

Taphonomic trade-offs in tropical marine death assemblages: Differential time averaging, shell loss, and probable bias in siliciclastic vs. carbonate facies

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ABSTRACT

Radiocarbon-calibrated amino-acid racemization ages of individually dated bivalve mollusk shells from Caribbean reef, nonreefal carbonate, and siliciclastic sediments in Panama indicate that siliciclastic sands and muds contain significantly older shells (median 375 yr, range up to ~5400 yr) than nearby carbonate seafloors (median 72 yr, range up to ~2900 yr; maximum shell ages differ significantly at $p < 0.02$ using extreme-value statistics). The implied difference in shell loss rates is contrary to physicochemical expectations but is consistent with observed differences in shell condition (greater bioerosion and dissolution in carbonates). Higher rates of shell loss in carbonate sediments should lead to greater compositional bias in surviving skeletal material, resulting in taphonomic trade-offs: less time averaging but probably higher taxonomic bias in pure carbonate sediments, and lower bias but greater time averaging in siliciclastic sediments from humid-weathered accretionary arc terrains, which are a widespread setting of tropical sedimentation.

Keywords: taphonomy, mollusks, tropical carbonates, sedimentology, time averaging.

INTRODUCTION

One of the major uncertainties in extracting biological and environmental information from fossil assemblages is that of time resolution: how many years of accumulation does a sample actually represent, i.e., how many generations have been mixed or “time averaged?” Understanding the magnitude and environmental variability of time averaging in shallow marine settings is also critical to questions of carbonate burial and recycling.

Magnitudes of time averaging (total range in shell ages) as estimated from degree of taphonomic damage, scattered radiocarbon dates, and stratigraphic context have ranged from 10 to 10^4 yr and, exceptionally, to 10^5 – 10^7 yr (Kidwell and Bosence, 1991). Syntheses of published radiocarbon dates (Flessa and Kowalewski, 1994) and targeted dating efforts (Flessa et al., 1993; Wehmiller et al., 1995; Martin et al., 1996; Meldahl et al., 1997; Kowalewski et al., 1998; Carroll et al., 2003) in modern sediments have verified the 10 – 10^4 yr range for mollusks, benthic foraminifera, and brachiopods, although shells are mostly young in a given death assemblage. Skeletal remains are thus capable of surviving reworking and prolonged residence at or near the shallow-marine sediment-water interface. However, with one exception (Brazilian brachiopods;

Carroll et al., 2003), no quantitative data are available on how time averaging and carbonate shell loss operate in the tropics, with their generally warmer waters, lower seasonality, distinctive seafloor types including photic-zone reefs, and carbonate sediments with low abrasive power and pore-water chemistry distinct from siliciclastics.

Here we present the first study of molluscan time averaging in a fully tropical setting. The San Blas Archipelago on the Caribbean coast of Panama provides an excellent test area, given the coexistence on a single open shelf of high-diversity coral reefs, hardgrounds, and a variety of siliciclastic, carbonate, and mixed-composition soft sediments (Best, 2000). Siliciclastic sediments are derived from humid weathering of accretionary volcanic arc deposits exposed on the Panama mainland (Coates et al., 2004). Volcanic arcs are common settings of shallow-marine mixed siliciclastic-carbonate sedimentation, known throughout the modern tropics of the eastern Caribbean, Central America, Pacific South America, Southeast Asia, and Indo-Pacific.

STUDY AREA AND METHODS

In the San Blas Archipelago (9° N), siliciclastic sediments (<30 wt% carbonate mud) occur in a 2–5 km belt along the mainland coast to ~20 m water depth, where they intergrade with a 2–5 km belt of mixed-

composition sediments (Best, 2000). Relatively pure carbonate sediments (50% to ~100% carbonate mud) occupy the rest of the modern open shelf (maximum depth ~60 m), which is edged by extensive reefs and carbonate cays ~15 km offshore. Seaward of the modern reef front is a sloping seafloor of drowned reefs and mixed-composition muddy sediments. Shell ages from that largely relict seafloor range from ca. 15.9 (calendar—cal.) ka offshore to ca. 8.6 cal. ka at the foot of the modern reef front, reflecting postglacial sea-level rise (Data Repository Appendix 1).¹ The modern San Blas shelf (area inboard of the actively growing reef front) yields shell dates exclusively younger than ca. 5 ka (this report), and thus was probably established ca. 6–7 ka.

