Time-averaged molluscan death assemblages: Palimpsests of richness, snapshots of abundance

Susan M. Kidwell*   Department of Geophysical Sciences, University of Chicago, 5734 South Ellis Avenue, Chicago, Illinois 60637, USA

ABSTRACT

Field tests that compare living communities to associated dead remains are the primary means of estimating the reliability of biological information in the fossil record; such tests also provide insights into the dynamics of skeletal accumulation. Contrary to expectations, molluscan death assemblages capture a strong signal of living species' rank-order abundances. This finding, combined with independent evidence for exponential postmortem destruction of dead cohorts, argues that, although the species richness of a death assemblage may be a time-averaged palimpsest of the habitat (molluscan death assemblages contain, on average, ~25% more species than any single census of the local live community, after sample-size standardization), species' relative-abundance data from the same assemblage probably constitute a much higher acuity record dominated by the most recent dead cohorts (e.g., from the past few hundred years or so, rather than the several thousand years recorded by the total assemblage and usually taken as the acuity of species-richness information). The pervasive excess species richness of molluscan death assemblages requires further analysis and modeling to discriminate among possible sources. However, time averaging alone cannot be responsible unless rare species (species with low rates of dead-shell production) are collectively more durable (have longer taphonomic half-lives) than abundant species. Species richness and abundance data thus appear to present fundamentally different taphonomic qualities for paleobiological analysis. Relative-abundance information is more snapshot-like and thus taphonomically more straightforward than expected, especially compared to the complex origins of dead-species richness.

Keywords: taphonomy, paleoecology, diversity, time resolution.

INTRODUCTION

Ever since R.G. Johnson's (1965) seminal quantitative comparison of living molluscan communities and locally accumulating shell material, paleontologists have used "live-dead agreement" to estimate the reliability of the marine fossil record and gain insights into the origins of postmortem bias. One key discovery from live-dead studies devoted to shelled mollusks has been that sedimentary death assemblages consistently contain more species—usually far more species—than are sampled in any single census of the local living community (e.g., Cadée, 1968; Warme et al., 1971; Peterson, 1976; Staff et al., 1986; Carthew and Bosence, 1986). Although this excess dead-species richness can result in part from postmortem delivery of exotic shells from other environments, most authors have argued that many (or most) "dead-only" species were actually indigenous to the local community, but simply had living populations that were too sparsely distributed, patchy, or ephemeral to have been encountered during sampling. That is, had the living community been sampled more intensively or over a longer period of time, its documented species richness would have more closely matched that of the death assemblage. Such findings strengthen the idea that a death assemblage is not biologically equivalent to a census of a living community, but instead sums dead-shell

input (minus shell destruction) over some longer period of time, permitting accrual of a time-averaged species richness (Johnson, 1965; Walker and Bambach, 1971).

These realizations (of excess dead-species richness, time averaging, and out-of-habitat exotics), combined with the potential for differential production and postmortem destruction of species and age classes during the period of time averaging, have led paleontologists to expect low live-dead agreement in species' abundances (Johnson, 1965; Walker and Bambach, 1971; Fürsich and Aberhan, 1990). Empirical results from molluscan live-dead studies have appeared to bear this out, in that individual authors who tested abundance agreement quantitatively usually found poor or highly variable levels of agreement (Cummins et al., 1986; and see Kidwell and Bosence, 1991).

However, a standardized reanalysis of 85 habitat-level live-dead molluscan data sets has shown that, although there is wide scatter in results and a previously unrecognized effect from sieve mesh size (which determines whether larval and early juvenile specimens are included in the analysis, and pervades all metrics of live-dead agreement; Kidwell, 2002), 92% of live-dead comparisons show a positive correlation in species' rank order (Kidwell, 2001). Overall, species that are dominant in a single live census also dominate the local death assemblage, and species that are rare or unsampled alive are also rare dead.

If species have different rates of dead-shell production (i.e., different rates of population turnover) and different rates of shell destruction, and if death assemblages are time-averaged over many generations, leading to the accrual of species richness, then why should death assemblages reflect species' original relative abundances so well? Here I argue that, although several scenarios are possible, the most likely explanation is that abundance information is simply not time averaged to the same degree as richness information. That is, death-assemblage richness may represent a time exposure of short-term fluctuations in local community composition over much or all of the period of time averaging, but dead species' relative abundances—here, the ranking of species according to their numerical abundance—is a higher acuity record that draws largely upon the most recent cohorts of dead shells.

