

## The preservational fidelity of evenness in molluscan death assemblages

Thomas D. Olszewski and Susan M. Kidwell

**Abstract.**—The richness (number of species) and evenness (uniformity of species abundances) of death assemblages can differ from corresponding living communities due to processes such as between-habitat transport, environmental condensation, and differential taphonomic destruction. Analysis of 132 single-census live-dead comparisons of benthic molluscs from a variety of soft-bottom marine settings indicates that *on average* evenness does not differ greatly between live and dead assemblages, regardless of the particular depositional setting or grain size of associated sediment. However, *individual* death assemblages can deviate quite substantially from their corresponding living assemblages, especially if processed using a fine mesh. In addition, death assemblages collected using sieves with 2 mm mesh or coarser showed consistently and significantly greater evenness than corresponding living assemblages. These results are encouraging for broad-scale assessments of evenness in the fossil record based on the comparison of *average* values (rather than for individual assemblages) and where *trends* in evenness are the aim of the study.

Our live-dead comparisons of richness sample-size corrected by rarefaction revealed that death assemblages were on average ~1.45 times richer than the corresponding living assemblages regardless of rarefied size. In 63.6% of death assemblages both dead richness and dead evenness were greater than live, suggesting sufficient time-averaging to catch significant random or directional changes in the living community and/or introduction of individuals from outside the sampled habitat. In 12.9% of collections both dead richness and dead evenness were less than live, suggesting either rapid loss of dead shells so that dead diversity is depressed below the local living community or selective loss of taphonomically vulnerable taxa. In 18.2% of data sets dead richness was elevated but dead evenness was depressed relative to live: these are interpreted to reflect the addition of low-evenness allochthonous material. The remaining 4.5% of data sets had elevated dead evenness but depressed dead richness, suggesting that live and dead in this case may not be closely related.

In seven available time series, temporal volatility in living communities over 6–24 months was considerable but could not account for observed (mostly higher) evenness values in corresponding death assemblages, whose evenness and composition were quite stable in the few examined studies. A densely sampled spatial transect shows that changes in living-assemblage evenness along an environmental gradient were preserved in the corresponding death assemblages, although dead evenness at any location on the gradient was substantially higher than living evenness.

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### Introduction

Taxonomic diversity is of fundamental interest to both ecologists and paleoecologists because it is interpreted to reflect how organisms in communities respond to their physical environment, divide available resources, interact with one another, and are distributed on ecological landscapes (MacArthur 1972; Tilman 1982, 2004; Magurran 1988, 2004; Dodd and Stanton 1990; Ricklefs and Schluter 1993; Rosenzweig 1995; Clarke and Warwick 2001; Hubbell 2001; Connolly et al. 2005; Holyoak et al. 2005). Paleontologists are particu-

larly interested in the state of past communities and how they have changed through time (e.g., Bambach 1977; Sepkoski 1988; Powell and Kowalewski 2002; Peters 2004; Bush and Bambach 2004), so understanding the preservation of diversity in the fossil record is critical to rigorous investigation of its nature and history. Because fossil assemblages are unlikely to be more reliable than their precursor death assemblages, better understanding of the reasons for the differences between live and dead diversity in modern environments is fundamental for accurate interpretation of paleocommunities. In addition to insight into di-

versity in the distant past, present-day death assemblages can also provide valuable information about recent changes in modern ecosystems (e.g., Powell et al. 1982; Kidwell 2001; Kowalewski 2001; Warwick and Light 2002; Warwick and Turk 2002; National Research Council 2005).

Comparison of modern living and death assemblages has a long history in paleontology, but individual case studies in the past have used different methods and focused on different aspects of communities, making it difficult to compare results or make generalizations. In order to establish a common basis for comparison, Kidwell (2001, 2002a,b) undertook a meta-analysis of original data from a compilation of older marine molluscan studies. She found that rank proportions of live molluscan species in single censuses from soft-sediment marine environments were generally preserved in death assemblages. In addition, she found that death assemblages generally had a surplus of species relative to their corresponding living assemblages, even when sample size was taken into account (Kidwell 2002a). In other words, as a general pattern, richness was altered in death assemblages despite the preservation of community abundance structure.

As has long been recognized, death assemblages are the complex product of time-averaging, spatial mixing, and taphonomic alteration (e.g., Johnson 1960, 1965, 1972; Walker and Bambach 1971; Fürsich and Aberhan 1990). Therefore, the first aim of this paper is simply to assess the fidelity of diversity, in particular, the evenness of death assemblages relative to their corresponding living assemblages. The second aim is to lay out the expected effect of various processes on death assemblages and use an enlarged version of Kidwell's (2001) database of live-dead studies to learn which of these processes may be dominant under different conditions. Although most assemblages in Kidwell's database are based on a one-time sampling of live and dead individuals in a habitat, a handful include temporal and spatial series of live and dead data. The third aim of this paper is to use this subset of studies as the basis for an initial assessment of the effects of spatial and temporal

variability in living communities on the diversity of death assemblages as they accumulate.

### Preservational Fidelity of Evenness Based on Single-Census Samples

A complete quantitative description of diversity requires knowing the abundances of all taxa, which are typically depicted as species abundance distributions, rank-abundance curves, and rarefaction lines (Tokeshi 1993; Magurran 2004). More commonly, complex abundance data are summarized as a single number or diversity index (e.g., Washington 1984; Magurran 1988, 2004; Smith and Wilson 1996; Hayek and Buzas 1997; Hubálek 2000; Clarke and Warwick 2001; Buzas and Hayek 2005). This is analogous to using the mean, variance, skewness, or kurtosis to describe a statistical distribution—each statistic describes a particular aspect of the data, making it easier to understand, but at the cost of a complete depiction. Two of the most common diversity statistics are richness (the number of taxa) and evenness (the uniformity of taxonomic abundances). We will return to a consideration of richness in death assemblages, but our aim in this section is to assess the preservational fidelity of evenness.

*Measurement of Evenness.*—In this paper, we use the Probability of Interspecific Encounter ( $PIE = [N/(N - 1)](1 - \sum_{i=1}^S p_i^2)$ ), where  $N$  = sample size,  $S$  = sample richness,  $p_i$  = proportion of species  $i$ ; Simpson 1949; Hurlbert 1971; Lande 1996) as the measure of evenness. PIE has several desirable properties for live-dead comparisons. First, like richness, PIE is additive—i.e., its value for a pooled set of samples equals or exceeds the average value of the individual samples (Lande 1996; Veech et al. 2002; Gering et al. 2003; Crist et al. 2003; Patzkowsky and Holland 2005; Layou and Holland 2005). The difference between the average PIE value of individual samples and the PIE value when the samples are pooled is due to nonrandom differences in taxonomic composition among the samples. Because spatial mixing, time-averaging, and taxon-specific differences in mortality and rate of taphonomic loss can alter the relative proportions of living species as they are pooled in a dead sam-

ple, the difference in PIE between corresponding live and dead samples provides a means of quantitatively assessing the effects of these processes on the preservation of evenness.

Second, PIE also has the benefit of equalizing the slope of the steepest segment of a rarefaction curve, which depicts richness as a function of number of individuals. This allows PIE to be visualized graphically and related directly to richness (Nei and Roychaudhury 1973; Gotelli and Graves 1996; Olszewski 2004).

Lastly, as implied by the relationship with rarefaction, the *accuracy* of PIE is unbiased by sample size, allowing direct comparison of live and dead evenness without the need for sample size correction (Gotelli and Graves 1996). Note that the *precision* of PIE, like that of all statistical measurements, remains a function of sample size, and this can introduce a large degree of uncertainty when comparing small samples.