Scuba and ship-based field work in 1995–1998 produced a dense network of data on subtidal environments and molluscan death assemblages (Best, 2000). Shells for age determination were selected primarily from sites on the modern shelf where we also have data from experimental shell deployments and pore-water geochemistry (Best et al., 1999; Best, 2000). Most dated shells come from surficial grabs of the seafloor (top 10 cm), and all but 2 were from the top 20 cm (Appendix 1; see footnote 1). Reef shells were collected from sandy pockets within the reef framework or from debris aprons.

Age control is based on analyses of single shell fragments by accelerator mass spectrometry (AMS; University of Arizona) 14 C, combined with amino-acid racemization (AAR; Northern Arizona University), together yielding 45 dated shells from the modern San Blas shelf (ages for all shells listed in Appendix 1 [see footnote 1], including additional shells from Bocas del Toro farther west in Caribbean Panama). For AAR analysis, we used the procedure of Kaufman and Manley (1998), which yields precise separations of D and L enantio-

¹Data Repository item 2005133, Appendices 1 and 2, is available online at www.geosociety.org/pubs/ft2005.htm or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, USA.

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mers of aspartic acid (Asp) and glutamic acid (Glu) from small shell fragments. To avoid variability in racemization rates within shells (Carroll et al., 2003) and among taxa, all specimens were sampled from a homologous position (posterior half used for AAR, umbo and anterior for AMS), and most dates are from a single bivalve genus (*Pitar*; 10 of 12 shells used to calibrate the age equation, and 26 of 33 additional shells dated by applying that equation to Glu AAR values; details in Appendix 1 [see footnote 1]).

To test the utility of shell preservation state as an indicator of shell age, all dated shells were scored for macroscopic damage (15 variables; following Best, 2000). The first dimension of a two-dimensional nonmetric multidimensional scaling (NMDS) ordination captured most of the variability (stress 0.079), with pristine shells and highly damaged shells plotting at the opposite ends of the axis, and so this is used as a proxy for damage (two-dimensional plot in Appendix 2; see footnote 1).

Because our aim was to determine maximum scales of time averaging per assemblage, we preferentially dated the poorest-condition shells at each site. Our sampling of shells and the resulting age frequency distribution are thus biased against recently dead specimens. To have sufficient mass for both AMS and AAR dating, only relatively large specimens (height ≥ 6 mm; Appendix 1; see footnote 1) were used. Estimates on time averaging are thus relevant primarily to death assemblages of biological adults, as in all other absolute calibrations of time averaging.

CALIBRATION OF SHELL AGES

Of the 30 shells from San Blas submitted for AMS ^{14}C dating, 16 yielded ages older than the assumed marine reservoir age of 450 yr, and their ages were calibrated using CALIB (Stuiver and Reimer, 1993). We used the midpoint of the 1 sigma age range for the calibrated ages. AAR analysis of these 16 ^{14}C dated shells predating A.D. 1950 shows that D/L ratios for Glu in shells younger than 6000 cal. yr B.P. increase systematically with increasing age (all of these shells are from the modern shelf, from sites at 1–42 m water depth), whereas Glu D/L ratios in the 4 shells with ^{14}C ages older than 8000 cal. yr B.P. do not increase with age (these are *Pitar* specimens from the relatively deep relict shelf; water depths 74–170 m; plot in Appendix 1 [see footnote 1]). Asp D/L ratios are generally more variable with respect to sample age compared with Glu D/L (Appendix 1; see footnote 1). We therefore base our AAR calibration for the modern shelf on Glu D/L in shells younger than 6000 cal. yr B.P. only, i.e., on the 12

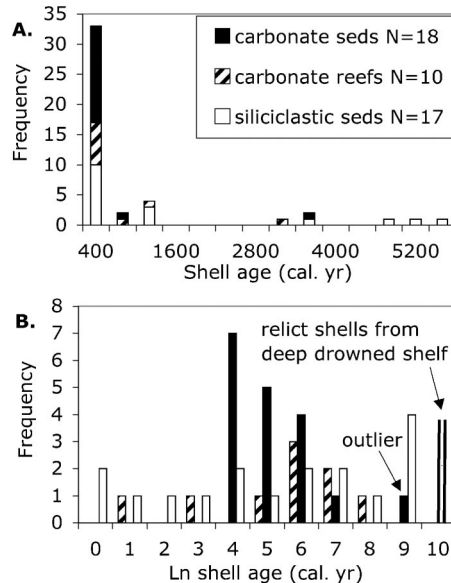


Figure 1. Frequency distribution of shell ages in calendar years from San Blas Archipelago. A: In all settings on modern shelf, majority of shells are young, but shells from siliciclastic and mixed-composition sediments (white bars) exhibit greater maximum shell age and greater dispersion of ages than shells from carbonate sediments and reefs. B: Differences are accentuated when shell ages are log-transformed.

shells with paired ^{14}C -AAR analyses that were collected from the modern shelf, which is known to have thermally nonstratified waters (D’Croz et al., 1999).

