

DOMINANCE OF REWORKED FOSSIL SHELLS IN MODERN ESTUARINE ENVIRONMENTS: IMPLICATIONS FOR PALEOENVIRONMENTAL RECONSTRUCTIONS BASED ON BIOLOGICAL REMAINS

CLAUDIO G. DE FRANCESCO* and GABRIELA S. HASSAN

Centro de Geología de Costas y del Cuaternario and Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET),

Universidad Nacional de Mar del Plata, CC 722, 7600, Mar del Plata, Argentina

e-mail: cgdefra@mdp.edu.ar

ABSTRACT

Death assemblages from contemporary marginal marine settings carved into ancient shell deposits are composed of fossil shells exhumed by currents or tides and shells derived from living populations. A better understanding of the bias produced by such a mixing process is of interest for studies that use modern death assemblages as analogues of similar past habitats. In order to evaluate the magnitude of reworking and redeposition of fossil shells in modern environments, a taxonomic (composition, abundance, and richness) and taphonomic (taphofacies) study was carried out in the Mar Chiquita coastal lagoon, Argentina (37°40'S, 57°20'W). The nature and extent of reworking was explored along a gradient in tidal energy from the outer to the inner reaches of the coastal lagoon. Results indicate that modern death assemblages in the lagoon are composed mostly of fossil (late Holocene) reworked shells and that reworking varies along a gradient in tidal energy, being higher in the outer reaches of the coastal lagoon, where tidal action is more significant. Temporal mixing in the coastal lagoon appears to be associated with condensation (remanié) rather than with a subtle mixing of shells, as occurs in time-averaged deposits. This reworking process leads to an abundance of old shells in modern death assemblages, which has negative consequences for their utilization as modern analogues of past lagoons. Multidisciplinary studies involving various biological indicators need to take this type of bias into consideration in order to avoid erroneous inferences on the Quaternary evolution of coastal lagoons.

INTRODUCTION

Modern depositional environments are a fertile source of taphonomic data, often fundamentally advancing our understanding of fossilization processes and the perception of the nature of biological information preserved in the sedimentary record (Kowalewski and LaBarbera, 2004). In the last 30 years, extensive research conducted in contemporary marginal marine settings demonstrated a good correlation between taphonomic condition of shelly remains accumulating in local death assemblages and the type of depositional environment. Examples include continental slope or shelf facies (e.g., Staff and Powell, 1990; Callender and Powell, 1992; Callender et al., 1992, 2002; Powell et al., 1998; Walker et al., 1998), mixed siliciclastic-carbonate shelf facies (e.g., Best and Kidwell, 2000; Kidwell et al., 2001; Parsons-Hubbard, 2005), and tidal-flat and tidal-inlet facies (e.g., Fürsich and Flessa, 1987; Meldahl and Flessa, 1990; Kowalewski et al., 1994; Meldahl, 1994; Meldahl et al., 1997). These actualistic studies provided a first step in the development of a conceptual framework for taphofacies models by revealing the variability that exists—both among environments and within single homogenous habitats—as well as the possible processes that produced them.

Death assemblages usually undergo some amount of temporal mixing on the scale of hundreds to thousands of years (Flessa et al., 1993; Martin et al., 1995, 1996; Meldahl et al., 1997; Kowalewski et al., 1998; Carroll et al., 2003). Specimens found together in death assemblages may represent mixed remains of organisms that lived at different times and never interacted with one another (Kowalewski and Bambach, 2003). The extent of temporal mixing varies as a function of rates of shell destruction and rates of shell burial. In fact, biological remains are subjected to repeated burial and exhumation cycles owing to physical reworking by currents and tides and can also be mixed within the sedimentary column by bioturbation (Kidwell, 1998). The more durable the hard parts, the greater the probability that hard parts from successive generations or communities at a site will survive short-term reworking events and become mixed into a single, time-averaged fossil assemblage (Kidwell, 1998). An exceptionally high level of mixing would be expected in the case of contemporary settings where ancient shell beds crop out in the shoreface or inner shelf of the region (Kowalewski and Bambach, 2003). In such cases, which are common in marginal marine environments developed after the last marine transgression, older shells are subject to reworking and redeposition in the littoral zone together with shells derived from living populations. The magnitude and incidence of the bias produced by this process, which would be of interest for studies that use modern death assemblages as analogues for paleoenvironmental reconstructions, remain unknown. To what degree is the original taxonomic composition of the living community distorted by this mixing process? How accurately do redeposited littoral shells reflect the local taphonomic damage that occurs in modern environments?

The Argentinean Mar Chiquita coastal lagoon (37°40'S, 57°20'W) provides an opportunity to explore these questions. The coastal lagoon originated during the regressive phase that followed a transgressive maximum at ca. 6.0–6.5 ka, which marked a sea level 2–2.5 m above the present level (Fasano et al., 1982). Well-defined horizons of late Holocene marine and estuarine shells are found in sediments surrounding the coastal lagoon and constitute the substratum of the upper marsh (marginal flat; Schnack et al., 1982). These sediments and the fossil shells contained in them are subject to erosional reworking along the edges of the coastal lagoon, leading to their redeposition in the littoral zone together with modern shells. Because physical and chemical factors (current speed, wave action, salinity, and nutrient availability) vary along a gradient in tidal energy (Schwindt et al., 2004), differential preservation of dead remains is expected, as a result of post mortem transportation, mixing, and differential destruction along the coastal lagoon.

The aims of the present study are to evaluate the magnitude of reworking and redeposition of fossil shells that occurs at present in the littoral zone of the Mar Chiquita coastal lagoon and to explore whether the nature and extent of the taphonomic processes that promote shell reworking vary along a gradient in tidal energy. Two main aspects of

* Corresponding author.

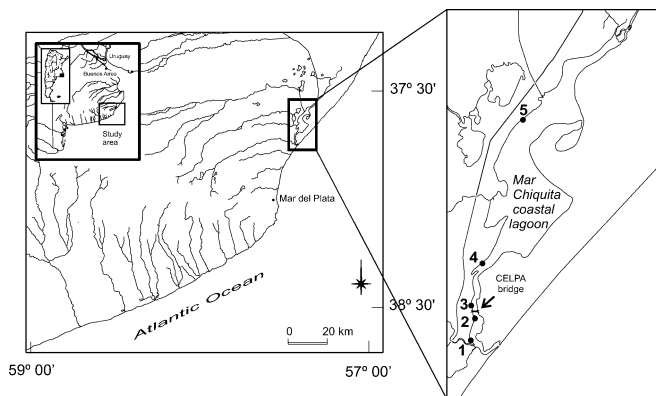


FIGURE 1—Schematic map of the study area. Regional map (Mar Chiquita coastal lagoon); inset, location of study sites.

shell assemblages are analyzed: (1) the taxonomic composition and (2) the state of preservation.

STUDY AREA

The Mar Chiquita coastal lagoon (Fig. 1) is a body of brackish water of ~ 46 km² located on a microtidal coast (0.6–1 m tidal range) and characterized by significant salinity changes (Fasano et al., 1982; De Francesco and Isla, 2003; Hassan et al., 2006). From a hydrological viewpoint, the coastal lagoon can be divided into an innermost shallow zone of 0.1–0.5 m in depth and a tidal inlet (a channel that connects the lagoon with the open sea) ≤ 2 m in depth (Reta et al., 2001; see Fig. 1). Nutrients and suspended sediment concentrations are higher in the innermost shallow zone than in the tidal inlet, whereas salinity, current speed, and depth show the opposite pattern (Table 1; Schwindt et al., 2004). The geomorphology of the coastal lagoon has changed since the building of a bridge in 1967 close to the upper reaches of the tidal inlet (Fig. 1). The bridge reduced the cross-sectional flow area to one-third of the original natural channel, not only restricting natural drainage of the coastal lagoon but also causing changes in turbidity, salinity, and temperature (Isla, 1997).