One of the limitations of PIE is that it estimates the evenness of a statistical community that is implicitly assumed to be of infinite size and can therefore include an infinite number of infinitesimally rare species (i.e., species whose  $p_i$  values are best approximated as 0.00). However, because real samples are finite by definition, their rarest species cannot have  $p_i$  values less than  $1/N$ . This limits the maximum value that PIE can take for a sample of given size and richness ( $\max(\text{PIE}) = [N/(N-1)][(S-1)/S]$ ; Hurlbert 1971; Olszewski 2004), a phenomenon referred to here as *maximum value truncation*. For example, if a sample with  $N = 50$  contains only a small number of species, say  $S = 2$ , then the abundance of both species would have to be equal for the sample to be as even as it possibly could. However, the calculated PIE value of such a sample is only 0.51 rather than the maximum theoretical PIE value of 1.00. Judging from this sample, the actual community being sampled is clearly dominated by only two species, even though it may contain many more that are much rarer—i.e., the sampled community is very unlikely to have a high evenness. A truly even community (one in which individuals are distributed at nearly the same abundance among many species) would be expected to show

many more than two species in a sample of 50 specimens. Attempts to correct this perceived problem (Hurlbert 1971; Peters 2004) result in metrics that are sensitive to sample size and violate additive partitioning (Olszewski 2004).

*Database.*—In order to recognize general patterns in benthic marine community preservation, Kidwell (2001, 2002a,b) previously compiled a database of 19 published and archived records (e.g., theses, government reports) that include both live and dead numerical abundance data for molluscan species from a wide variety of places and environments (85 habitat-level data sets). The database used here expands the earlier version to include 32 studies, yielding 132 habitat-level data sets. (Four of the 19 previously used studies have been excluded here because they represent numerical data digitized from spindle diagrams, which were adequate for presence-absence and rank-order analyses but not for calculations of evenness.)

The 32 studies provide information on 45 different areas worldwide (latitudes ranging from  $0^\circ$  to  $56^\circ\text{N}$ ). All are based on sieved, quantitative samples of soft-sediment seafloors (usually acquired using Petersen grabs or hand-trenched volumes and various mesh sizes from 0.3 to 5 mm), with sediments ranging in grain size from mud to gravel (lithic and shell). Environments ranged from supratidal marsh to outer shelf; no reefs or hardgrounds were included. For each study area (e.g., Mugu Lagoon [Warme 1969]), raw live and dead data from individual samples were pooled into habitat-level data sets based on features like those used to define lithofacies in the stratigraphic record—e.g., grain size, sedimentary bedforms. In many instances, these groupings of samples diverged from those of the original authors, who were more likely to cluster samples on the basis of biological content and then compare them to the sedimentary matrix. This step provided more-complete estimates of the living species pool in a habitat than individual samples would have, and it helped to mitigate stochastic differences due to the small size of many individual samples. Although combining individual samples from distinct patches could have influenced evenness, we found no relationship between

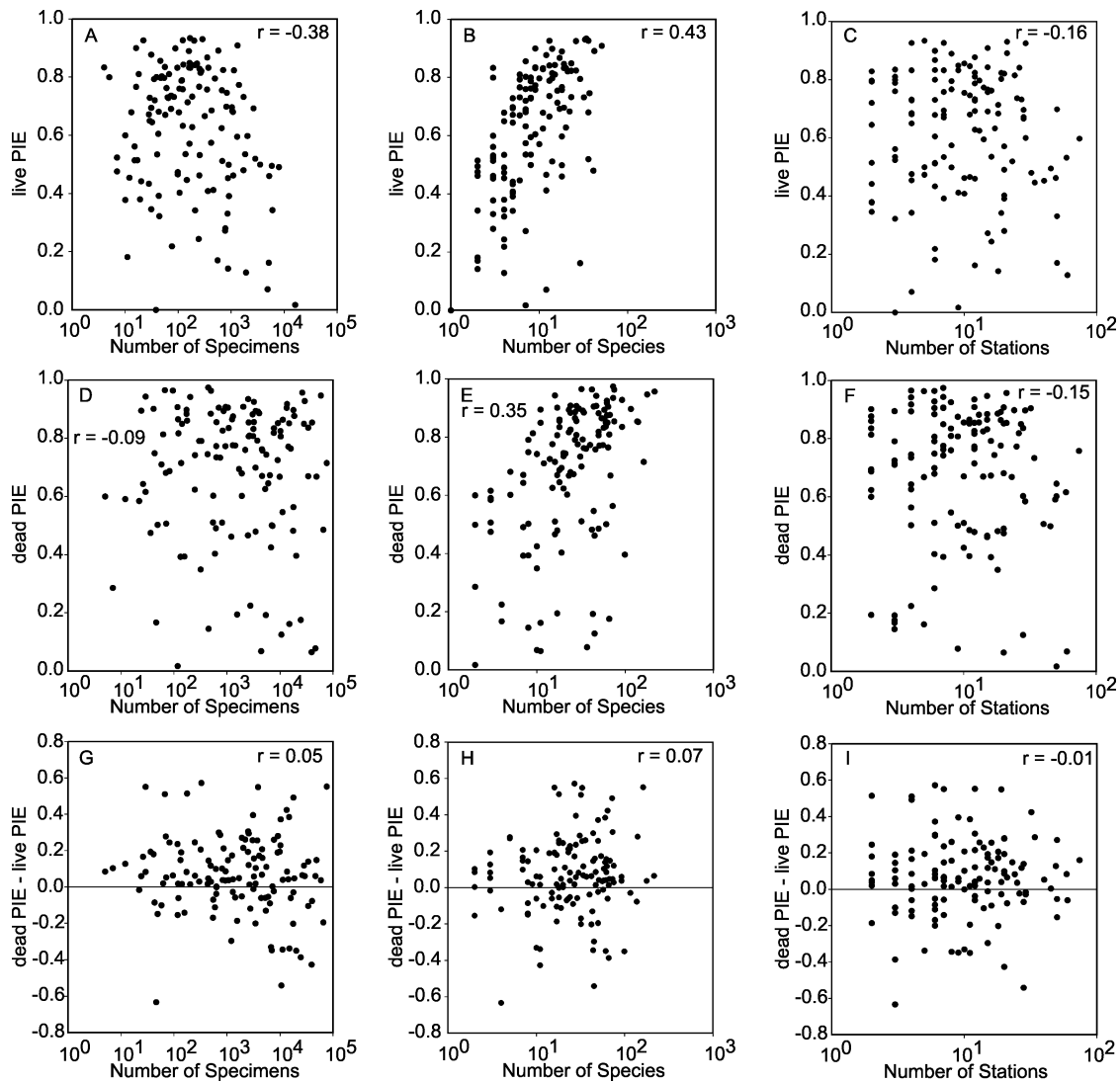


FIGURE 1. The relationship of live PIE, dead PIE, and  $\Delta$ PIE with various sample properties based on 132 molluscan data sets. Top row depicts the relationship between live evenness and live sample size (A), live richness (B), and number of stations per single census (C). Middle row depicts the relationship between dead evenness and dead sample size (D), dead richness (E), and number of stations per single census (F). Bottom row depicts the relationship between  $\Delta$ PIE (dead PIE - live PIE) and dead sample size (G), dead richness (H), and number of stations per single census (I). Number of data sets is 132, so  $r_{0.01} = 0.228$  and  $r_{0.05} = 0.174$ . None of the  $\Delta$ PIE correlations are significant; significant correlations of live and dead PIE and number of species (B and E) reflect the maximum value truncation of PIE in low-richness samples (see text for further explanation). Negative correlations between live and dead PIE and number of collections (C and F) are opposite to expectation if samples from individual stations that were pooled into composite samples differed significantly in composition, in which case evenness would be expected to increase with number of stations.

both live or dead PIE and the number of individual sampling stations combined (Fig. 1).