Of the various equations that have been used to model reaction pathways of amino acids, the rate of Glu racemization in San Blas shells best fits a parabolic model, which produces a linear relationship between the D/L and square root of sample age ($R^2 = 0.863$). The ages of undated samples (33 specimens, including the 14 shells that ^{14}C proved were younger than A.D. 1950) is estimated by a least-squares linear regression equation for D/L Glu: $t = (262.2 \text{ D/L} - 4.5)^{0.5}$, where $t = \text{age in cal. yr B.P.}$ Shells from genera other than *Pitar* (one *Codakia* specimen, one *Callista* specimen) fell sufficiently close to the regression line to use in the calibration (Fig. DR1; see footnote 1) and lend confidence to our application of the equation to Glu D/L values from other non-*Pitar* specimens (four *Codakia*, three *Macoma*). All of the Glu-dated non-*Pitar* specimens fall well within the variation described by dated *Pitar* specimens (e.g., in plots and analyses that follow here).

MAGNITUDES OF TIME AVERAGING

The maximum shell age among the 45 dated shells from the modern San Blas shelf is ca. 5400 cal. yr B.P. (Fig. 1A). Despite the preferential dating of damaged shells, the age

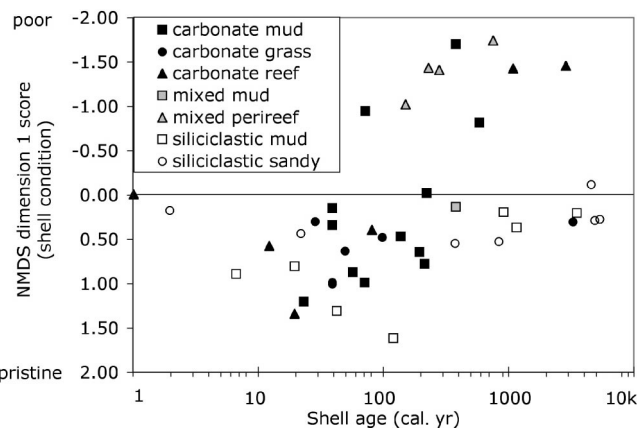
frequency distribution is strongly right skewed, i.e., most shells are young (median age = 120 yr), as are siliciclastic- and carbonate-derived subsets of shells (Fig. 1A). However, shells from siliciclastics have higher median, semiquartile range $[(Q3 - Q1)/2]$, and maximum values (375 yr, 1743 yr, ~ 5400 yr old; $N = 15$) than shells from carbonate seafloors (72 yr, 90 yr, ~ 3300 yr old; $N = 24$); shells from sediments of mixed composition yield intermediate values ($N = 6$) (Table DR3; see footnote 1). Log transformation accentuates differences in the shapes of the age frequency distributions of these different sets of “worst-condition” shells (Fig. 1B). Shells from carbonate muds and sandy grassbeds remain right skewed, even if an AAR-dated outlier of ca. 3300 cal. yr is excluded (maximum shell age from carbonate soft sediments becomes ca. 2900 cal. yr); shells from reefs show greater dispersion but a similar mode to nonreefal carbonate sediments; and shells from siliciclastic muds and sands show greatest dispersion and a left skew.

Nonrandom sampling of shells precludes standard statistical tests of the differences described here, but differences in maximum shell ages can be evaluated using extreme-value statistics (Denny and Gaines, 2000; Kinison, 1985; see Appendix 2 [see footnote 1]). Using this method, the magnitude of time averaging in siliciclastic and mixed-composition sediments is significantly greater than in carbonate seafloors ($p = 0.018$ for the four siliciclastic shell dates that exceeded the maximum known from carbonates; Table DR2 [see footnote 1]). Time averaging in siliciclastics does not differ significantly from reefs ($p = 0.13$), but in both siliciclastic and reef assemblages, time averaging is significantly greater than in carbonate nonreefal sediments ($p = 0.004$ and 0.041 , respectively).