In the tidal inlet, the living mollusk fauna is dominated by dense populations of the infaunal, stout razor clam *Tagelus plebeius* (10–200 individuals per m²; Iribarne et al., 1998) and the rissooidean snail *Heleobia australis* (1120 individuals per m²; De Francesco and Isla, 2003; see

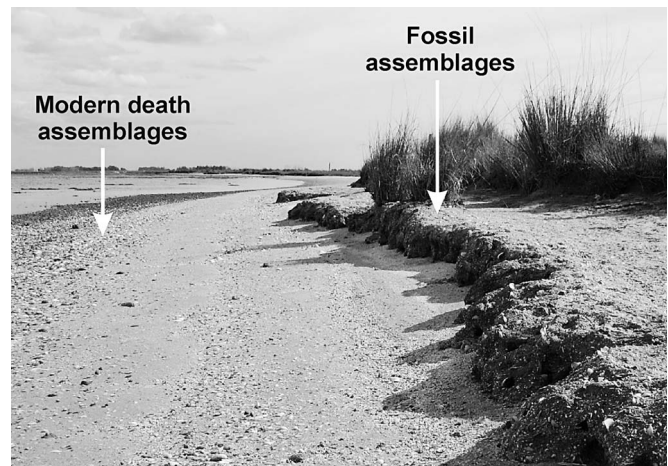


FIGURE 2—Fossil and modern death assemblages at a single site in the Mar Chiquita coastal lagoon.

Table 1). The epifaunal bivalve *Brachidontes rodriguezii* is also present, although in minor densities (Olivier et al., 1972). In the innermost shallow zone, the only molluscan species is the rissooidean *Heleobia conexa*, which inhabits reefs of the invasive serpulid polychaete *Ficopomatus enigmaticus* at average densities between 0.95 and 3.30 individuals per cm³ (De Francesco and Isla, 2003). No other mollusk species has been recorded in previous surveys (Olivier et al., 1972; De Francesco and Isla, 2003).

Beds of late Holocene marine and estuarine shells deposited during the last marine regression form the substratum of the upper marsh (marginal flat) of the coastal lagoon (Fig. 2; Schnack et al., 1982). These deposits have been dated from 1340 ± 50 to 3850 ± 60 yr using ¹⁴C (Fasano et al., 1982; Schnack et al., 1982) and are dominated by the bivalves *Maetra isabelleana* and *Tagelus plebeius*, as well as by rissooidean gastropods of the genus *Heleobia*. Most *T. plebeius* and *M. isabelleana* shells are found articulated and in life position and have been interpreted as autochthonous assemblages (Fasano et al., 1982).

MATERIAL AND METHODS

The study was performed in five sites representing a gradient in tidal energy from the outer to the inner reaches of the coastal lagoon (Fig. 1, Table

TABLE 1—Summary of physical and chemical characteristics and live mollusk fauna composition of the sites at Mar Chiquita coastal lagoon. Data represent mean values (minimum and maximum values are given in parentheses). + = presence; – = absence.

| Site | 1 | 2 | 3 | 4 | 5 |
|--|-------------------|-------------------|-------------------|-------------------|-------------------|
| Physical and chemical variables¹ | | | | | |
| Distance from mouth of lagoon (km) | 2.3 | 3.3 | 3.4 | 5.2 | 17.4 |
| Depth (m) | 1.7 | 1.5 | 1.5 | 1.0 | 0.7 |
| Tidal range (m) | 0.96 | 0.77 | 0.77 | 0.30 | 0.05 |
| Current speed (m/s) | 1.87 (1.77–2.00) | 1.32 (1.18–1.73) | N/A | 1.21 (0.85–1.55) | 1.06 (0.73–1.20) |
| Salinity (‰) | 24.32 (10.3–31.8) | 21.27 (8.1–35.5) | 20.43 (7.6–34.8) | 20.23 (7.3–34.3) | 2.92 (0.7–12.4) |
| Temperature (°C) | 19.02 (11.7–28.3) | 19.61 (13.3–29.7) | 19.65 (13.5–29.1) | 19.72 (14.6–29.3) | 20.66 (14.3–30.1) |
| pH | 8.07 (7.58–8.51) | 8.19 (7.51–8.51) | 8.27 (8.17–8.43) | 8.18 (7.01–8.8) | 8.65 (7.98–9.03) |
| Suspended sediment concentration (g/l) | 0.63 (0.54–0.68) | 0.72 (0.58–0.88) | N/A | 1.35 (1.01–1.63) | 1.49 (1.22–1.67) |
| Chlorophyll (mg/m ³) | 0.48 (0.39–0.57) | 0.71 (0.40–1.05) | N/A | 0.75 (0.52–1.22) | 1.55 (1.37–1.98) |
| Detritus (g/l) | 0.33 (0.12–0.58) | 0.51 (0.14–0.89) | N/A | 1.78 (1.49–2.04) | 2.46 (1.66–3.09) |
| Live mollusk species² | | | | | |
| <i>Brachidontes rodriguezii</i> | + | – | – | – | – |
| <i>Tagelus plebeius</i> | + | + | + | – | – |
| <i>Heleobia australis</i> | + | + | + | + | – |
| <i>Heleobia conexa</i> | – | – | – | + | + |

Data from: ¹Reta et al. (2001), Schwindt et al. (2004), and Hassan et al. (2006); ²Olivier et al. (1972), Iribarne et al. (1998), and De Francesco and Isla (2003).

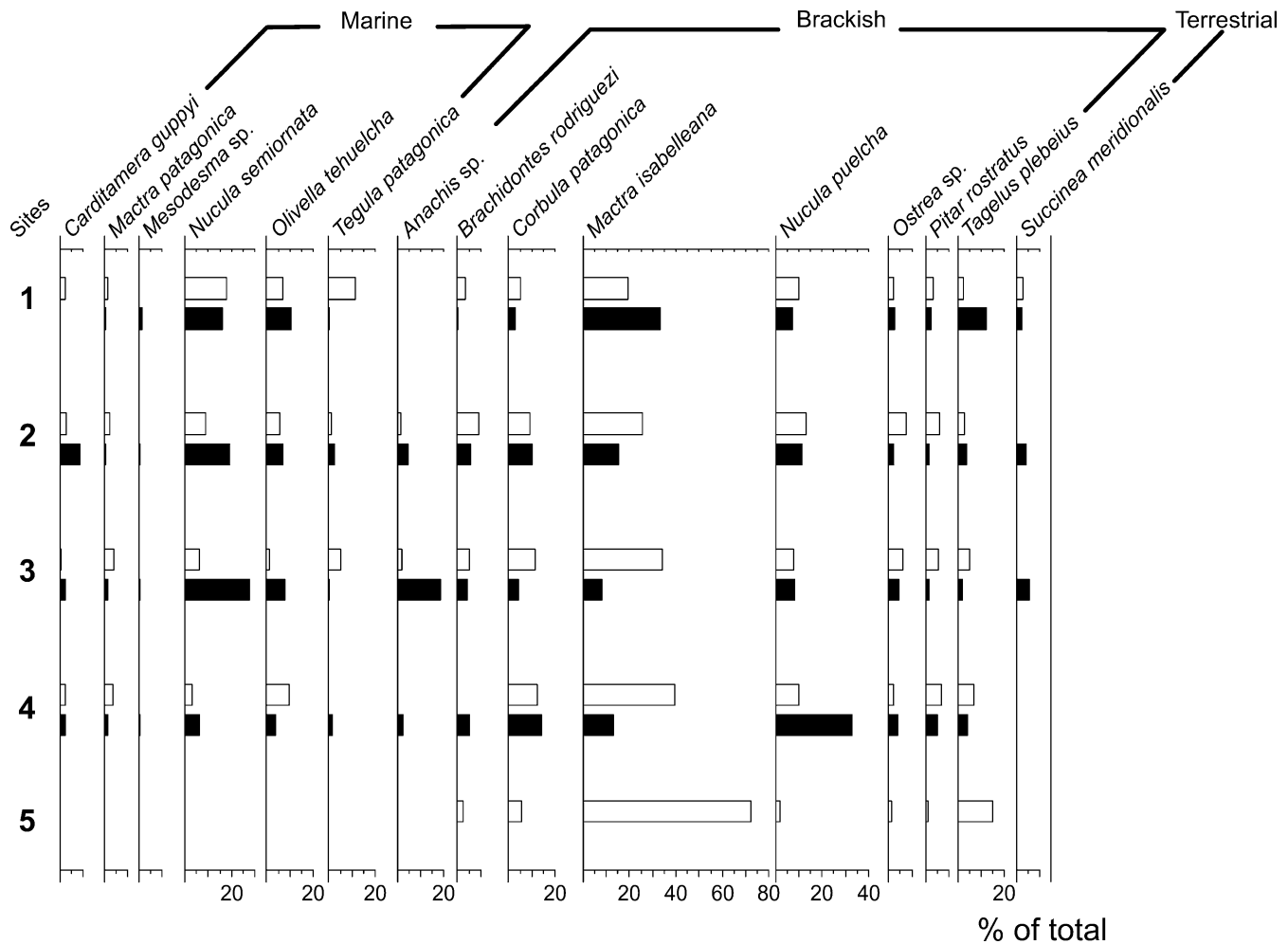


FIGURE 3—Relative abundance of dominant species in modern death assemblages (empty bars) and fossil assemblages (filled bars). Only those species representing >2% of total abundance were included. Data on salinity preferences of species from Castellanos (1967), Giberto et al. (2004), and Soares-Gomes and Pires-Vanin (2005). For locations of sites, see Figure 1.