MATERIALS

Molluscan live-dead data sets were gathered from the published literature and from data archives and are based on live and dead material sieved from samples of the top 10 or 20 cm of marine and estuarine sediments (marsh to middle shelf; see Data Repository Appendix[1]). Studies were included only if numerical abundance data were available for the complete molluscan fauna, including rare species, and if live and dead data were generated using a single specified mesh size (range 0.3–5 mm; 1 mm median). There were 19 independent studies covering 30 different study areas in low and middle latitudes (0–54°N) that met these criteria: 26 additional studies did not meet these criteria and are excluded (see footnote 1).

For each study area, live and dead species abundances from individual samples were pooled into habitat-level data sets on the basis of similar sedimentary grain size, seafloor features (vegetation, mass

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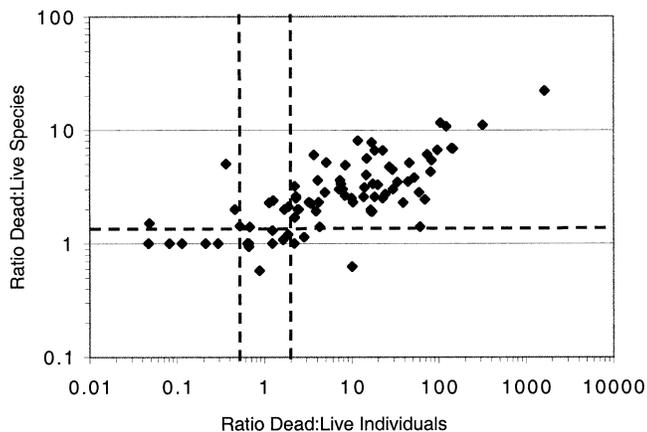*E-mail: skidwell@midway.uchicago.edu.

Figure 1. In all but 2 of 85 data sets, species richness of death assemblage matches or exceeds that of sampled live community (as shown by dead:live ratio >1; median ratio of dead:live species is 2.57), even where live individuals are more numerous than dead individuals. For data sets where live and dead data are based on similar numbers of individuals (area between vertical dashed lines, $n = 14$), median dead:live species ratio decreases to 1.25 (dashed horizontal line; death assemblage is 25% richer than comparably sized census of local live community).

properties), and salinity of the sample site. These habitats are comparable in scale and distinctiveness to stratigraphic facies and were defined independently of faunal data. Sediment grain sizes ranged from mud to gravel (no hardgrounds or reefs). All 85 habitat-level data sets compiled in this way are from settings where the uppermost sediments of the column can be assumed to be time averaged to some degree.

In the majority of studies, live data came from a single census of the community (single visit), thus providing a very conservative estimate of true live-species richness. In 12 of the 85 habitats, several seasons of live census data are available (1.75 yr maximum duration of sampling program; see footnote 1). In the present analysis, these 12 data sets are each represented by only one single-census value (census with maximum number of live individuals).

MAGNITUDE OF EXCESS DEAD RICHNESS

The ratio of dead:live species in the 85 data sets ranges from 0.6 to 22.0, with a median value of 2.6 (Fig. 1).

However, as virtually every original author noted, dead individuals are usually far more abundant than live individuals, and thus, although the effect has never been quantified, part of the excess dead richness might be explained by differences in sample size. In the present database, ratios of dead:live individuals range from 0.05 (1:20) to 1637 (median 8; Fig. 1). This result leads to the question: would death assemblages still be enriched relative to the live community—and thus be presumed to be time averaged—if sample sizes were comparable?

Examination of the scatter plot (Fig. 1) indicates that, although the ratio of dead:live species declines as the ratio of dead:live individuals approaches 1, excess dead richness exists across the entire range of data sets, even where dead individuals are outnumbered by live individuals. The magnitude of this discrepancy can be estimated in two ways. First, among data sets containing similar numbers of live and dead individuals, i.e., where the ratio of dead:live individuals ranges between 1:2 and 2:1 (area between dashed vertical lines in Fig. 1), the median dead:live species ratio is 1.25. That is, death assemblages are on average 25% more species rich than their local live communities when live and dead sample sizes are comparable.