These are all one-tailed tests; p values would approximately double for two-tailed tests. This would eliminate any significant difference between reefs and carbonate soft sediments, but all other differences are robust. Statistical power is lost if data are further partitioned to test for variation as a function of both grain size and sediment composition. However, ranked by maximum shell age, time averaging in siliciclastic sands $>$ siliciclastic muds $>$ carbonate muds $>$ carbonate sands, suggesting that the effects of sediment composition supersede those of grain size. Moreover, shell ages from sands (siliciclastic and carbonate data pooled) do not differ significantly from muds as a group ($p = 0.09$, two-tailed test).

As in all other analyses of time averaging, we assume that rates of skeletal input have been steady, and thus that differences in the magni-

Figure 2. Relationship between shell age and shell condition, as scored by multivariate analysis (nonmetric multidimensional scaling; NMDS) of taphonomic damage (see text). Young shells (younger than ~100 yr) in both siliciclastic and carbonate settings can exhibit range of damage states, indicating that early damage accrual is erratic but can be rapid in both settings. Based on full age spectrum, however, shells from carbonates range to poorer conditions than shells of similar or greater age from siliciclastic and mixed-composition sediments, suggesting more intense recycling.



tude of time averaging reflect patterns of taphonomic loss rather than changes in biological supply. Differences in sedimentation rate can also produce differences in maximum shell ages. However, given the bathymetric ramping of siliciclastics and mixed-composition sediments along the mainland coast, which is fed by a series of short sediment-rich rivers, we suspect that net sediment accumulation rates in onshore siliciclastic facies of the San Blas shelf probably are as high or higher than in coeval carbonate facies. This should cause maximum shell ages in siliciclastic facies to be lower than in carbonate facies, opposite to what we observe.

ACCRAAL OF SHELL DAMAGE WITH POSTMORTEM AGE

These differences in time averaging and their attribution to different loss rates are corroborated by observations that bivalve shells in San Blas carbonate sediments accrue taphonomic damage at higher long-term rates than shells in siliciclastic sediments (Fig. 2). Overall, shell-condition scores range from +2.00 (pristine; no macroscopic damage) to 0.00 (moderate; microbial maceration, mineral precipitates) to -2.00 (poor; extensive bioerosion, bioencrustation, and/or corrosion). Shells from carbonate environments exhibit this full range, from +1.5 (slight discoloration from micritization) to -1.75, with shells only a few hundred years old exhibiting relatively intense damage (Fig. 2).

Shells from siliciclastics exhibit at worst only moderate damage (-0.1), despite greater maximum ages (~5400 yr old; Fig. 2; see Best, 2000, for a much larger data set supporting this narrow range in damage). At worst, shells from siliciclastics exhibit a surface sheen and staining from diagenetic precipitation of very fine grained calcium carbonate and other minerals: there is no evidence of pitting from dissolution, macroscopic fouling is rare, and microbial macera-

tion is comparable to that in shells from carbonate settings. This same total range of shell damage and same qualitative differences between carbonate and siliciclastic facies occurs in bivalve death assemblages from the Bocas del Toro area of Caribbean Panama (Best and Kidwell, 2000).

Although it seems axiomatic that damage should be positively correlated with age, most studies have found high degrees of damage in very young shells and thus a weak or nonexistent relationship between shell condition and shell age (Powell and Davies, 1990; Flessa et al., 1993; Martin et al., 1996; Meldahl et al., 1997; Carroll et al., 2003). San Blas death assemblages produce generally low correlation values owing to a scatter of damage states among young shells (in carbonates, linear regression of log-transformed age yields $R^2 = 0.27$, $p = 0.01$; within siliciclastic sediments $R^2 = 0.23$, $p = 0.07$; Fig. 2). However, old shells (whether defined as older than 500 yr or older than the median shell age) exhibit significantly greater damage than young shells (Fig. 2; t-test, $p = 0.004$ in carbonates, $p = 0.008$ in siliciclastics; approach of Carroll et al., 2003; see Appendix 2 [see footnote 1] for implications on resegregating cohorts using shell damage, i.e., "taphonomic clock").

DIFFERENCES IN TIME AVERAGING AND SHELL PERSISTENCE: WHY?

The lower degree of time averaging and higher implied rates of shell loss for bivalve shells in carbonate sediments may seem counterintuitive: these sediments consist mostly of carbonate grains, which have lower abrasive power than siliciclastic grains and imply favorable pore-water (and overlying water) chemistry. However, the dating results are consistent with the higher damage levels observed in carbonate death assemblages (Fig. 2; see Best, 2000, for a much larger data set), primarily from bioerosion and dissolution (verified by Scanning electron microscope),

relative to nearby siliciclastic sediments. Dating results are also consistent with the higher short-term (3 yr) rates of shell deterioration and weight loss determined experimentally by Best (2000) at these same carbonate sites.