For every habitat-level data set, information was recorded on live and dead sample sizes, live and dead richnesses, depositional setting, mesh size used to process the collection, and sediment grain size (including a category for

seagrass meadows, which can significantly alter sediment cohesion and epifaunal attachment).

Live and dead data usually reflect only a single census or collecting visit to the area by the original author. Several studies in the database, however, record multi-season time se-

TABLE 1. Difference in evenness and log of rarefied richness between live and dead single-census data.  $\Delta\text{PIE} = \text{dead PIE} - \text{live PIE}$ ;  $\Delta S = \log(\text{rarefied dead } S) - \log(\text{rarefied live } S)$ . Values in parentheses exclude a coarse-mesh outlier (Tanabe et al. 1986; see text for further explanation).

|                                  | No. of data sets | Min.          | Max. | Median      | Mean        | SE            |
|----------------------------------|------------------|---------------|------|-------------|-------------|---------------|
| $\Delta\text{PIE}$ all data sets | 132              | -0.63         | 0.57 | 0.061       | 0.066       | 0.019         |
| $\Delta\text{PIE}$ fine-mesh     | 104              | -0.63         | 0.57 | 0.038       | 0.030       | 0.020         |
| $\Delta\text{PIE}$ coarse-mesh   | 28               | -0.33 (0.038) | 0.55 | 0.16 (0.18) | 0.20 (0.22) | 0.034 (0.029) |
| $\Delta S$ all data sets         | 132              | -0.61         | 0.74 | 0.17        | 0.16        | 0.020         |
| $\Delta S$ fine-mesh             | 104              | -0.61         | 0.70 | 0.14        | 0.13        | 0.022         |
| $\Delta S$ coarse-mesh           | 28               | -0.29 (0.08)  | 0.74 | c0.24       | 0.28 (0.30) | 0.036 (0.031) |

ries of the living community. The multi-census data sets are represented in the single-census analyses by only one live-dead comparison value based on the single census in the series with the maximum number of live individuals.

The 32 studies yielded 132 habitat-level, single-census data sets ranging in size from 4 to 16,109 live individuals and from 5 to 75,839 dead individuals per data set (medians of 160 and 1896, respectively). In species richness, they range up to 51 live and 215 dead taxa (medians of 8 and 27), and in number of stations per data set, they range from 2 to 74 (median of 10). In the vast majority of data sets, the number of dead individuals is larger than the number of live individuals: ratios of dead to live individuals vary from 0.047 to 1637 with a median of 8.83. Of these, marsh and tidal creek data sets have a median dead to live ratio of  $\sim 1.2$ , whereas data sets from intertidal settings, subtidal coastal embayments, and subtidal open shelves all exhibit a median ratio of  $\sim 10$ . (The nearly equivalent numbers of live and dead individuals, and the unusually high average live-dead agreement in species richness, rank abundance, and other metrics in marsh and tidal creek data sets, implies much faster postmortem loss rates—i.e., more snapshot-like in terms of time-averaging—than in other environments [Kidwell 2001, 2002a].)

*How Well Does Death Assemblage Evenness Match a Single Census of the Living Assemblage?*—Taphonomic fidelity of evenness is measured here as the difference ( $\Delta\text{PIE}$ ) between the evenness value of a death assemblage (dead PIE) and that of the corresponding living assemblage (live PIE). Zero differ-

ence indicates that live and dead yield identical evenness values, positive differences (up to +1) indicate that the sampled death assemblage is more even than the corresponding living assemblage, and negative differences (down to -1) indicate that the death assemblage is less even than the corresponding living assemblage.

Death assemblages are on average significantly more even than their associated living assemblages but the offset is very slight in absolute terms, as indicated by the mean  $\Delta\text{PIE}$  value of  $0.066 \pm 0.037$  (Table 1; 95% confidence interval calculated using standard error; median  $\Delta\text{PIE} = 0.061$ ). Live and dead PIE values are not sensitive to the total number of individuals or the number of physical stations incorporated into an individual data set, but at low species richness ( $S < 10$ ), both show the effects of maximum value truncation (Fig. 1). Despite its small mean value,  $\Delta\text{PIE}$  ranges widely from -0.63 to 0.57 (Table 1) and the variance among individual data sets in the database is very large ( $SD = 0.35$ ). Like live and dead PIE values,  $\Delta\text{PIE}$  is not sensitive to sample size, richness, or number of physical stations incorporated into each data set (Fig. 1). Therefore, although average live-dead agreement is very good, with death assemblages tending to be only slightly more even than their corresponding living assemblages, the evenness of any *particular* death assemblage can be quite different from a single census of the corresponding living community, although the postmortem change in any particular death assemblage is *on average* more likely to be slightly positive than negative.

Excluding data sets having either low live or low dead richness in order to account for max-

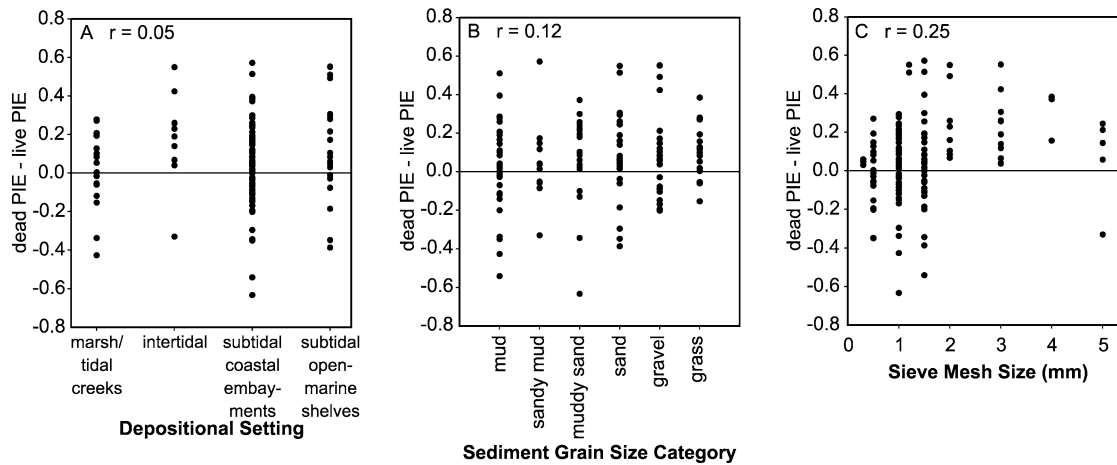


FIGURE 2. Live-dead differences in evenness ( $\Delta$ PIE) do not vary as a function of depositional setting (A) or sediment grain size (B), but are sensitive to the mesh size used to process samples (C). Number of data sets is 132, so  $r_{0.01} = 0.228$  and  $r_{0.05} = 0.174$ .

imum value truncation seen in live PIE and dead PIE has no substantial effect on the  $\Delta$ PIE results (Fig. 1): If only the 21 data sets having live  $S \geq 20$  are used, mean and median  $\Delta$ PIE are 0.037 and 0.040 respectively, and the total range is  $-0.35$  to  $0.55$  ( $SD = 0.21$ ); if only the 55 data sets having live  $S \geq 10$  are used, corresponding values are 0.044, 0.040, and  $-0.54$  to  $0.55$  ( $SD = 0.22$ ).

