahuel Rucá (NR) mollusk abundance in LIT and OW. **B**) Nahuel Rucá (NR) mollusk abundance at each depth zone in LIT and OW. **C**) Las Mostazas (LM) species abundance in LIT and OW. **D**) Las Mostazas (LM) mollusk abundance in each depth zone. **E**) Los Carpinchos (LC) species abundance in each depth zone. Abbreviations: Hp = *Heleobia parchappii*; Bp = *Biomphalaria peregrina*; Uc = *Uncancylus concentricus*; Ma = *Musculium argentinum*; Sm = *Succinea meridionalis*; An = *Antillorbis nordestensis*; Ha = *Heleobia australis*; Pc = *Pomacea canaliculata*; Dk = *Drepanotrema kermatoides*; LIT = littoral; OW = open water; Z1–Z5 = depths 1–5, respectively.

assemblages, which indicates very low specific richness fidelity. This could be due to the more acidic conditions than the other two lakes.

In some cores from NR, *H. australis,* an estuarine species that is very abundant in the tidally influenced Mar Chiquita coastal lagoon (De Francesco and Isla 2003), was also recorded (see Fig. 1). This species had been previously recorded as a fossil in sedimentary cores extracted from NR and also in two other lakes in the area, Hinojales-San Leoncio and Lonkoy located close to NR (De Francesco et al. 2013). Possibly, a connection among water bodies allowed this species to migrate into the interior from the coast in the past (which does not occur today) (De Francesco et al. 2013). If so, the *H. australis* shells recorded in the surficial

sediments of the cores may correspond to those fossil levels reported by De Francesco et al. (2013).

The higher abundance of shells in OW suggests geochemical conditions less destructive than those of LIT. The abundant vegetation in LIT provides a source of organic matter available for degradation contrary to OW, which is in general free of vegetation. This pattern is clearly seen in NR, where shells recovered from OW are better preserved than those from LIT. In fact, fine-scale surface alteration exhibits low values (better preservation) in OW, the opposite of the higher values (poor preservation) obtained in LIT (Fig. 7A). The fact that LIT in LC was completely sterile suggests that dissolution may have destroyed all shells
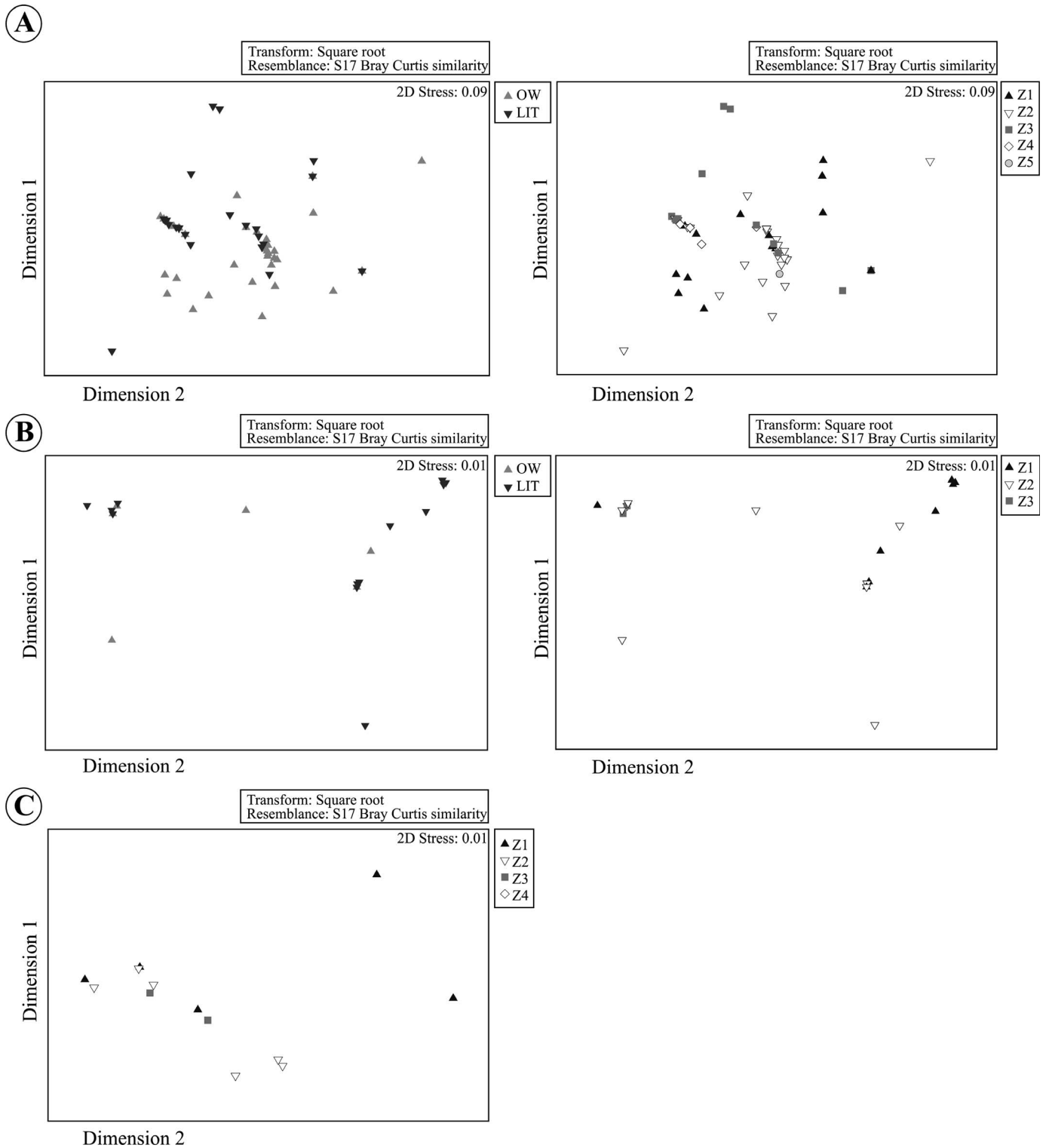
FIG. 6.—Two-dimensional Non metric MDS plot based on species abundances. **A**) Nahuel Rucá (NR). **B**) Las Mostazas (LM). **C**) Los Carpinchos (LC). Abbreviations: LIT = littoral; OW = open water; Z1–Z5 = depths 1–5, respectively.