Second, a null-model value of dead-species richness can be calculated for each data set in which dead individuals outnumber the live, by using information on species proportions to calculate how many

dead species would be sampled if live and dead samples were the same size (this method is used to determine whether an island fauna is unambiguously depauperate relative to the mainland, or if the lower richness can instead be explained by the smaller area available to sample; see Gotelli and Graves, 1996). For the 72 data sets where dead individuals outnumber live individuals, the median percentage of dead-only species in a sample-size–corrected death assemblage is 22%. If individual data sets are weighted by the number of live species (target sample size), the metaanalytic average weighted mean is 22.00% ± 0.06% (95% confidence interval, calculated with variance defined as 1 over the sum of weights; see Gurevitch and Hedges, 2001). This ~25% discrepancy is much lower than the two- to threefold difference estimated from raw data (e.g., Kidwell and Bosence, 1991), but species enrichment of death assemblages is clearly significant, pervasive, and not simply an artifact of oversampling the dead.

The vast majority of these excess dead-only species are numerically rare (each constitutes ≤1% of dead individuals; Kidwell, 1999). In shoreface sands and in muds adjacent to rocky or vegetated shores, a few species (characterized by large numbers of individuals) are exotics washed in from shallower habitats. However, in these as well as other settings, the majority of dead-only species are each represented by few individuals and appear to be indigenous species not captured by the live census, thus supporting the idea that excess dead richness is largely a product of within-habitat time averaging.

LIVE-DEAD AGREEMENT IN SPECIES RANK ORDER

Spearman rank-order correlation coefficients (r values; Sokal and Rohlf, 1995) indicate whether dead species ranked according to numerical abundance occur in opposite order to those species when alive ($r = -1$), random order ($r = 0$), or identical order ($r = +1$). Coefficients for the 85 data sets range from -1 to $+1$, but 92% are positive with an overall median of 0.48 (Kidwell, 2001). The metaanalytic average r value, in which data sets are weighted according to the total number of species in the comparison, is 0.45 ± 0.03. Average live-dead correlations are thus less than perfect, but significantly positive, meaning that species that are abundant in the death assemblage are also abundant in the live data, and species that are rare dead are also rare or absent alive.

EXPLAINING GOOD RANK CORRELATION: RAPID FADING OF DEAD COHORTS

The capture of rank-order information by a time-averaged death assemblage could arise two ways.

1. Species' relative abundances were stable in the source live community over the entire duration of time averaging. This scenario becomes less reasonable ecologically with increasing periods of time averaging, especially in environments that undergo fluctuating salinity or substratal conditions (i.e., changes sufficient to reset ecological succession or to shift community gradients). Unfortunately, this scenario is impossible to test directly: continuous time series for live communities are generally available for a few years at most and, even then, sampling is usually seasonal at best.

2. The majority of dead individuals was contributed by only the most recent generations of organisms to live in the habitat, and thus, although still time averaged, reflect input over a much shorter interval of time than the total death assemblage. Thus, the taxon-specific abundance structure of the live community need only have been stable for the final phase of time averaging rather than for the entire duration.

This second scenario—that dead species' abundances largely reflect only the most recent phase of live community structure—fits expectations about the taphonomic age structure of time-averaged death assemblages, namely that younger (more recently dead) shells should dominate because they have been subject to destructive postmortem processes for less time than old shells (Kidwell and Bosence, 1991;

Olszewski, 1999). It is also supported by (1) short-term rates of shell destruction and (2) direct dating. For example, by sampling sediments at 6-week intervals over an 18–21 month period, Cummins et al. (1986) observed rapid ''decay'' in numbers of dead individuals following each pulse of larval settlement and death: ''taphonomic half-lives'' on the order of months were calculated for these predominantly small shells (<~3 mm). Although a few species and larger shells in general showed ''immeasurably long'' half-lives relative to study duration, the implication was that newly generated shells underwent very rapid initial loss rates, resulting in a hollow, right-skewed, frequency distribution of shell ages in the time-averaged death assemblage.

Direct dating of mollusk shells in modern marine sediments also yields strongly right-skewed, exponential age distributions (e.g., Flessa and Kowalewski, 1994; Olszewski, 1999). In studies designed to calibrate time averaging in coastal depositional facies, shell ages range to several thousand years, but most are <500 yr (Meldahl et al., 1997; Kidwell and Best, 2001).