Despite the excellent average correspondence between live and dead PIE on average, the large observed variance in  $\Delta$ PIE indicates that measurement of evenness for any individual molluscan death assemblage may be unreliable unless the sources of variance can be identified. Factors related to sampling intensity—i.e., live and dead sample size, richness, and number of physical stations—show no significant correlation with  $\Delta$ PIE in the total database (Fig. 1). Environmental factors—i.e., depositional setting and sediment grain size—also do not significantly influence  $\Delta$ PIE (Fig. 2A,B; intertidal data sets appear to have higher  $\Delta$ PIE, but these are exclusively coarse-mesh studies; see below).

In contrast, mesh size (Fig. 2C) does yield a significant pattern, as also found in studies of live-dead agreement in rank abundance and taxonomic composition (Kidwell 2001, 2002b; Kowalewski and Hoffmeister 2003). For data sets collected using mesh of 2 mm or larger,  $\Delta$ PIE varies between 0.038 and 0.55 (not in-

cluding an outlier with  $\Delta$ PIE =  $-0.33$ ) with a mean value of 0.22 (mean  $\Delta$ PIE including the outlier equals 0.20). (The outlier is from an intertidal area subject to intense clam-digging [Tanabe et al. 1986], which biases against living specimens of dominant species, thereby raising live PIE above dead PIE.) This contrasts with finer-mesh data sets, which range from  $-0.63$  to  $0.57$  but have a mean  $\Delta$ PIE of 0.03 (Table 1). A  $t$ -test of the means (including the coarse-mesh outlier) confirms the obvious difference in  $\Delta$ PIE between coarse- and fine-mesh data sets (coarse mean = 0.20, coarse  $n = 28$ ; fine mean = 0.030, fine  $n = 104$ ;  $t = -3.97$ ,  $t_{\alpha=0.05} = 1.98$ ). An  $F$ -test indicates that the variances of coarse- and fine-mesh  $\Delta$ PIE values are not significantly different (fine variance = 0.043, coarse variance = 0.033;  $F = 1.302$ ,  $F_{(103,27),\alpha=0.05} = 1.74$ ). Rerunning the  $F$ -test without the coarse-mesh outlier, however, does result in a significant difference (coarse variance without outlier = 0.023;  $F = 1.836$ ,  $F_{(103,26),\alpha=0.05} = 1.76$ ). Overall, these results suggest that, given a reasonable number of sampled assemblages, (1) fine-mesh death assemblages show little offset in PIE from corresponding living assemblages on average but with very large variance, whereas (2) dead data generated using coarse mesh consistently overestimate live PIE by an average amount of about 0.2.

To explore the possibility that the influence

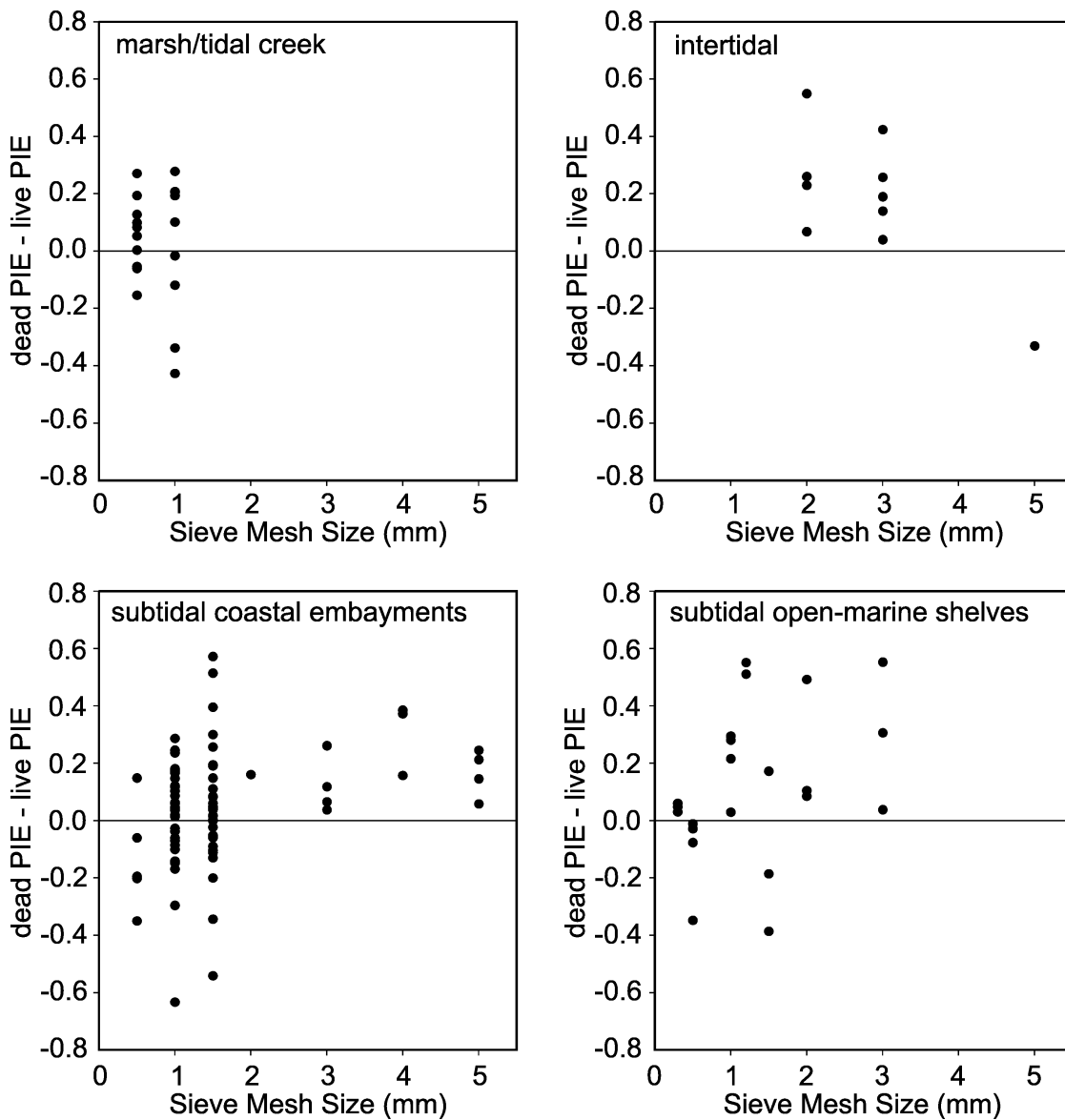


FIGURE 3. Live-dead differences in evenness ( $\Delta$ PIE) among depositional settings as a function of mesh size. The mesh size effect on  $\Delta$ PIE is apparently not limited to any single environment; also, bias does not vary among environments once mesh size is controlled.

of environmental factors on  $\Delta$ PIE would be apparent if mesh size effects were accounted for, Figure 3 shows the mesh size plot of Figure 2C broken down by depositional setting. Because marsh/tidal creek and intertidal settings were not sampled with the full range of sieve sizes in the database (the former limited to fine-mesh data and the latter to coarse-mesh data), it is not possible to confirm the relationship between mesh size and  $\Delta$ PIE within

these environments; however, the patterns seen in these two settings are at least consistent with (i.e., do not refute) an increase in  $\Delta$ PIE at mesh sizes  $\geq 2$  mm. The much larger number of data points from subtidal coastal embayments (estuaries, lagoons, back-reef areas, shallow bights protected by shoals) and subtidal open-marine settings (shoreface to outer shelf; stenohaline) show the increase in  $\Delta$ PIE associated with coarser mesh size that is

seen in the entire database. Overall, the data from all four depositional settings, as defined by water depth and onshore-offshore position, do not indicate that mesh size effects differ among environments, or that environments differ in  $\Delta$ PIE once mesh size is controlled for.