1). Sites 1, 2, and 3 were located in the inlet (main channel), site 5 in the innermost shallow zone, and site 4 in the zone where the constricted tidal channel opens into the lagoon proper. Sites 2 and 3 were located immediately landward and seaward of the bridge in order to account for differences in taphonomic signature caused by its influence.

Both modern (littoral) and fossil (upper marsh) mollusk assemblages were sampled (Fig. 2). For modern death assemblages, three randomly located replicate quadrats (25 × 25 cm) were delimited in the littoral zone and the uppermost 2 cm of the sediment collected. For fossil assemblages, three replicate bulk samples of ~1 kg of sediment were collected directly from Holocene deposits outcropping in the marginal flat (Fig. 2). Site 5 lacked Holocene outcrops. Taxonomic and taphofacies analyses were conducted in both fossil and modern mollusk assemblages. Both analytical approaches provide different and complementary types of information about sedimentary environments and often covary along large-scale environmental gradients (Kowalewski et al., 1994; Meldahl, 1994).

Taxonomic Analysis

Samples were sieved through a 1 mm mesh screen in order to retain mollusk shells, and complete shells were separated from fragments. Any fragment of a shell that included the umbo (bivalves) or the apex (gastropods) was considered a complete specimen. All specimens contained in the complete subfraction were counted and identified to species. Bivalve abundance was estimated by dividing the number of shells by two.

Multidimensional scaling (MDS) was used to analyze sample distributions based on relative frequency data. Multidimensional scaling is an exploratory statistical technique that allows the mapping of similarities between points in a high dimensional space into a lower dimensional space. Unlike such traditional approaches as cluster analysis or discriminant function analysis, MDS does not rigidly define species associations, and, consequently, the approach is biologically more realistic (Meldahl and Flessa, 1990; Springer and Flessa, 1996). The stress is defined as a numerical measure of the closeness between similarities in the lower dimensional space and the original space. Stress has a value between 0 and 1, with 0 indicating perfect fit and 1 indicating worst possible fit. The MDS plot was constructed based on similarities of correlation matrices using the computer program STATISTICA (StatSoft, 1998). Analysis of similarity was used to test for significant taxonomic composition differences between modern and fossil assemblages with the program PAST 1.34 (Hammer et al., 2001).

Species richness was calculated for each site using Margalef's index of species richness: $D = (S - 1) / \ln N$, where D = species richness value, S = number of species, and N = number of shells collected. This index minimizes the effect of sample size bias (Dodd and Stanton, 1990), allowing for comparison between modern and fossil samples. A Kruskal-Wallis test was used to evaluate differences in richness indices among sites. A posteriori multiple comparisons were performed with nonparametric Tukey-type tests (Zar, 1984).

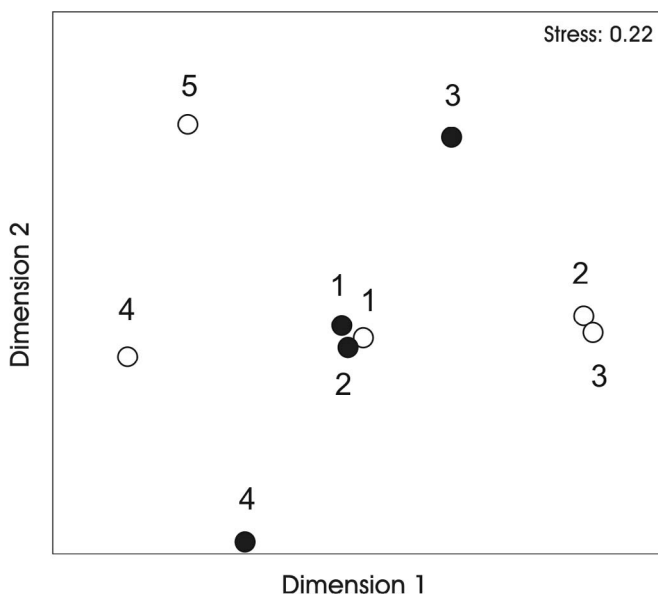


FIGURE 4—Multidimensional scaling ordination plot of samples from modern death assemblages (empty circles) and fossil assemblages (filled circles) in Mar Chiquita coastal lagoon. For locations of sites, see Figure 1.

Taphofacies Analysis

The methods used to describe taphonomic characteristics of mollusk shells vary greatly among researchers. Generally, taphonomic analysis can be done either by including all the specimens found in samples or by restricting analysis to selected target species. The former method may not always be appropriate as taphonomic characteristics often vary among species (because of differences in size, geometry, architecture, and composition of shells), and therefore, pooling different taxa may generate noise in the data (Kowalewski et al., 1994). In the present work, the two dominant bivalve species present in all sites (*Macra isabelleana* and *Tagelus plebeius*) were targeted for taphonomic analysis. Both are infaunal bivalves of similar size. Thirty specimens of each species were selected randomly from each site, and ten replicate samples per site were taken. The taphonomic condition of the specimens was described using semiquantitative taphonomic ranks. Three taphonomic grades (0, 1, 2) were erected for each attribute, and all specimens were classified as good (0 = best preservation), fair (1 = intermediate), and poor (2 = poorest; Kowalewski et al., 1995). Taphonomic attributes included (1) fragmentation, (2) edge preservation, (3) external luster, (4) internal luster, (5) external encrustation, (6) internal encrustation, and (7) bioerosion. The characterization of each taphonomic grade was erected following Kowalewski et al. (1994). Each taphonomic variable was analyzed individually at the sample level with the use of ternary taphograms (Kowalewski et al., 1995). 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.

Additional taphonomically informative variables included articulation and proportion of left to right valves. The variations in the percentage of articulated shells among sites were evaluated using Kruskal-Wallis tests (Zar, 1984). Tukey-type nonparametric, multiple-comparison tests were used to determine significant differences between sites at $p = 0.05$. Chi-square tests were performed to evaluate the fit of proportions of left to right valves to random distributions (Zar, 1984).

RESULTS

Taxonomic Analysis

A total of 281,324 shells belonging to 50 species were recovered from the sites sampled (169,659 from modern death assemblages and 111,665

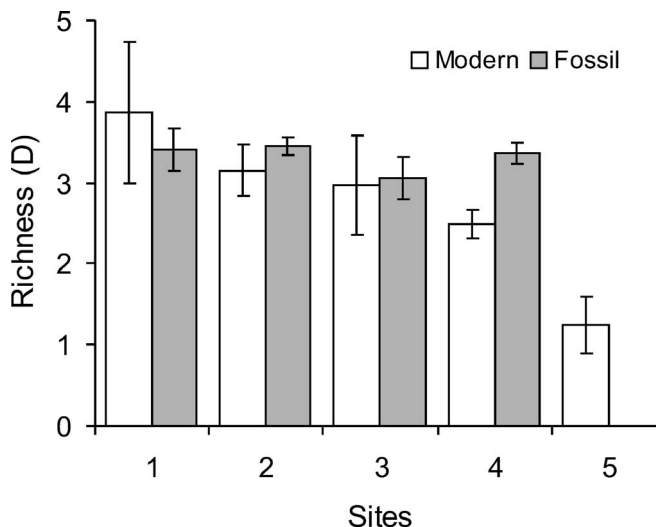


FIGURE 5—Variation in species richness (D) along the Mar Chiquita coastal lagoon, including standard error bars. For locations of sites, see Figure 1.

from fossil assemblages). Both modern and fossil mollusk assemblages were dominated by minute gastropods (usually 2–4 mm total shell length) of the genus *Heleobia*, which constituted 98% of the total shells. Meta-analysis of preservation potential and rank-order tests from a wide array of settings provided robust evidence that small-bodied individuals—presumably both those that are ontogenetically young and those that have reached adulthood at small size because of opportunistic strategies—are more prone to being underrepresented or overrepresented in local death assemblages (Kidwell, 2002a). Since its dominance may mask the results, *Heleobia* shells were discarded from later analyses. A total of 15 species reached relative abundances >2% in at least one sample (Fig. 3).