Field evidence thus indicates that (1) time-averaged molluscan death assemblages are dominated numerically by relatively recently dead shells, despite the presence of significantly older shells in the assemblage and (2) ''relatively recently dead'' means on the order of a few hundreds of years in settings where shell input is primarily from local (within habitat) living communities and the focus is on adult (versus larval and early juvenile) specimens.

EXCESS RICHNESS: IS TIME AVERAGING ALONE SUFFICIENT?

Molluscan death assemblages are thus dominated numerically by recently dead shells, preserve on average a strong signature of species' original relative abundances, and, even after correcting for live and dead sample sizes, contain a significant tail of rare, dead-only species. Paleontologists and taphonomists generally conceive of this excess richness as accruing during time averaging and thus occupying the tail of the shell-age distribution: the more time averaged the assemblage, the greater its potential richness (including ecological relicts) and the greater the disparity with the richness of any single census of the live community.

However, if each cohort of dead shells (i.e., the dead shells added to the sedimentary system in a unit time) undergoes exponential decay, then the subset of shells surviving into each successive interval should contain fewer and fewer of the initially rare species. That is, rare species (or, more precisely, species that for whatever reason contribute few dead shells per unit time) should be preferentially lost, not preferentially accumulated, through random (proportional) sampling of survivors over the course of time averaging (solid lines in Fig. 2). How, then, can time averaging yield a long tail of rare, dead-only species?

One possible explanation is that taphonomic half-lives are neither uniform nor random among species, but vary inversely with species' initial abundance. If rare taxa as a group have longer half-lives than abundant taxa, then rare taxa would persist despite their initially low numbers of individuals, and would become disproportionately abundant within the tail of the shell-age distribution (dashed lines in Fig. 2; the analogy is to a rock containing two radiogenic isotopes of different initial concentrations and half-lives). Because new cohorts of dead shells, dominated by abundant taxa, are continually added to the death assemblage during the period of time averaging, the initially rare species would remain rare in the total death assemblage even though they persist for longer periods of time (compare areas under curves).

An inverse relationship between abundance (productivity) and postmortem half-life is ecologically and taphonomically plausible for mollusks. The most abundant species in any quantitatively sampled community tend to be larvae and early juveniles (if mesh size is fine enough) or, among adults, small-bodied opportunists and other com-
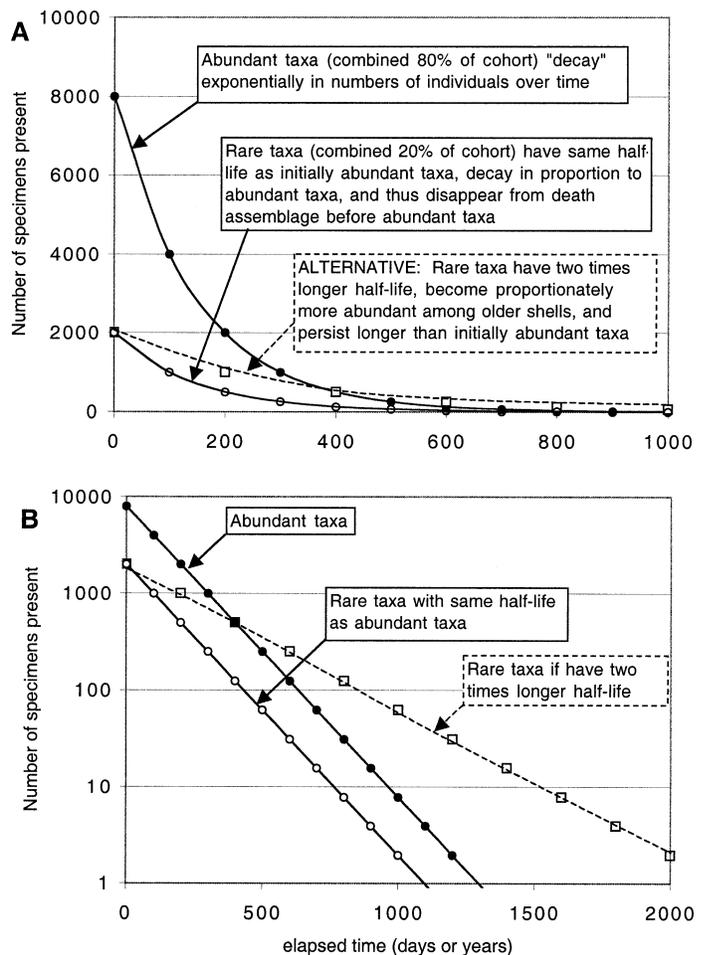