#### Live-Dead Differences in Diversity as Signatures of Postmortem Processes

In an earlier version of the database that included 85 habitat-level data sets, Kidwell (2002a) found that even after sample size differences were accounted for, death assemblage richness on average exceeded live community richness by  $\sim 22\%$ . More data and use of rarefied richnesses in the current analysis have not changed the fundamental finding that death assemblages are substantially richer than living assemblages. However, combining information on live-dead differences in richness with  $\Delta$ PIE provides a means of assessing the relative importance of a variety of processes that alter the diversity of death assemblages relative to their corresponding living assemblages.

*Predicted Effects of Taphonomic Processes on Death Assemblage Diversity.*—Although decades of research have shown that the formation of death assemblages is complex (e.g., Johnson 1960, 1965, 1972; Walker and Bambach 1971; Warme et al. 1976; Fürsich and Aberhan 1990), a naïve view of them as cumulative samples of a compositionally static local living community, without the input of allochthonous material or differential loss or addition of local species, provides a useful heuristic benchmark for recognizing the effects of various processes on dead diversity. Three broad categories of processes can change diversity by adding, removing, or changing the relative proportions of species: (1) *Ergodic* or *within-habitat* mixing (parautochthonous transport and within-habitat time-averaging), (2) *non-ergodic* or *out-of-habitat* mixing (allochthonous transport and environmentally condensed time-averaging), and (3) *differential addition via mortality rates* or *selective postmortem destruction* of taxa, age classes, etc. during death assemblage accumulation (Fig. 4).

*Ergodic mixing* draws individuals that co-

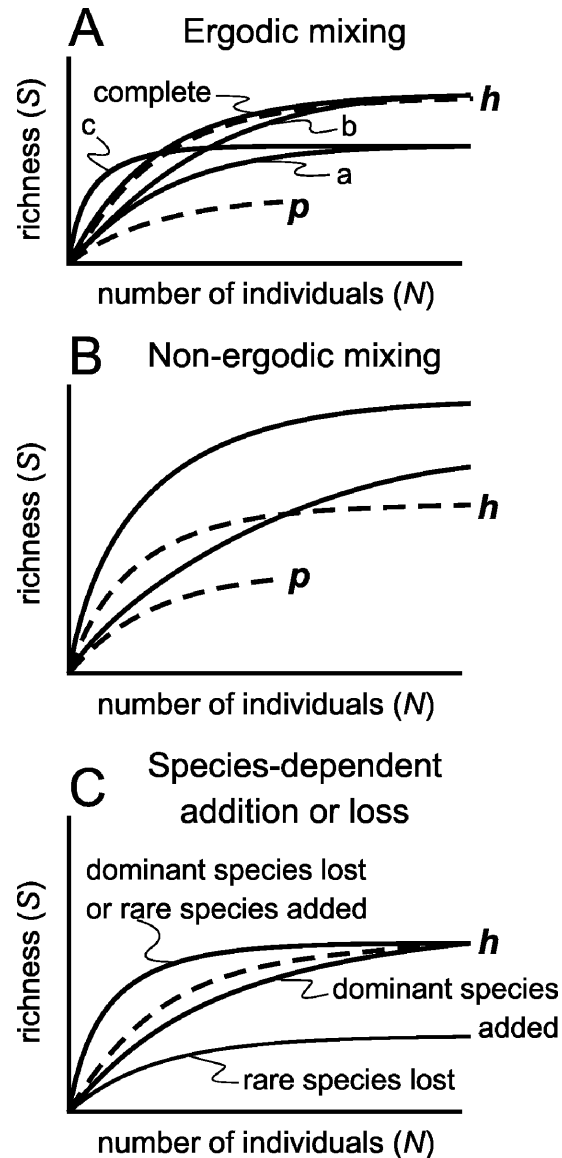


FIGURE 4. Predicted effect of various processes on death assemblage diversity. Solid line = death assemblage, dashed line = living assemblage,  $p$  = mean diversity of living community in local patches, and  $h$  = diversity of living community in entire habitat. A, Ergodic, within-habitat mixing;  $a$ ,  $b$ , and  $c$  refer to different scenarios of incomplete mixing. B, Non-ergodic mixing due to admixture of allochthonous material or of in situ communities over a period of environmental change. C, Species-selective loss or addition to death assemblage due to differential taphonomy or mortality. Rarefaction curves rise to the total richness of a patch ( $p$ ) or habitat ( $h$ ) as  $N$  approaches  $\infty$ . The initial slope of the rarefaction curves (i.e., their steepest segment) equals PIE, and so the more steeply rising curves, regardless of their terminal richness, are more even than those rising less steeply.

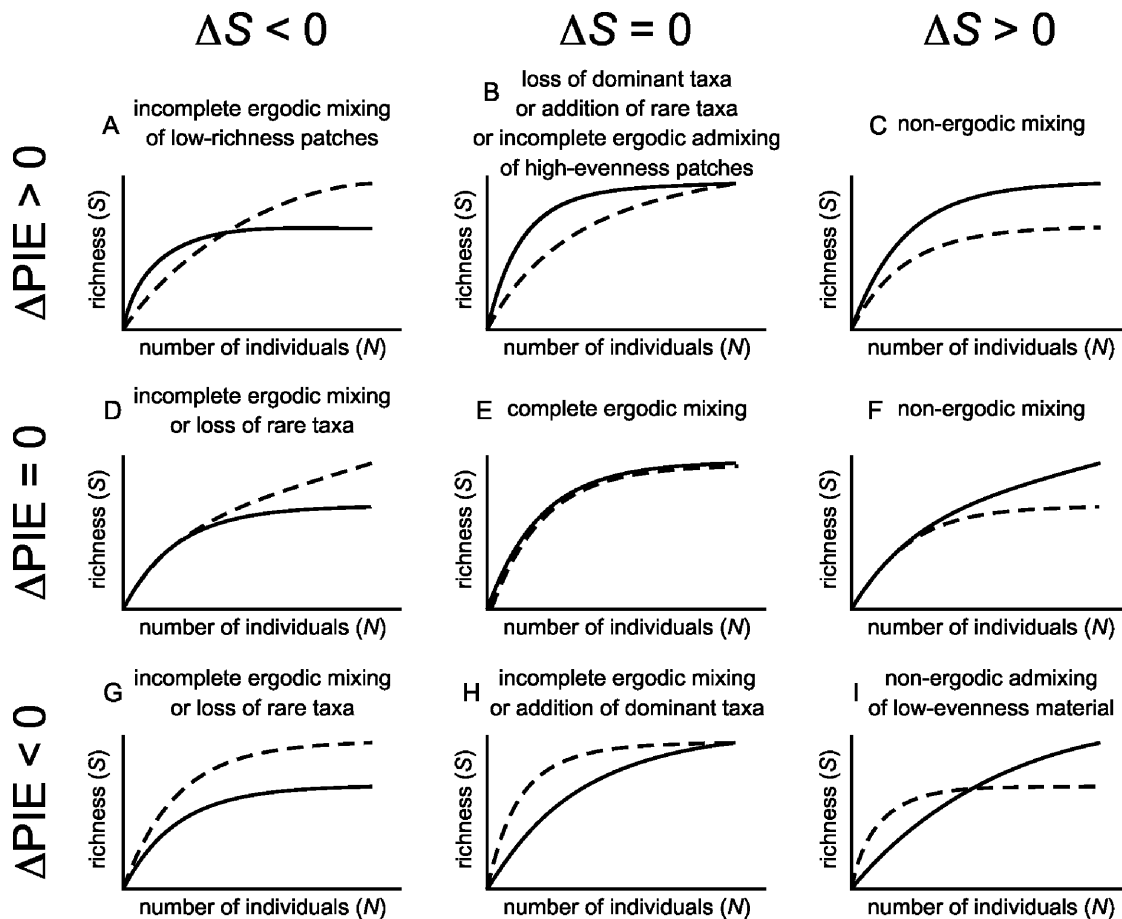


FIGURE 5. All possible combinations of diversity change from live to dead. Labels describe the action of single processes that could result in the depicted outcome. Solid line = death assemblage; dashed line = living assemblage. Living assemblages in this figure are assumed to reflect diversity of the habitat, not just a local patch or single community state. The initial slope of the rarefaction curves (i.e., their steepest segment) equals PIE, so the more steeply rising curves, regardless of their terminal richness, are more even than those rising less steeply.