from death assemblages below the sediment-water interface. The exception was LM, which did not show differences between compartments of the lakes, possibly because the depositional environments had similar pH values (Fig. 2).

Best et al. (2007) found that chemical dissolution dominantly occurs in the upper centimeters of sediments because of decomposition of organic matter resulting in corrosive pore waters. In a recent study performed in the same lakes of the present work, Cristini et al. (2017) analyzed the chemical
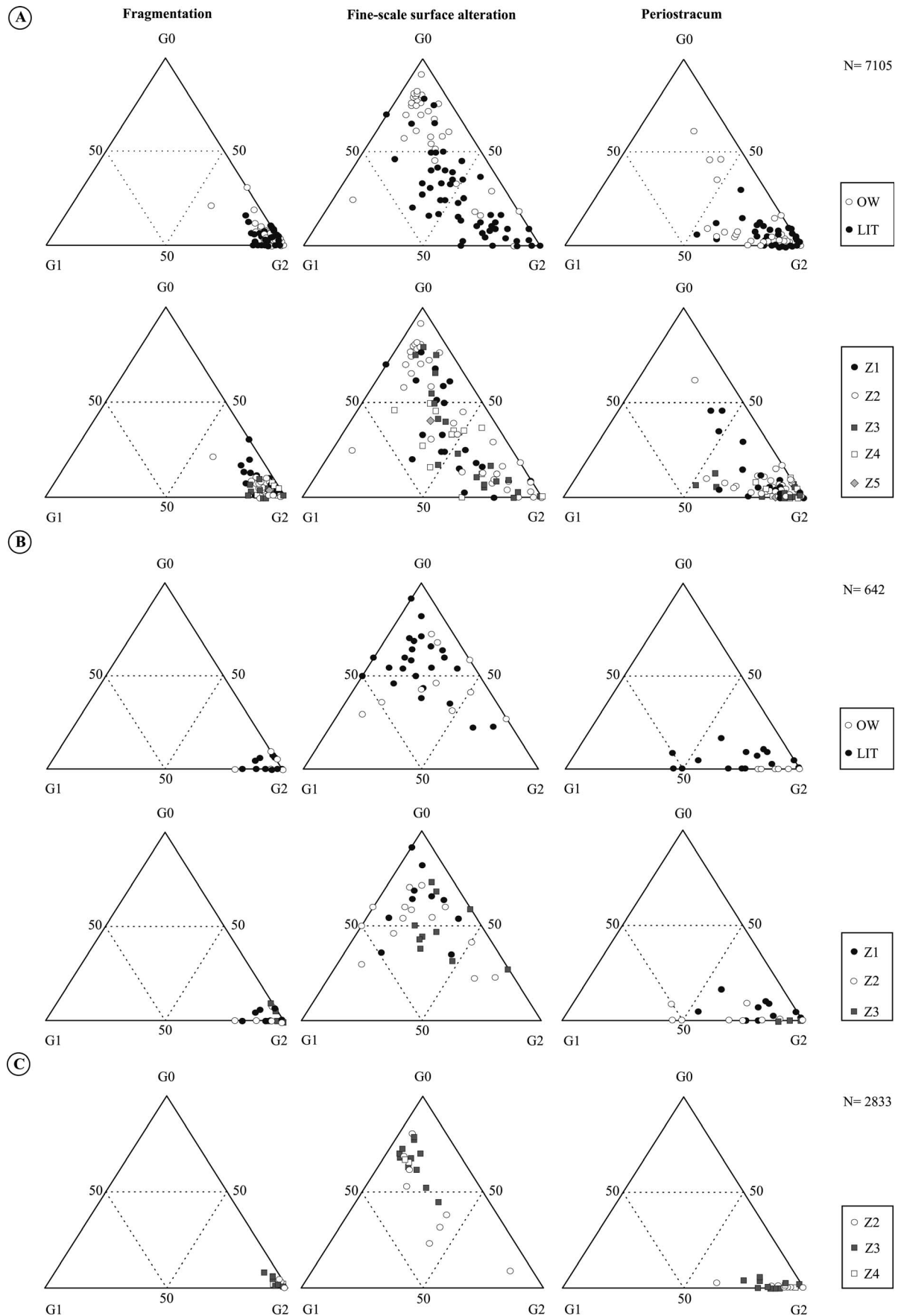