Two factors appear to drive these differences. First, on carbonate seafloors, dead shells are attacked by boring and encrusting taxa during even brief exposure at the seafloor, whereas in siliciclastic settings, frequent plumes of sediment from rivers and easy re-suspension of the organic-rich flocculant that mantles the seafloor apparently severely limit the colonization and survival of foulers other than microbes (Best, 2000).

Second, in both natural death assemblages and experimentally deployed shells, shell pitting consistent with dissolution is observed only in carbonate settings, whereas in siliciclastic sediments, diagenesis favors carbonate and other mineral precipitation onto shells (Best, 2000; Best et al., 2001). Pore-water analyses at these same experimental sites (Ku et al., 2000) indicate that rapid sulfur redox cycles starting immediately below the sediment-water interface would probably generate net acidic conditions in carbonate sediments, promoting shell dissolution such as observed year-round in Florida Bay (e.g., Ku et al., 1999) and seasonally in temperate siliciclastics (e.g., Green and Aller, 1998). In contrast, in San Blas siliciclastic sediments, which are rich in reactive iron from humid weathering of mainland arc deposits, pore waters from the top 20 cm are alkaline and show no downcore buildup of calcium ions consistent with carbonate dissolution; anaerobic organic decomposition is apparently strongly influenced by Fe (and probably Mn) reduction, given the downcore increase in pore-water reduced iron (no sulfate reduction detected; Ku et al., 2000). The products of these microbial pathways prevent acid accumulation and favor shell preservation as well as early diagenetic precipitation of calcium carbonate, siderite, and other mineral crusts (Best et al., 2001; Ku and Walter, 2003). The very young ages of shells exhibiting such precipitates (documented here as a few hundred to few thousand years old; Fig. 2) demonstrate how rapidly and shallowly within the sedimentary column such precipitation can occur in San Blas siliciclastics, and this is also confirmed by the appearance of such precipitates on shells deployed experimentally for 1-3 yr (Best, 2000).

CONCLUSIONS AND IMPLICATIONS

Larger numbers of (randomly) dated shells would improve our confidence in these estimated scales of time averaging. However, we expect the sign of the between-facies difference to be robust given its consistency with

other independent lines of evidence (differences in damage levels in natural death assemblages, shell loss rates during experimental shell deployments, pore-water geochemistry). These findings are noteworthy (1) as a first investigation of this major metazoan group in tropical reef and siliciclastic settings, and (2) because the between-facies contrast discovered in San Blas—higher shell loss rates and less time averaging in carbonate sediments than in siliciclastic sediments—is contrary to geological intuition.

Owing to more intense bioerosion and greater interstitial dissolution, we predict a lower proportion of carbonate shell input to survive to permanent burial within tropical carbonate facies than in siliciclastic facies, where negligible bioerosion and, at least in arc terrains like Panama, relatively alkaline pore waters promote shell preservation. Paleobiologically, the higher rates of shell loss in carbonate facies result in less time averaging, which is favorable to ecological and environmental analysis of surviving shell material. However, the relatively rapid recycling of shells should also result in stronger filtering of shell input according to taxonomic differences in shell durability and original abundance, leading to greater compositional bias in surviving skeletal material.

We thus expect a taphonomic trade-off between relatively high temporal resolution and low compositional fidelity in carbonate facies, with the opposite combination in siliciclastic sediments. The question of whether these facies-level differences in time averaging and shell loss lead to significant net bias in ecological information—e.g., an underestimation of species richness or infaunal/epifaunal ratio in carbonates—requires direct testing, for example via live-dead comparisons. However, shallow-marine arc-related siliciclastics, which are widespread in tropical latitudes today, can clearly be effective sinks of locally produced molluscan shell carbonate and would constitute a good target facies for ecological and evolutionary comparisons across geologic time. Siliciclastic death assemblages from nonhumid, nonvolcanic settings probably undergo less favorable diagenetic conditions (more standard sulfate-reduction regimes) and higher fouling (if there is less mud in the system). The conditions found in San Blas carbonate environments, however, are probably relatively general: carbonate sediments and reefs are not inherently favorable refuges of shell preservation. Per capita rates of molluscan shell recycling there are at least comparable to those found in siliciclastic en-

vironments from other latitudes and are less favorable than in tropical arc-hosted siliciclastics. Inventories of tropical diversity from carbonate records are thus almost certainly conservative estimates.

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