existed or potentially coexisted in the same habitat into a death assemblage (within-habitat time-averaging of Kidwell and Bosence 1991). Mixing can be achieved by the migration of living populations in and out of a local patch as a death assemblage accumulates and/or by postmortem transport among patches; either way, mixing occurs strictly within a single habitat. (In this paper, the term “patch” is used for an area over which there is no significant spatial variation in community composition or structure, and “habitat” represents a set of patches that reflect similar extrinsic environmental conditions, including all the potential community states that naturally occur under given conditions [Leibold et al. 2004; Holyoak et al. 2005].)

A death assemblage resulting from *complete ergodic mixing*—i.e., proportional representation of all living patches within a habitat—produces an unbiased sample of the living community in a habitat and is therefore expected to have richness and evenness equal to that of the living habitat sampled (Figs. 4A, 5E). (Note that richness is assumed to be compared between samples of sufficient size so that both live and dead values are reasonable characterizations of the underlying live and dead species pools. Also, richness in this context is assumed to be rarefied in order to account for differences in live and dead sample size.)

*Incomplete ergodic mixing* occurs when death assemblages do not include the full variety of

living patches in proportion to their occurrence in a habitat. As a result, both richness and evenness of a death assemblage can fall below the corresponding living habitat but above that of an average living patch (scenario *a* Fig. 4A; Fig. 5G). It is possible for death assemblage richness to equal living habitat richness if all species are represented, but not in their correct proportions; in this case, death assemblage evenness is expected to remain depressed (scenario *b* in Fig. 4A; Fig. 5H). Alternatively, it is possible that a death assemblage represents a subset of patches that are all above average evenness but do not include all the species in the habitat; this situation is expected to result in depressed dead richness but elevated dead evenness (scenario *c* in Fig. 4A; Fig. 5A). Incomplete mixing can occur when within-habitat spatial mixing does not result in homogenization of dead skeletal material because transportation is non-uniform (e.g., postmortem movement down a depositional gradient) or the duration of time-averaging is insufficient for all possible states of the community living in the habitat to be fairly represented in the death assemblage. Whether complete or incomplete, ergodic mixing cannot produce a local death assemblage having richness greater than the total living richness of the habitat.

*Non-ergodic mixing* introduces species to a local death assemblage that do not or would not be expected to co-occur alive in the same habitat. These additions could be from postmortem out-of-habitat transport (introduction of allochthonous material) or environmental condensation (in situ time-averaging over a period of environmental change, leading to faunal condensation (Fürsich 1978; Kidwell and Bosence 1991]). Non-ergodic mixing is predicted to result in a death assemblage with total richness greater than that of the corresponding living assemblage in a local patch or an entire habitat (Figs. 4B, 5C, 5E, 5I). Introduction of allochthonous material is generally expected to raise evenness by adding specimens of different taxa than present in the local living assemblage and thereby increasing the uniformity of dead species abundances. Nevertheless, a large influx of low evenness ma-

terial could depress evenness in the death assemblage despite raising total richness.

The extent of mixing (which governs the degree of completeness when mixing is ergodic) in a death assemblage is limited by the duration of time-averaging, which is a reflection of the rate of postmortem loss. If loss is rapid—i.e., there is rapid *postmortem fading* of added material—then the number of successive generations, patches, and non-ergodic contributions that are likely to be mixed in a death assemblage will be reduced. This is the case regardless of the rate of sediment accumulation or depth of advective mixing of skeletal remains within the sedimentary column; the result is a death assemblage that resembles a census or snapshot assemblage (Kidwell 1998). Such death assemblages should on average be substantially more similar in terms of diversity (both richness and evenness) and composition to their local living patch (their immediate and most recent source of dead skeletal material) than to other patches in the habitat or other habitats on the broader ecological landscape. Evenness would therefore be depressed relative to the living habitat, although the large-scale richness could remain high because dead individuals of some species would survive in the death assemblage at low abundances (Figs. 4B, 5I).

The duration of time-averaging in death assemblages also influences the degree to which the population dynamics of different species in a community can influence dead relative abundances (Van Valen 1964; Vermeij and Herbert 2004). Greater duration of time-averaging should result in greater over-representation of species with high mortality rates in the death assemblage relative to the living community. This is not expected to increase total richness but could alter evenness: evenness would be decreased if dominant taxa have higher mortality rates, but would be increased if rare taxa have higher mortality rates (Figs. 4C, 5B,D,G).

Just as differences in life histories can influence dead species abundances, so can differences in intrinsic preservability (Cummins et al. 1986c; Tomašových and Rothfus 2005; Tomašových in press). If individuals of dominant species are lost at a higher rate than those of rare species, richness will be relatively un-

affected because common species are not expected to disappear entirely (they are quickly replaced). In contrast, evenness should increase because species that are very different in living abundance will appear to be more similar in death (Figs. 4C, 5B). Kidwell (2002a) postulated that excess dead richness despite the high fidelity of rank order in death assemblages could reflect the tendency for the most numerically abundant species in the living assemblage to be relatively small bodied, even as adults, making them particularly susceptible to destruction or transport out of their life habitat. Conversely, preferential loss of rare species would be expected to decrease death assemblage richness because already rare taxa would no longer be registered as present (i.e., a drop in richness) and decrease evenness by making the most abundant species appear even more dominant (Figs. 4C, 5G).

The expected effects of mixing at varying spatial and temporal scales and of variability in the life histories and preservabilities of different species on live-dead differences in both evenness and richness provide a conceptual framework that can be used to identify the likely processes influencing death assemblages in the database (Fig. 5).

*Observed Patterns of Live-Dead Diversity Differences.*—In a manner analogous to  $\Delta$ PIE, live-dead differences in richness are measured as the difference between the logarithmic values of rarefied dead and live richness:  $\Delta S = \log(\text{dead } S) - \log(\text{live } S) = \log(\text{dead } S / \text{live } S)$ . Taking the logarithm of dead and live richness values transforms  $\Delta S$  from a skewed to a symmetrical distribution, making statistics such as mean and standard deviation unbiased and more readily interpretable. Comparing richness values of different collections, unlike comparing PIE, requires rarefaction in order to account for differences in sample size. Comparisons of live and dead richness in this framework should be made on the rarefaction plateau of both samples rather than on their rising limbs: This provides a closer estimate of richness in the community being sampled and minimizes the likelihood that the live and dead rarefaction trajectories will cross with further sampling. Because the point where