Figure 2. Time averaging is not sufficient to generate death assemblage with long tail of dead-only species, even if composition of rare species varies over time, unless taxa that are initially rare (here constituting 20% of newly generated dead individuals) have significantly longer taphonomic half-lives than taxa that are initially abundant (together constituting 80% of dead individuals). A: Rare taxa (open circles) are reduced to fewer than one individual sooner than abundant taxa (solid circles) if both sets of taxa have same half-life, whereas rare taxa could persist and thus permit death assemblage to accrue richness if they had longer half-lives (open squares, dashed line). For larval and early juvenile molluscan specimens, half-lives are measured in months (x-axis in days); for adult specimens, half-lives are hundreds of years. B: Log-linear plot of same information.

paratively short-lived organisms. By virtue of their small, thin, and/or rapidly made shells, individuals of these numerically abundant taxa can be expected to have lower preservation potential than larger bodied— and always numerically rarer—shells in the same assemblage (and see discussion by Cummins et al., 1986; Powell et al., 1992; Kidwell and Flessa, 1995).

Taphonomic half-lives thus might vary with species' original abundances (shell-production rates) not because of abundance per se, but because abundance is linked to maximum adult body size and/or typical ontogenetic stage at death. This postulated variation does not negate other potential sources of variation (e.g., shell-mineral composition, mechanical robustness, life habit, environment). This effect is utterly testable, albeit with great labor, either (1) by direct dating of death assemblages (is the median shell age for the set of rare taxa significantly greater than that for abundant taxa?), or (2) by determining body size and other key attributes for species in the live-dead data sets used here (ongoing analysis; do rare taxa have on average higher expected preservation potential than abundant taxa?). The implication

of this line of reasoning, however, is that time averaging alone is probably not sufficient to generate excess dead richness: in a simple model of steady shell input, species accrual should require a bias toward longer taphonomic half-lives among ecologically rare taxa.

RICHNESS VERSUS ABUNDANCE: THE OVERALL PICTURE

Excess species richness in a molluscan assemblage can derive from many sources. Rare dead-only species might, on the one hand, be the ghosts of earlier cohorts in which these species were abundant (i.e., earlier community states were dominated by species different from those of today; dead-only species are relicts), or, at the other age extreme, comprise recently dead shells produced by rare settlement events during the most recent phase of time averaging (the last several hundred years; i.e., rare dead-only shells might not preferentially occupy the tail of the shell-age distribution, because even a few hundred years would permit many rare settlement events not captured by a single live census). In addition, some dead-only species are true exotics, which may consist of recently dead to old shells in any abundance. Given the new finding here that the sample-size–standardized richness of a death assemblage is on average only ~25% above that achieved in a single census of the local living community, these "conventional" sources of dead-only species might be perfectly adequate, without recourse to the abundance-linked variation in taphonomic half-lives postulated here. Studies such as this metaanalysis (but also including field-based calibrations of shell age, structure, etc.) should be useful both in identifying potential variables and in setting increasingly realistic boundary conditions for next-generation modeling of death-assemblage genesis.

Paleobiologically, the key implication of molluscan live-dead studies is that, at the scale of individual death assemblages (bed-scale collections) and contrary to expectations, species abundance data are taphonomically far less complex and ambiguous than species richness. The palimpsest nature of dead-species richness is not new here: the image of multiple shell sources contributing material, and multiple agents acting to destroy it, over ecologically or geologically long periods pervades the paleontologic literature. Such time-averaged richness data would be disadvantageous for some studies, but not for others. On the other hand, high fidelity and high temporal acuity data on species' relative abundance would be an immense advantage to any number of paleobiological applications.

Richness and abundance data thus present fundamentally different taphonomic qualities to the paleobiologist. The factors that cause these differences—rapid postmortem fading of dead cohorts, higher mortality rates of very young individuals and of species with rapid population turnover, lower preservation potential of young and/or small individuals, and abundant species (in a single census) characterized on average by small body sizes and/or rapid population turnover—should not be unique to shelled marine mollusks. Thus these findings may well find application among other environments and groups.

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