FIG. 7.—Taphograms. **A**) Nahuel Rucá (NR). **B**) Las Mostazas (LM). **C**) Los Carpinchos (LC). Abbreviations: G0 = good preservation; G1 = intermediate preservation; G2 = poor preservation; LIT = littoral; OW = open water; Z1–Z5 = depths 1–5, respectively.
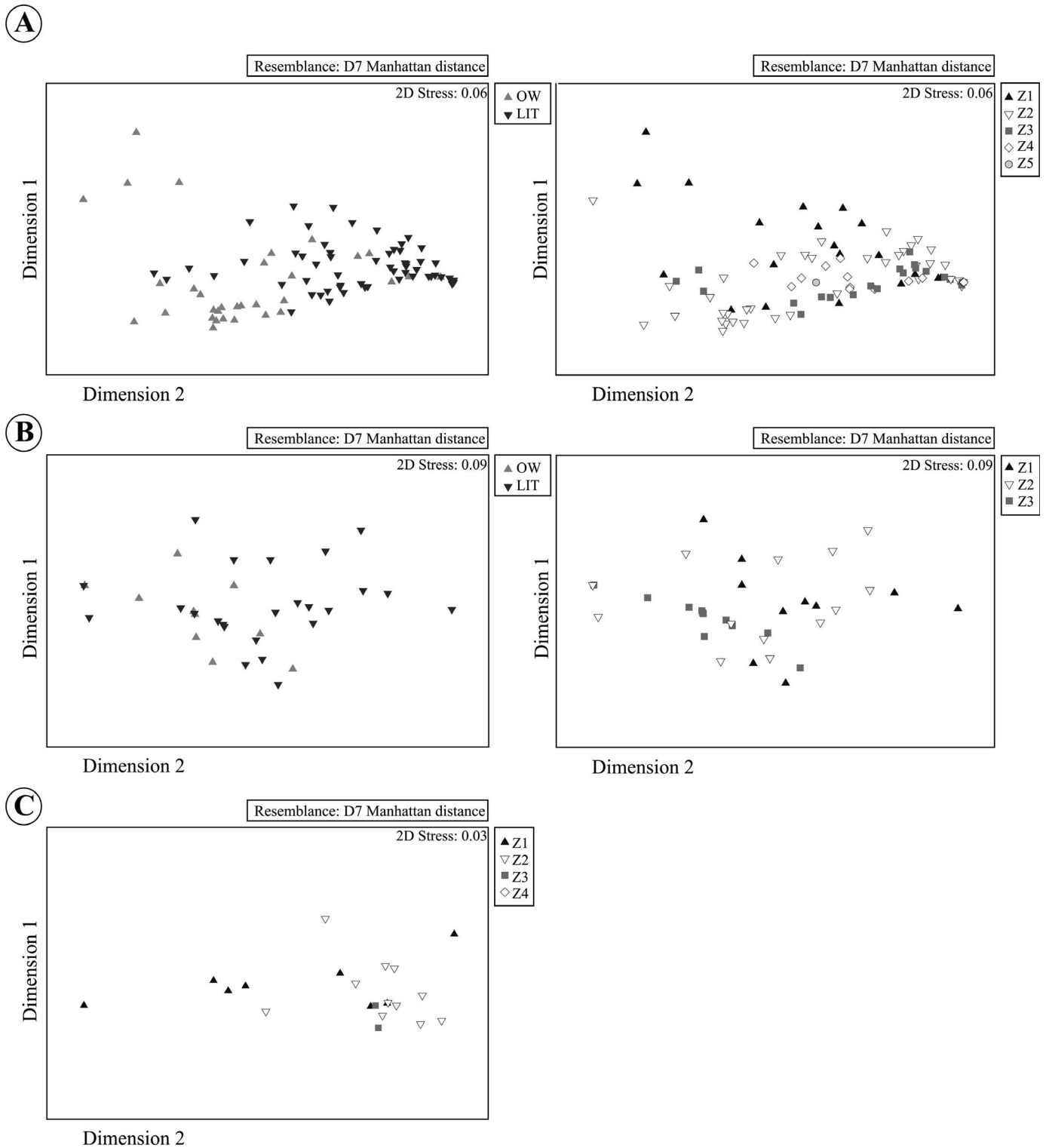
FIG. 8.—Two-dimensional Non metric MDS plot of taphonomic variables. **A)** Nahuel Rucá (NR). **B)** Las Mostazas (LM). **C)** Los Carpinchos (LC). Abbreviations: LIT = littoral; OW = open water; Z1–Z5 = depths 1–5, respectively.