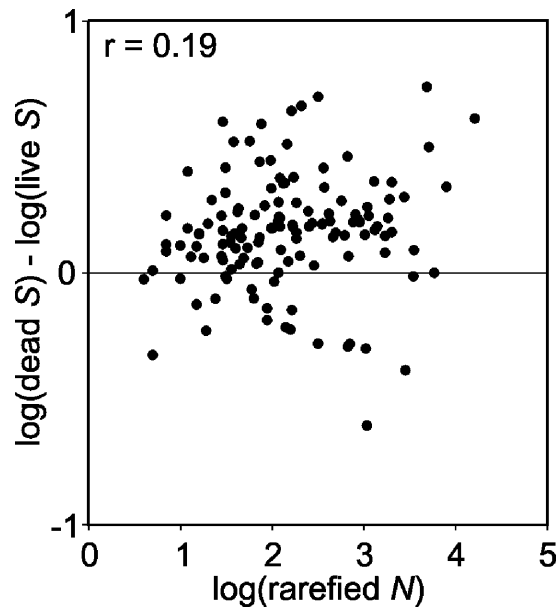


FIGURE 6. Live-dead differences in the logarithm of rarefied richness ( $\Delta S$ ) are not related to the rarefied sample size used for each comparison ( $N$ ). Richness values were rarefied to the smaller assemblage, living or dead, for any given data set. Number of data sets is 132, so  $r_{0.01} = 0.228$  and  $r_{0.05} = 0.174$ .

curves level off could be different for each live-dead comparison, each pair was rarefied to the smaller of the two (the live collection in 113 of 132 cases) rather than all data sets being rarefied to the same size.  $\Delta S$  is not correlated to rarefied sample size in the database (Fig. 6), so rarefying each live-dead pair to a different sample size should not bias interpretations. This lack of correlation also indicates that the average ratio between live and death assemblages richness does not change with sample size.

Prior to rarefaction, 120 of 132 data sets had dead richness greater than live, nine data sets had dead richness equal to live, and three had dead richness less than live. This is not surprising, given that death assemblages are larger than living assemblages in 113 of 132 data sets, usually by two to three times (minimum ratio of dead:live individuals is 0.58, maximum is 22, and median is 2.85). After rarefaction,  $\Delta S > 0$  in 108 data sets,  $\Delta S = 0$  in one, and  $\Delta S < 0$  in 23;  $\Delta S$  ranges from  $-0.61$  to  $0.74$  with a mean of  $0.16$  and a median of  $0.17$  (Table 1). According to these values, death assemblages in the database are on average 1.45 to

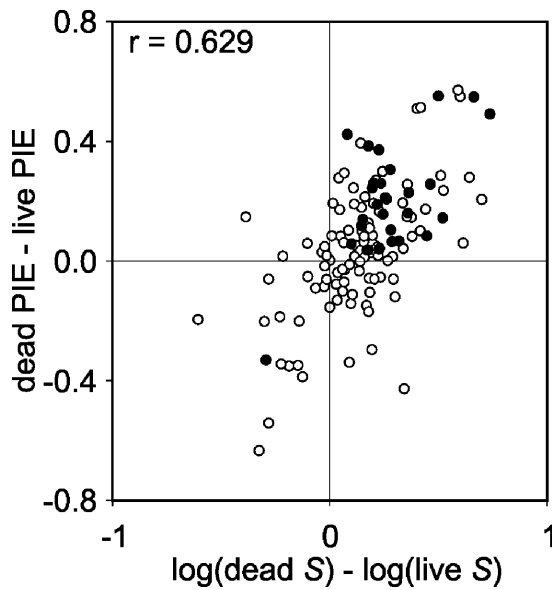


FIGURE 7. Cross-plot of live-dead differences in evenness versus richness. Compare with Figure 5 for interpretation of main processes influencing each quadrant. Richness values were rarefied to the smaller assemblage, living or dead, for any given data set. Open circles indicate collections made with mesh size  $< 2$  mm; solid circles indicate collections made with mesh size  $\geq 2$  mm. Number of data sets is 132, so  $r_{0.01} = 0.228$  and  $r_{0.05} = 0.174$ .

1.48 times richer than living assemblages at all sample sizes, although at the extremes they can be as low as 0.24 times smaller and 5.45 times larger.

Cross-plotting  $\Delta S$  against  $\Delta PIE$  (Fig. 7) allows direct comparison of these single-census live-dead data sets with the conceptual framework summarized in Figure 5. The most obvious aspect of the pattern is the strong correlation between  $\Delta S$  and  $\Delta PIE$ . However, this is not surprising given that  $\Delta PIE$  measures the difference between the slopes of live and dead rarefaction trajectories and  $\Delta S$  measures the difference between richness values rarefied to the same sample size—the steeper the initial rise, the higher the expected rarefaction trajectory. The 84 points (63.6%) in the upper right quadrant are consistent with non-ergodic mixing, indicating either time-averaging of sufficient duration to catch either temporal volatility or significant directional change in the species composition of the living community (relative to the single live censuses used in this analysis) and/or the introduction

of individuals from outside the sampled habitat, so that both richness and evenness increase in the death assemblage. The 24 points (18.2%) in the lower right quadrant are also associated with non-ergodic mixing, which is required to explain the surplus dead species, but evenness is lower in the death assemblage than the living community, suggesting extrinsic input is dominated by one or a few abundant species. The two left quadrants are consistent with incomplete ergodic mixing due to taphonomic fading of admixed material, which is required to explain the deficit of dead richness. The 17 collections (12.9%) in the lower left quadrant indicate addition of individuals from dominant taxa. The remaining six data sets (4.5%) in the upper left quadrant suggest a degree of inconsistency between the live census and the death assemblage—i.e., the death assemblage essentially reflects a different living community. (One collection has  $\Delta S = 0$  and a positive  $\Delta PIE$ , so it falls on the boundary between the upper two quadrants.) These values change little if the collections near the origin of the plot are interpreted to reflect death assemblages that are closely comparable to corresponding living assemblages in both evenness and richness: If we eliminate 17 collections that fall within a square bounded by  $-0.1$  and  $0.1$   $\Delta PIE$  and  $-0.1$  and  $0.1$   $\Delta S$ , three data sets (2.6%) occur in the upper left, 81 (70.4%) occur in the upper right, 13 (11.3%) in the lower left, and 18 (15.7%) in the lower right.

Although differences in spatial mixing and selective destruction could explain the observed pattern (Fig. 7), the consistent factor influencing the diversity of death assemblages relative to corresponding living communities from lower left to upper right is the duration of time-averaging. Short time-averaging relative to living-community variation prevents complete mixing by losing older cohorts from the death assemblage before all possible community states are fairly represented—these death assemblages are represented by the lower left quadrant. Long time-averaging allows a greater chance for the introduction of exotic taxa or for changes to occur in the composition and abundances of species inhabiting

a habitat—these death assemblages are represented by the upper right quadrant.

All but one of the 28 coarse-mesh data sets fall in the upper right quadrant (Fig. 7). Not including the previously identified outlier in the lower left quadrant (Tanabe et al. 1986), the  $\Delta S$  of data sets (Table 1) analyzed with mesh size  $\geq 2$  mm ranges from 0.08 to 0.74 with a mean of 0.30, a median of 0.24, and a standard deviation of 0.16. These high average values are consistent with higher per capita durability of large shells, thus longer effective duration of time-averaging per assemblage—i.e., less fading of mortality cohorts and greater potential for both ergodic mixing (of patches within habitats) and non-ergodic mixing (of temporal states or allochthonous shells) to be reflected by the death assemblage.