The most common species represented in modern death assemblages were the bivalves *Macra isabelleana* (19%–72%), *Nucula semiornata* (3%–17%), *N. puelcha* (7%–13%), *Corbula patagonica* (5%–12%), and the stout razor clam *Tagelus plebeius* (2%–14%; see Fig. 3). Except for *T. plebeius*, which is a strictly brackish species, the other bivalves represented here are marine-brackish species that inhabit salinities between 13‰–34‰ in the Río de La Plata Estuary (Giberto et al., 2004). Although the same species dominated all sampling sites, their relative abundances varied along the tidal gradient. Sites 1 and 2 were dominated by *M. isabelleana* (19%–25%), accompanied by *N. semiornata* (9%–17%), *N. puelcha* (9%–13%), and scarce specimens of *T. plebeius* (2%–3%). The terrestrial snail *Succinea meridionalis* (2.5%) was recorded only in site 1 (Fig. 3). Many other marine taxa were also recorded in these sites (*Entodesma patagonicum*, *Turbonilla* sp., *Buccinanops cochlidium*, *Fisurella* sp., *Mesodesma* sp., and *Strigilla carnaria*), although in relative abundances <2%. In contrast, sites 3, 4, and 5 showed higher percentages of *M. isabelleana* (34%–72%) and *T. plebeius* (5%–14%) and lower percentages of *N. semiornata* (3%–6%) and *N. puelcha* (7%–10%). In this innermost shallow zone, the marine taxa *Plicatula gibbosa*, *Buccinanops* sp., and *Crepidula aculeata* were also recorded, although in relative abundances <2%.

Fossil assemblages were dominated by the same species as in modern assemblages (Fig. 3): *M. isabelleana* (8%–33%), *N. puelcha* (7%–32%), *N. semiornata* (6%–27%), *C. patagonica* (2%–14%), and *T. plebeius* (2%–12%). Contrary to modern assemblages, the relative abundance of *M. isabelleana* and *T. plebeius* decreased toward the innermost shallow zone (from 33% to 8%–12% and from 12% to 2%–4%, respectively), whereas *N. puelcha* increased in the same direction (from 7% to 32%; see Fig. 3). The MDS results (Fig. 4) indicated that the taxonomic composition of fossil assemblages was not significantly different than that of the modern ones (analysis of similarity, $R = 0.1375$; $p > 0.05$).

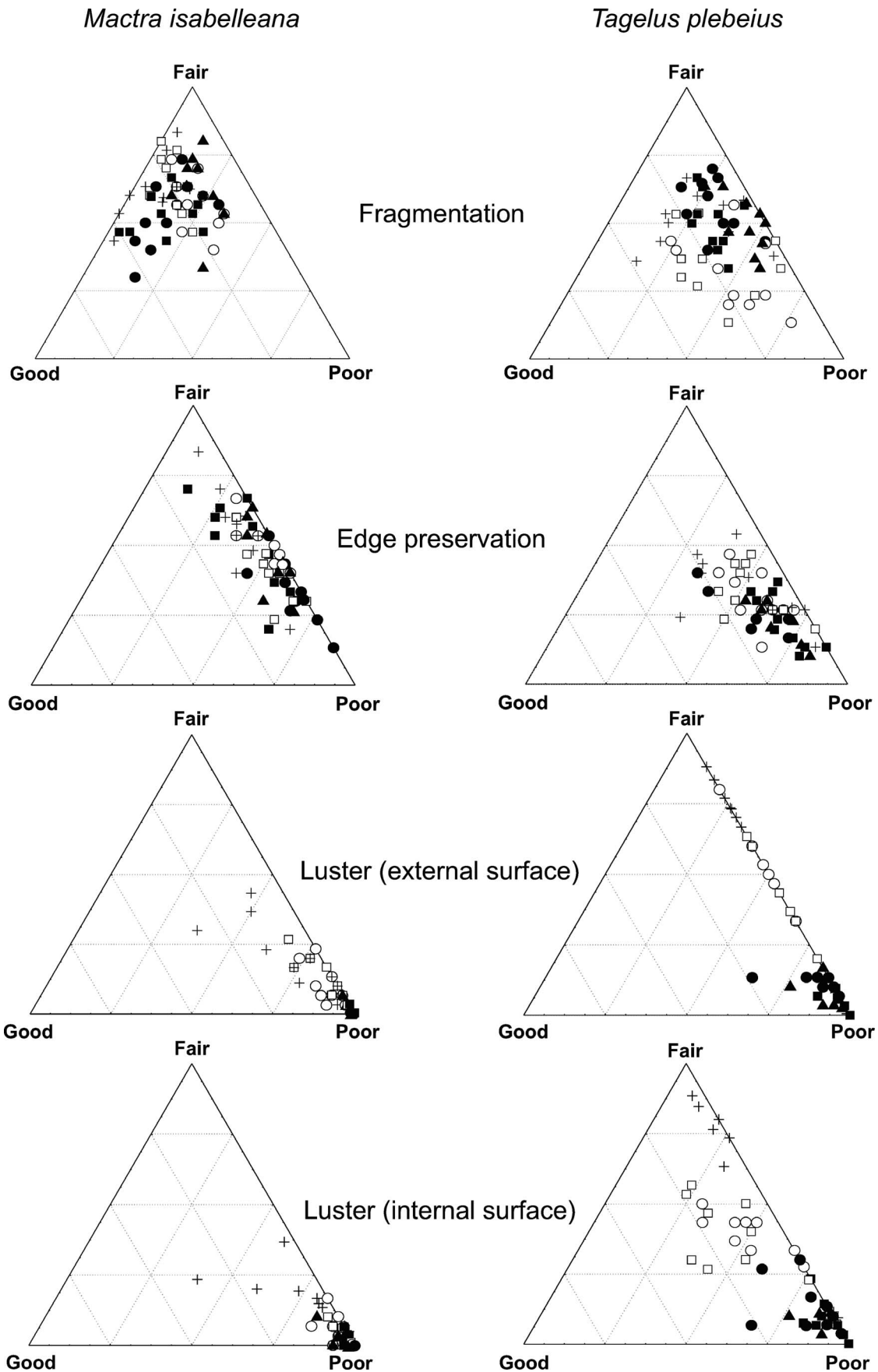


FIGURE 6—Ternary taphograms showing variation among sampling sites for taphonomic attributes of *Mactra isabelleana* and *Tagelus plebeius* shells. Symbols for modern death assemblages: ● site 1; ■ site 2; ▲ site 3; □ site 4; ○ site 5; Fossil assemblages are represented by + (only average values for each site shown).