composition of sediments (first 10 cm below the sediment-water interface, depth Z1 in this work), interstitial water (IW) and column water (CW). They also analyzed the redox environments and compared the saturation state of carbonates between IW and CW. They found that sediments are

highly reducer indicating that organic matter decomposition mainly occur by methanogenesis and sulfate reduction, acidifying the milieu and producing subsaturation of calcium carbonate. This idea is supported by aragonite and calcite indices in equilibrium or slightly subsaturated which

lead to think that carbonate remains within sediments would be probably subject to dissolution. The detection of sulfide in the pore water of the studied environments indicates a redox state belonging to the sulfidic zone in the Berner (1981) zonification. Besides, it is also possible that the methanogenic state was reached in some cases where bubbling gasses were observed (personal observation). The iron recorded in the sediments makes possible the formation of iron sulfides (solid phase), avoiding accumulation of H_2S that lower pH, but the concentration would have not been high enough since saturation indices reported are near to equilibrium or slightly subsaturated in sediments. It is well known that redox mechanisms are able to affect the saturation state of carbonates due to changes in pH (Candfield and Raiswell 1991; Cherns et al. 2011). Consequently, the preservation potential of shell remains could be negatively affected. Indeed, previous taphonomic studies performed in these lakes indicated the existence of destructive processes, such as dissolution, that diminish the abundance of individuals and the richness of species through depth (Cristini and De Francesco 2012; this work) compared to those remains placed at the sediment-water interface (Tietze and De Francesco 2012, 2014). Certainly, mollusk shells are not expected to dissolve if they are in contact with column water which is strongly oversaturated with respect to calcium carbonate (Cristini et al. 2017). In the present work, less alkaline conditions in Z1 would explain the lower abundance of mollusks in NR and the sterile level found in LC. In LM, pH was rather alkaline and constant through depth suggesting that lower alkalinity conditions in the upper centimeters were not an important factor in this case. Differences found among lakes could be consequence of lower mollusk abundance in life assemblages, since LM exhibits physico-chemical conditions unfavorable for mollusks, such as higher conductivity, in contrast to NR and LC (Cristini et al. 2017). It is important to emphasize that the more acid environments in LC, compared to NR and LM, strongly affect the abundance and species richness of the lake.