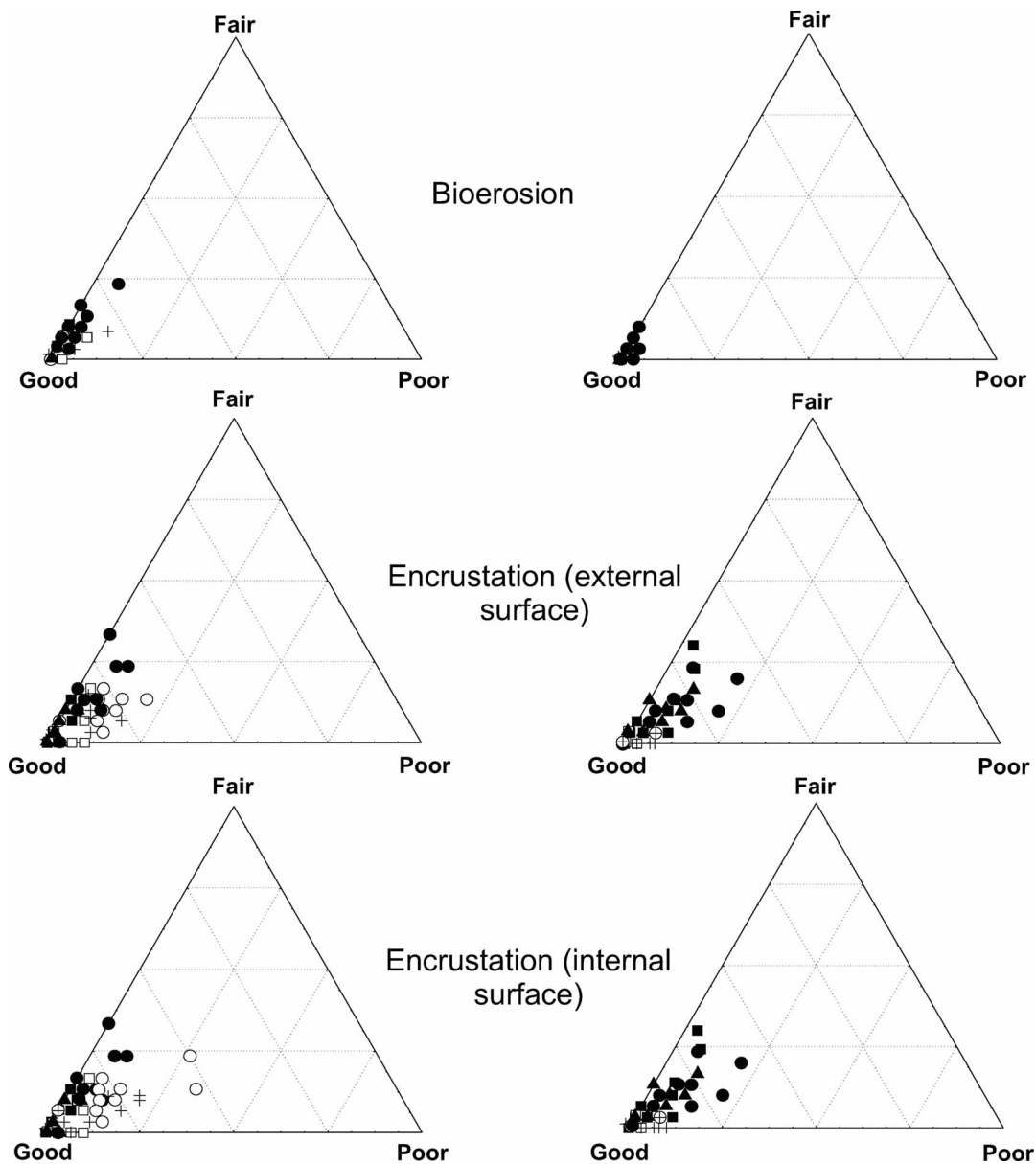


FIGURE 6—Continued.

Species richness in modern death assemblages decreased significantly toward the inner reaches of the coastal lagoon (Kruskal-Wallis Corrected Chi-Square = 10.6; $p < 0.05$; Fig. 5). The sites located in the tidal inlet (sites 1–3) displayed higher values than those located toward the inner reaches. Species richness, however, did not reveal differences among fossil assemblages along the spatial gradient (Kruskal-Wallis Corrected Chi-Square = 3.8; $p = 0.28$). These values were similar to those obtained in sites located at the outer reaches of the coastal lagoon (closer to the mouth) in modern death assemblages (Fig. 5).

Taphofacies Analysis

The taphonomic condition of shells improved toward the inner reaches of the coastal lagoon (Fig. 6). This pattern was stronger in *T. plebeius* than in *M. isabelleana* shells. In both species, the taphonomic condition of fossil shells most closely resembled modern shells from the innermost sites (sites 3–5).

Ternary diagrams offered insight into variation in taphonomic vari-

ables. Fragmentation showed considerable variation among samples (Fig. 6). Shells of *T. plebeius* were on average more fragmented (fair-poor) than those of *M. isabelleana* (good-fair). The most fragmented *T. plebeius* shells were represented in the innermost shallow zone (sites 4 and 5). Fossil shells varied from good-fair and fair condition (*M. isabelleana*) to good-fair and fair-poor condition (*T. plebeius*). In addition, edge preservation exhibited a fair-poor condition in most samples (Fig. 6). A poor taphonomic degree was observed in some shells from the tidal inlet.

The luster variables (external and internal surface) exhibited a similar pattern of variation along the coastal lagoon (Fig. 6). Shells of *M. isabelleana* were on average more abraded than those of *T. plebeius*. For *T. plebeius*, both external and internal surfaces were ranked poor in the tidal inlet and fair-poor toward the innermost area. For *M. isabelleana*, these attributes were poor in all samples, although the sites from the tidal inlet were on average poorer than those represented in the innermost area. For both species, fossil shells displayed a better preservation than those of modern ones (fair for *T. plebeius*; fair-poor for *M. isabelleana*).

Bioerosion did not provide important differences among sites and

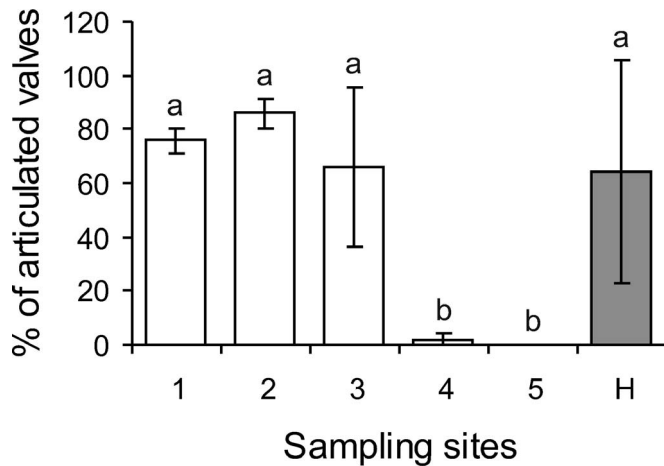


FIGURE 7—Variation in the percentage of *Tagelus plebeius* articulated shells along the Mar Chiquita coastal lagoon. Same letters mean no significant differences (Tukey test, $p < 0.05$). All fossil sites were grouped in H (Holocene). For locations of sites, see Figure 1.

species. All shells exhibited a very low degree of bioerosion and were classified as good (Fig. 6). Similarly, the encrustation variables (external and internal) exhibited a good condition in most sites without variation between species (Fig. 6). Shells from the tidal inlet, however, displayed on average more encrusted organisms than those represented in the innermost sites. Rank orders of the different encrusting taxa were quite similar among sites, with bryozoans most abundant in all, followed by barnacles (*Balanus* sp.). Fossil shells exhibited a very low degree of encrustation.

Only *T. plebeius* shells were found articulated. In modern death assemblages, the percentage of articulated valves increased gradually from the inlet (63%–86%) to the innermost area (0%–1.6%; $H = 25.34$, $p < 0.001$; see Fig. 7). Fossil assemblages showed, on average, 67% articulated valves, which is similar to modern shells in the sites located closer to the mouth. No divergences from random in the proportion of left to right valves were observed. All sites displayed values between 47% and 53% for *T. plebeius* shells ($\chi^2 = 0.52$, $p > 0.90$) and between 45% and 55% for *M. isabelleana* shells ($\chi^2 = 1.28$, $p > 0.90$).

DISCUSSION

Taxonomic Analysis

This analysis reveals a high similarity in taxonomic composition and relative abundance of taxa between modern and fossil assemblages. Except for *Heleobia* spp. and *Tagelus plebeius*, assemblages were composed of species not represented in the living fauna of the coastal lagoon. Consequently, modern assemblages are probably largely derived from late Holocene reworked shells and, thus, have a low ecological fidelity to the living fauna. These results bring new insights into the nature of temporal mixing in lagoonal environments that originated in the last transgressive-regressive cycle, with implications for depositional resolution. Despite their young age (ca. 4 ka), temporal mixing appears to be associated with condensation or reworking of older fossils into younger deposits (remanié) rather than to a subtle mixing of shells as occurs in time-averaged deposits (see Kidwell and Bosence, 1991; Kowalewski and Bambach, 2003). This reworking process leads to an abundance of old shells in modern death assemblages. Therefore, any ecological parameter inferred from such a collection will reflect values closer to the late Holocene rather than values from more recent times.

Fossil assemblages exhibited similar richness values along the gradient in tidal energy. In contrast, a decrease in species richness in the same direction was observed in modern death assemblages. Moreover, the sites

located in the tidal inlet exhibited values similar to those recorded in fossil assemblages. This pattern may be explained by a differential effect of taphonomic processes acting at the tidal inlet and the innermost shallow area of the coastal lagoon. The significant effect of tides in the inlet may lead to strong removal of fossil shells from this zone and, therefore, to a higher abundance of redeposited shells in the littoral zone of the lagoon. It has been pointed out that erosion is the dominant process mixing older assemblages into younger sediments (Martin, 1999, and references therein). Consequently, a higher shelliness in the tidal inlet increases the probability that different species will be represented in modern death assemblages. In other words, the higher temporal mixing recorded here is directly related to an overcompleteness in modern death assemblages. The palimpsest nature of dead-species richness has been mentioned in several works (e.g. Kowalewski, 1996; Kidwell, 2002b).

Taphofacies Analysis

Shells of *T. plebeius* were more sensitive to taphonomic alteration than those of *M. isabelleana*, exhibiting a clearer pattern of variation among samples. This difference may be explained by the fact that *T. plebeius* has a much weaker and lighter shell. In general, modern death assemblages exhibited poorer preservation than fossil assemblages, which may be a consequence of the additional mechanical reworking suffered by fossil shells prior to their redeposition in modern assemblages. Moreover, most fossil shells cropping out along the Mar Chiquita coastal lagoon exhibited excellent preservation, because some bivalves were articulated and in life position within the sedimentary column and were interpreted as autochthonous assemblages.

Luster varied significantly between the tidal inlet and the innermost shallow area of the coastal lagoon. Luster was poorest in the tidal inlet, supporting the hypothesis of major shell reworking there, which agrees with the conclusion obtained from taxonomic analysis. Many factors are responsible for surface alteration in mollusk shells. Physical processes such as currents and waves generated by storms and tides (see Kowalewski et al., 1994, and references therein) are common in intermittently high energy environments, such as those represented in the tidal inlet of Mar Chiquita. Here, the cyclic nature of the tidal action provides more opportunities for physical abrasion. Chemical dissolution is another important process that occurs in modern marginal marine settings, mostly related to higher rates of sulfate reduction and greater reoxidation of reduced sulfide (e.g., Best and Kidwell, 2000). Algal and fungal micro-boring and microbial maceration of organic matrix are important biological sources of fine-scale alteration in surfaces, producing chalky and pitted textures (e.g., Best and Kidwell, 2000). According to the differences in both physical and chemical factors between the tidal inlet and the innermost shallow zone, it appears that all of these are probable factors in the differential pattern of fine-scale alteration of shells found in the Mar Chiquita coastal lagoon. In general, an increase in the quality of preservation of death assemblages along a gradient is related to residence time on the sediment-water interface and frequency of reworking events (Parsons-Hubbard and Brett, 1991). In the present case, as energy decreased toward the inner lagoon, the probability that shells would be exhumed and reworked went down as well.

Bioerosion and encrustation did not experience significant variation among assemblages, and the overwhelming majority of shells were neither bioeroded nor encrusted. Previous results of experiments carried out on mollusk shells demonstrated the rapid colonization of deployed shells by epibionts (Parsons-Hubbard et al., 1999). In addition, Rodland et al. (2006), working on brachiopod shells, pointed out that encrustation occurred mainly during a brief interval between host death and burial rather than by recolonization of exhumed shells. Therefore, the low encrustation values registered here suggest that the rare colonization by epibionts that did occur was primarily during the late Holocene, prior to burial or shell destruction. This is also supported by the fact that the dominant encrusting organisms are marine bryozoans that do not live in the coastal lagoon

today. Modern death assemblages, however, exhibit higher alteration by encrusting organisms, indicating some degree of recolonization of shells by modern epibionts after late Holocene shells were redeposited in the modern littoral area.

Fragmentation did not show significant differences along the tidal-energy gradient. In general, the interpretation of fragments to reconstruct the depositional environment is still very rudimentary. Shell breakage is well known from high-energy habitats but is also extremely common in low-energy habitats where biogenic interactions are a major source of fragmentation (e.g., Meldahl and Flessa, 1990; Best and Kidwell, 2000; Zuschin and Stanton, 2001, and references therein). Important biogenic interactions include predation, bioturbation, and breakage of empty shells by crabs. In fact, the littoral surface of the Mar Chiquita coastal lagoon is dominated by dense populations of the crabs *Chasmagnathus granulatus* and *Cyrtograpsus angulatus* (Spivak et al., 1996). Their activity may promote shell damage in redeposited fossil shells. Human impact (trampling) is another variable that may promote shell breakage because most of the sampling sites are frequently used by fishermen as boat jetties. The higher fragmentation of *T. plebeius* shells may be a consequence of their thinner shells and, thus, lower strength compared to *M. isabelleana* shells. The strength of a shell is a function of a multitude of morphologic variables—such as size, thickness, shape, mass, microstructure, organic matrix, and sculpture—and taphonomic variables—such as taphonomic grade, presence of drill-holes, and progressive degradation of skeleton and organic matrix (Zuschin and Stanton, 2001; Zuschin et al., 2003). In summary, these processes obscure the paleoecological and taphonomic information that can be inferred from this taphonomic attribute.

It has been suggested that the high frequency of disarticulation in samples from quiet-water, soft sediments is biogenic rather than physical in origin (Best and Kidwell, 2000). Articulation, in contrast, constitutes a valuable indicator of the time of exposure since death or of the energy of the depositional environment (Parsons-Hubbard and Brett, 1991). In this study, only *T. plebeius* shells were found articulated, which may be explained by the fact that this species actually inhabits the coastal lagoon. Therefore, it is likely that a significant number of articulated shells may arise from modern populations and represent recently dead specimens. This hypothesis is also supported by the fact that the higher percentage of articulated valves has been recorded in the tidal inlet, which coincides with the modern distributional area of *T. plebeius* in Mar Chiquita (see Table 1). The only *T. plebeius* predator recorded in the coastal lagoon is the American oystercatcher *Haematopus palliatus*. To extract the clam from its burrow, the bird uses its long bill to grasp the clam. In the process, the soft parts of the clams are extracted without exhuming or splitting the valves (Iribarne et al., 1998). Thus, it is probable that most articulated *T. plebeius* shells found in the tidal inlet may correspond to modern predated shells. Although clams with their tough ligament can hold together much longer than other organisms, it is still less probable that they remain articulated after reworking by tidal currents.

Overall, shells deposited in the littoral zone of the Mar Chiquita tidal inlet showed poorer preservation than those deposited in the innermost shallow area. This difference results from the differential effect of tides along the lagoonal gradient. An important conclusion that can be drawn from the present taphonomic analysis is that taphofacies appear to be a far more informative and reliable indicator of original depositional environment than either taxonomic categorization or ecological characteristics of mollusk species, owing to the redeposition of fossil shells. Regardless of their previous taphonomic history, reworked fossil shells are still sensitive to taphonomic alteration by modern processes and can be used to infer depositional subenvironments along a tidal energy gradient with high confidence. These results indicate that comparative taphonomy provides valuable environmental information despite the age and previous taphonomic history of shells.

The process of shell reworking and redeposition observed in the Mar Chiquita coastal lagoon may not be limited to this site since most lagoons along the low-lying southwestern Atlantic coast have arisen in a similar

way—during the regressive phase of the Holocene transgressive-regressive cycle (Isla, 1995). Several coastal lagoons from Brazil and Uruguay have been used to reconstruct variation in sea level during the Quaternary (e.g., Carreño et al., 1999; García-Rodríguez et al., 2004a, 2004b, and references therein). These studies have been based on the paleoecological analysis of different microfossils, such as diatoms and pollen, recovered from core samples. It would be interesting to carry out detailed taphonomic analyses of the mollusk shells (if any) preserved in such habitats in order to assess whether the mixing process documented in Mar Chiquita is also applicable elsewhere in the region. If community-level characteristics of a fossil assemblage are to be interpreted, it is essential to understand the taphonomic pathways that have altered the original signal in a variety of related environments.