Despite the less favorable conditions for shell preservation in the upper centimeters, taphonomic variables did not exhibit significant differences with depth. Fine-scale surface alteration was very variable at each depth and did not show a clear pattern throughout the sedimentary succession. In NR, the state of preservation varied between low to high degree of fine-scale surface alteration, while in LM and LC, fine-scale surface alteration varied between intermediate to good preservation (see Fig. 7A–7C). Recovered mollusks had a high degree of fragmentation and loss of periostracum at all depths, even superficial sediments. The lack of significant differences together with the lack of a clear pattern for taphonomic variables could be a consequence of dissolution, which destroys most shells coming from the sediment-water interface and it is only possible to record those shells that have by-passed those conditions. This suggests a strong influence of the TAZ even below the first 10 centimeters of the sediment-water interface.

The high degree of fragmentation may be a consequence of bioturbation. In fact, the presence of roots in the three lakes could alter the degree of mollusk fragmentation. Roots produce corrosive pore waters due to the decomposition of organic matter, favoring weakening of mollusks by dissolution. Hence, mollusks would be prone to fragmentation. Fragmentation could also be due to trampling by cows. At some times of the year, water level decreases because of drought and cows graze within the LIT sampling area. The periostracum has several functions necessary for the survival of mollusks, one of which is to work as a waterproof layer that protects the shell from acids in the environment (e.g., dissolution and bioeroding processes) (Walker and Goldstein 1999; Nakayama et al. 2013). However, because the periostracum is an uncalcified outer organic covering mainly composed of organic material (e.g., amino acids, quinone-tanned proteins, mucopolysacharides, and lipids) (Meenakshi et al. 1969; Revathy et al. 1989; Nakayama et al. 2013) it is most likely to decay and rarely preserve in the fossil record (Hare 1962; Nielsen et al. 2008; Erthal et al. 2015) except in exceptional circumstances (e.g., Klommaker and Fraaije 2012).

According to the results obtained here, the first 10 cm below the sediment-water interface (Z1) of LIT had less favorable conditions for shell preservation. This coincides with the highest concentrations of organic matter and less alkaline pH values (Fig. 2). It is also in agreement with recently results obtained in the same lakes (Cristini et al. 2017). According to the scarce information available on the TAZ worldwide, this value appears to be lower than those recorded for the TAZ in marine settings (e.g., 50 cm, Walker 2001). The presence of deep burrowers in marine environments may be responsible for the deeper extent of the TAZ recorded there. For instance, Walker (2001) estimated a TAZ of nearly 50 cm in sandy marsh environments and 20 cm in silty/clay rich sediments. In contrast, in freshwater environments where there is a lack of deep burrowers, the TAZ is expected to be shallower.

De Francesco et al. (2013) studied variations in taxonomic composition, abundance, and preservation of freshwater mollusks during the mid- to late Holocene in three freshwater shallow lakes from the same study area. They inferred that shell preservation was favored when water bodies developed brackish conditions and preservation was poorer in times of freshwater input. The first 30 cm of sediment obtained from the cores in the present study correspond to the upper zone described by De Francesco et al (2013), which records a highly vegetated freshwater body with conditions very similar to modern ones, circa 700 cal. year B.P. The poor preservation observed in this zone together with the lowest shell abundance, in particular for the top 15 cm is coincident with the higher taphonomic destruction that occurring in the present. This suggests that the taphonomic processes acting in the first 30 cm below the sediment-water interface have been occurring since at least 700 year BP. Although no studies on time averaging in the TAZ have been conducted, indirect evidence suggests a relatively long interval for shell destruction before reaching the DFB. On the other hand, the first 30 cm would not be a good analogue of deeper parts of the succession (Z3, in De Francesco et al. 2013) since modern conditions are very different from those in the past and probably the dynamics and extent of the TAZ were also different.

SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive: http://www.sepm.org/pages.aspx?pageid=332.

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