CONCLUSIONS

Modern death assemblages from Mar Chiquita coastal lagoon are composed mostly of late Holocene reworked shells. Reworking of older deposits by modern tidal currents leads to an abundance of fossil shells in modern death assemblages, which has important implications for their utilization as modern analogues of past lagoonal habitats. In fact, any ecological or environmental parameter inferred from such a mixed assemblage will reflect values closer to the late Holocene than values from more recent times, and, for this reason, strict uniformitarian interpretations should be regarded with great caution. These results have important consequences for Quaternary studies aimed at reconstructing coastal paleoenvironments associated with sea-level fluctuations. Such studies usually involve different proxy records (e.g., diatoms, foraminifera, ostracods, pollen, and mollusks) and use the relationship between death assemblages and environmental parameters in contemporary settings as analogues for past environments. Death assemblages integrate small-scale perturbations (temporal and spatial) in a more definable assemblage, becoming a more accurate indicator of general environmental conditions than the biocoenosis (living community; Scott and Medioli, 1980). It is thus very important that researchers involved in such multidisciplinary studies consider all possible sources of bias in interpreting the Quaternary evolution of coastal lagoons.

Finally, the present study provides the first evidence that reworking of older material occurs not only under transgressive conditions but also during highstand-early regression and the slight alternations of relative sea level that characterize it. This mixing process is probably more common than generally appreciated, and further taphonomic analyses should be focused on determining its regional extent. A comprehensive study might provide data that would allow recognition of a regional pattern of taphonomic alteration related to the evolution of coastal lagoons during the Holocene, which would help in the outline of retrospective paleoenvironmental inference.

ACKNOWLEDGMENTS

Financial support for this study was provided by Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET), Resolución 1273/04. We thank Mónica Hassan for her assistance with data preparation and Ron Martin and Susan Kidwell for constructive and supportive review of this manuscript. C.G.D.F. is a member of the Scientific Research Career of CONICET. G.S.H. was supported by a CONICET fellowship.

REFERENCES

- BEST, M.M.R., and KIDWELL, S.M., 2000, Bivalve taphonomy in tropical mixed siliclastic-carbonate settings: I. Environmental variation in shell condition: *Paleobiology*, v. 26, p. 80–102.
- CALLENDER, W.R., and POWELL, E.N., 1992, Taphonomic signature of petroleum seep assemblages on the Louisiana upper continental slope: Recognition of autochthonous shell beds in the fossil record: *PALAIOS*, v. 7, p. 388–408.
- CALLENDER, W.R., POWELL, E.N., STAFF, G.M., and DAVIES, D.J., 1992, Distinguishing autochthony, parautochthony and allochthony using taphofacies analysis: Can cold

- seep assemblages be discriminated from assemblages of the nearshore and continental shelf?: *PALAIOS*, v. 7, p. 409–421.
- CALLENDER, W.R., STAFF, G.M., PARSONS-HUBBARD, K.M., POWELL, E.N., ROWE, G.T., WALKER, S.E., BRETT, C.E., RAYMOND, A., CARLSON, D.D., WHITE, S., and HEISE, E.A., 2002, Taphonomic trends along a foreereef slope: Lee Stocking Island, Bahamas: I. Location and water depth: *PALAIOS*, v. 17, p. 50–65.
- CARREÑO, A.L., COIMBRA, J.C., and CARMO, D.A., 1999, Late Cenozoic sea level changes evidenced by ostracodes in the Pelotas Basin, southernmost Brazil: *Marine Micropaleontology*, v. 37, p. 117–129.
- CARROLL, M., KOWALEWSKI, M., SIMÕES, M.G., and GOODFRIEND, G.A., 2003, Quantitative estimates of time-averaging in terebratulid brachiopod shell accumulations from a modern tropical shelf: *Paleobiology*, v. 29, p. 381–402.
- CASTELLANOS, Z.J.A. DE, 1967, Catálogo de los moluscos marinos bonaerenses: Anales de la Comisión de Investigación Científica, La Plata, v. 8, 365 p.
- DE FRANCESCO, C.G., and ISLA, F.I., 2003, Distribution and abundance of hydrobiid snails in a mixed estuary and a coastal lagoon, Argentina: *Estuaries*, v. 26, p. 790–797.
- DODD, J.R., and STANTON, R.J., JR., 1990, *Paleoecology: Concepts and Applications*: Wiley-Interscience, New York, 502 p.
- FASANO, J.L., HERNÁNDEZ, M.A., ISLA, F.I., and SCHNACK, E.J., 1982, Aspectos evolutivos y ambientales de la laguna Mar Chiquita (Provincia de Buenos Aires, Argentina), in Lasserre, P., and Postma, H., eds., *Coastal Lagoons: Proceedings of the International Symposium on Coastal Lagoons, Bordeaux, France: Oceanologica Acta*, v. 4, suppl., p. 285–292.
- FLESSA, K.W., CUTLER, A.H., and MELDAHL, K.H., 1993, Time and taphonomy: Quantitative estimates of time-averaging and stratigraphic disorder in a shallow marine habitat: *Paleobiology*, v. 19, p. 266–286.
- FÜRSICH, F.T., and FLESSA, K.W., 1987, Taphonomy of tidal flat molluscs in the northern Gulf of California: Paleoenvironmental analysis despite the perils of preservation: *PALAIOS*, v. 2, p. 543–559.
- GARCÍA-RODRÍGUEZ, F., METZELTIN, D., SPRECHMANN, P., TRETTIN, R., STAMS, G., and BELTRÁN-MORALES, L.F., 2004a, Upper Pleistocene and Holocene paleosalinity and trophic state changes in relation to sea level variation in Rocha Lagoon, southern Uruguay: *Journal of Paleolimnology*, v. 32, p. 117–135.
- GARCÍA-RODRÍGUEZ, F., SPRECHMANN, P., METZELTIN, D., SCAFATI, L., MELENDI, D.L., VOLKHEIMER, W., MAZZEO, N., HILLER, A., VON TÜMLING, W., and SCASSO, F., 2004b, Holocene trophic state changes in relation to sea level variation in Lake Blanca, SE Uruguay: *Journal of Paleolimnology*, v. 31, p. 99–115.
- GIBERTO, D.A., BREMEC, C.S., ACHA, E.M., and MIANZAN, H., 2004, Large-scale spatial patterns of benthic assemblages in the SW Atlantic: The Río de La Plata estuary and adjacent shelf waters: *Estuarine, Coastal and Shelf Science*, v. 61, p. 1–13.
- HAMMER, Ø., HARPER, D.A.T., and RYAN, P., 2001, PAST: Paleontological Statistics Software Package for Education and Data Analysis: *Palaeontologia Electronica*, v. 4, no. 1, 184 KB, http://palaeo-electronica.org/2001_1/past/issue1_01.htm.
- HASSAN, G.S., ESPINOSA, M.A., and ISLA, F.I., 2006, Modern diatom assemblages in surface sediments from estuarine systems in the southeastern Buenos Aires Province, Argentina: *Journal of Paleolimnology*, v. 35, p. 39–53.
- IRIBARNE, O.O., VALERO, J.L., MARTÍNEZ, M.M., LUCIFORA, L., and BACHMANN, S., 1998, Shorebird predation may explain the origin of Holocene beds of stout razor clams in life position: *Marine Ecology Progress Series*, v. 162, p. 301–306.
- ISLA, F.I., 1995, Coastal lagoons, in Perillo, G.M.E., ed., *Geomorphology and Sedimentology of Estuaries: Developments in Sedimentology 53*, Elsevier Science, Amsterdam, p. 241–272.
- ISLA, F.I., 1997, Seasonal behaviour of Mar Chiquita tidal inlet in relation to adjacent beaches, Argentina: *Journal of Coastal Research*, v. 13, p. 1221–1232.
- KIDWELL, S.M., 1998, Time-averaging in the marine fossil record: Overview of strategies and uncertainties: *Géobios*, v. 30, p. 977–995.
- KIDWELL, S.M., 2002a, Mesh-size effects on the ecological fidelity of death assemblages: A meta-analysis of molluscan live-dead studies: *Géobios*, v. 35, *mémoire special* 24, p. 107–119.
- KIDWELL, S.M., 2002b, Time-averaged molluscan death assemblages: Palimpsests of richness, snapshots of abundance: *Geology*, v. 30, p. 803–806.
- 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 Data Locked in the Fossil Record: Topics in Geobiology*, vol. 9, Plenum, New York, p. 115–209.
- KIDWELL, S.M., ROTHFUS, T.A., and BEST, M.M.R., 2001, Sensitivity of taphonomic signatures to sample size, sieve size, damage scoring system, and target taxa: *PALAIOS*, v. 16, p. 26–52.
- KOWALEWSKI, M., 1996, Time-averaging, overcompleteness, and the geological record: *Journal of Geology*, v. 104, p. 317–326.
- KOWALEWSKI, M., and BAMBACH, R.K., 2003, The limits of paleontological resolution, in Harries, P.J., ed., *Approaches in High-Resolution Stratigraphic Paleontology: Kluwer Academic/Plenum Publishers*, New York, p. 1–48.
- KOWALEWSKI, M., FLESSA, K.W., and AGGEN, J.A., 1994, Taphofacies analysis of recent shelly cheniers (beach ridges), northeastern Baja California, Mexico: *Facies*, v. 31, p. 209–242.
- KOWALEWSKI, M., FLESSA, K.W., and HALLMAN, D.P., 1995, Ternary taphograms: Triangular diagrams applied to taphonomic analysis: *PALAIOS*, v. 10, p. 478–483.
- KOWALEWSKI, M., GOODFRIEND, G.A., and FLESSA, K.W., 1998, High-resolution estimates of temporal mixing within shell beds: The evils and virtues of time-averaging: *Paleobiology*, v. 24, p. 287–304.
- KOWALEWSKI, M., and LABARBERA, M., 2004, Actualistic taphonomy: Death, decay, and disintegration in contemporary settings: *PALAIOS*, v. 19, p. 423–427.
- MARTIN, R.E., 1999, *Taphonomy: A Process Approach*: Cambridge University Press, Cambridge, UK, 508 p.
- MARTIN, R.E., HARRIS, M.S., and LIDDELL, W.D., 1995, Taphonomy and time-averaging of foraminiferal assemblages in Holocene tidal flat sediments, Bahía La Choya, Sonora, Mexico (northern Gulf of California): *Marine Micropaleontology*, v. 26, p. 187–206.
- MARTIN, R.E., WEHMILLER, J.F., HARRIS, M.S., and LIDDELL, W.D., 1996, Comparative taphonomy of bivalves and foraminifera from Holocene tidal flat sediments, Bahía La Choya, Sonora, Mexico (Northern Gulf of California): *Taphonomic grades and temporal resolution*: *Paleobiology*, v. 22, p. 80–90.
- MELDAHL, K.H., 1994, Biofacies and taphofacies of a Holocene macrotidal environment: Bahía La Cholla, northern Gulf of California: *Ciencias Marinas*, v. 20, p. 555–583.
- MELDAHL, K.H., and FLESSA, K.W., 1990, Taphonomic pathways and comparative biofacies and taphofacies in a Recent intertidal/shallow shelf environment: *Lethaia*, v. 23, p. 43–60.
- MELDAHL, K.H., FLESSA, K.W., and CUTLER, A.H., 1997, Time-averaging and post-mortem skeletal survival in benthic fossil assemblages: Quantitative comparisons among Holocene environments: *Paleobiology*, v. 23, p. 207–229.
- OLIVIER, S.R., ESCOFET, A., PENCHASZADEH, P., and ORENSANZ, J.M., 1972, Estudios ecológicos de la región estuarial de Mar Chiquita (Buenos Aires, Argentina): I. Las comunidades bentónicas: *Anales de la Sociedad Científica Argentina*, v. 193, p. 237–262.
- PARSONS-HUBBARD, K.M., 2005, Molluscan taphofacies in recent carbonate reef/lagoon systems and their application to sub-fossil samples from reef cores: *PALAIOS*, v. 20, p. 175–191.
- PARSONS-HUBBARD, K.M., and BRETT, C.E., 1991, Taphonomic processes and biases in modern marine environments: An actualistic perspective on fossil assemblage preservation, in Donovan, S.K., ed., *The Processes of Fossilization*: Belhaven Press, London, p. 22–65.
- PARSONS-HUBBARD, K.M., CALLENDER, W.R., POWELL, E.N., BRETT, C.E., WALKER, S.E., RAYMOND, A.L., and STAFF, G.M., 1999, Rates of burial and disturbance of experimentally-deployed molluscs: Implications for preservation potential: *PALAIOS*, v. 14, p. 337–351.
- POWELL, E.N., CALLENDER, W.R., and STANTON, R.J., JR., 1998, Can shallow- and deep-water chemoautotrophic and heterotrophic communities be discriminated in the fossil record?: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 144, p. 85–114.
- RETA, R., MARTOS, P., PERILLO, G.M.E., PICCOLO, M.C., and FERRANTE, A., 2001, Características hidrográficas del estuario de la laguna Mar Chiquita, in Iribarne, O.O., ed., *Reserva de Biosfera Mar Chiquita: Características Físicas, Biológicas y Ecológicas*: Editorial Martín, Mar del Plata, Argentina, p. 31–52.
- RODLAND, D.L., KOWALEWSKI, M., CARROLL, M., and SIMÕES, M.G., 2006, The temporal resolution of epibiont assemblages: Are they ecological snapshots or over-exposures?: *Journal of Geology*, v. 114, p. 313–324.
- SCHNACK, E.J., FASANO, J.L., and ISLA, F.I., 1982, The evolution of Mar Chiquita lagoon coast, Buenos Aires Province, Argentina, in *Holocene Sea Level Fluctuations—Magnitude and Causes: International Geological Correlation Programme, Project 61, International Union for Quaternary Research, Columbia, South Carolina*, p. 143–155.
- SCHWINDT, E., DE FRANCESCO, C.G., and IRIBARNE, O.O., 2004, Individual and reef growth of the introduced reef-building polychaete *Ficopomatus enigmaticus* in a south-western Atlantic coastal lagoon: *Journal of the Marine Biological Association of the United Kingdom*, v. 84, p. 987–993.
- SCOTT, D.B., and MEDIOLI, F.S., 1980, Living vs. total foraminiferal populations: Their relative usefulness in paleoecology: *Journal of Paleontology*, v. 54, p. 814–831.
- SOARES-GOMES, A., and PIRES-VANIN, A.M.S., 2005, Bivalve mollusk assemblages on São Paulo's northern continental shelf, southeast Brazil: *Brazilian Journal of Zoology*, v. 65, p. 717–727.
- SPIVAK, E.D., ANGER, K., LUPPI, T.A., and ISMAEL, D., 1996, Size structure, sex ratio, and breeding season in two intertidal grapsid crab species from Mar Chiquita Lagoon, Argentina: *Nerítica (Curitiba, Brazil)*, v. 10, p. 7–26.
- SPRINGER, D.A., and FLESSA, K.W., 1996, Faunal gradients in surface and subsurface shelly accumulations from a recent clastic tidal flat, Bahía la Choya, northern Gulf of California, Mexico: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 126, p. 261–279.

- STAFF, G.M., and POWELL, E.N., 1990, Local variability of taphonomic attributes in a parautochthonous assemblage: Can taphonomic signature distinguish a heterogeneous environment?: *Journal of Paleontology*, v. 64, p. 648–658.
- STATSOFT, 1998, STATISTICA for Windows, ver. 5.1: StatSoft Inc., Tulsa, Oklahoma.
- WALKER, S.E., PARSONS-HUBBARD, K.M., POWELL, E.N., and BRETT, C.E., 1998, Bioerosion or bioaccumulation? Shelf-slope trends for epi- and endobionts on experimentally deployed gastropod shells: *Historical Biology*, v. 13, p. 61–72.
- ZAR, J.H., 1984, *Biostatistical Analysis*: Prentice-Hall, Englewood Cliffs, New Jersey, 718 p.
- 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.
- ZUSCHIN, M., and STANTON, R.J., JR., 2001, Experimental measurement of shell strength and its taphonomic interpretation: *PALAIOS*, v. 16, p. 161–170.

ACCEPTED FEBRUARY 17, 2007