$\Delta S$  of the 104 fine-mesh data sets ( $< 2$  mm sieve size) ranges more widely but has a lower average value than the coarse-mesh samples (Table 1, Fig. 7). Again, this is consistent with the tendency for finer meshes to include shells of larvae and early juveniles from all species plus the adults of small-bodied opportunistic and parasitic or commensal species. These small-bodied individuals are prone not only to significant out-of-habitat transport but also to selective destruction and rapid cohort loss (e.g., Staff et al. 1986; Cummins et al. 1986a; Aller 1995). These same intrinsic differences in the ecological and taphonomic volatility of larval and juvenile versus adult components were postulated to explain comparable effects of mesh size on rank order of death assemblages (Kidwell 2001, 2002a,b). This result is consistent with Kowalewski's (1996) hypothesis that variation in the durability of groups, including body-size fractions, might result in different degrees of time-averaging and thus differently biased diversity in various segments of a single death assemblage. However, no live-dead data sets having species lists partitioned by size fraction are yet available in the database to test whether these different components diverge in live-dead agreement (but see Kowalewski et al. 2003 for an evaluation of live-dead agreement in rank abundance and several taphonomic metrics among size fractions  $> 2$  mm).

Examination of  $\Delta \text{PIE}$  versus  $\Delta S$  cross-plots

separated by depositional setting suggests differences in the nature of death assemblage alteration in different environments (Fig. 8). Despite the fact that marsh and tidal creek data sets are all fine mesh (Fig. 3), very few occur in the lower left quadrant and most show some degree of non-ergodic mixing (Fig. 5). All intertidal collections (except the outlier of Tanabe et al. 1986) occur in the upper right quadrant (Fig. 8), indicating extensive non-ergodic mixing. However, these were all collected using coarse mesh (Fig. 3), making generalizations about this environmental setting difficult. Most of the points in the lower left quadrant of Figure 7 are from subtidal coastal embayments (Fig. 8), suggesting that these settings are favorable for incomplete ergodic mixing. In addition to the upper right and lower left quadrants, subtidal coastal embayments are also well represented in the lower right quadrant, suggesting the influence of non-ergodic inputs of low evenness and short time-averaging. Data sets from subtidal open-marine shelves show a wide scatter (Fig. 8), although relative to subtidal coastal embayments and marsh/tidal creek settings they are poorly represented in the lower right quadrant, suggesting that their non-ergodic component has accumulated as a result of protracted time-averaging rather than a recent influx of a single or few abundant species.

#### Case Studies of Temporal and Spatial Variability

The 132 live-dead data sets analyzed above are all based on multiple sampling stations from a habitat but were only visited one time (i.e., single census). Although this approach allows assessment of how well death assemblages reflect the standing crop of a habitat at a moment in time, it does not allow variability in live and dead diversity over time or among patches to be assessed. Seven data sets from three studies provide time series and sufficiently large samples to allow the assessment of temporal variability (Table 2)—two lagoons in Texas (Staff et al. 1986), two lagoons in California (Peterson 1976, 1977), and three shell gravels from the English Channel (Carthew and Bosence 1986). A fourth study (three facies from the Amazonian shelf; Aller 1995)

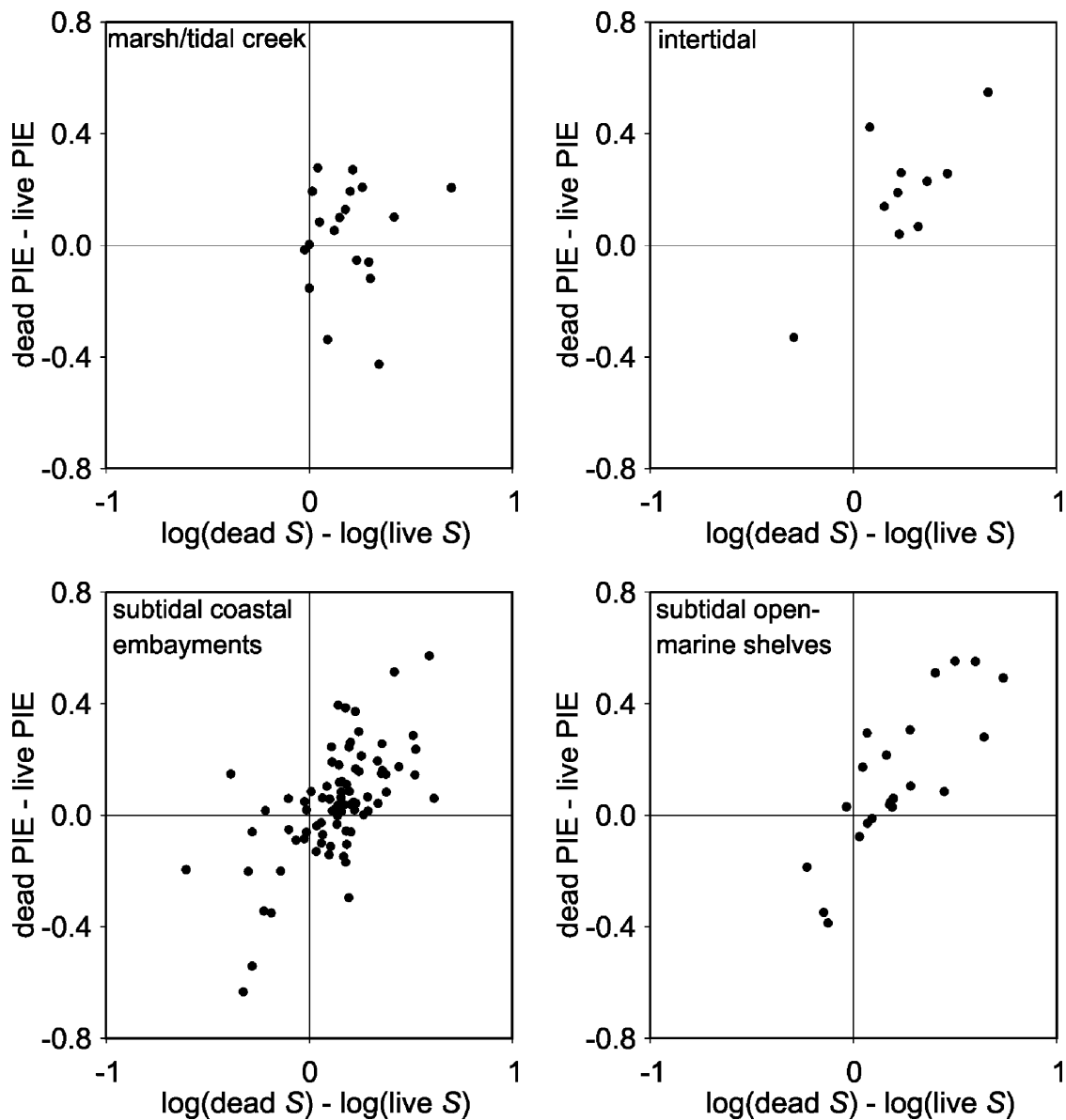


FIGURE 8. Cross-plot of live-dead differences in evenness versus rarefied richness separated by environmental setting.

with temporal replicates of the living communities is excluded here because the dead data were pooled across censuses and could not be deconvolved. A study from the Virgin Islands (Miller 1988) allows assessment of live and dead spatial variations by providing data from a closely sampled transect of an environmental gradient (Table 2). Any generalizations based on these case studies must remain provisional because of their limited number, lim-

ited duration, and limited areal coverage, but they demonstrate possible patterns and suggest profitable directions for future research.

*Time Series of Live Diversity: Sampling Temporal Variation.*—Over what period of time must a living community be repeatedly censused before the full range of temporal variation in a habitat has been captured? One way to address this issue is to use collector's curves of time series of live data. Collector's curves

TABLE 2. Evenness statistics for time series and gradient studies.  $N$  = sample size,  $S$  = sample richness,  $X$  = number of collections,  $\Sigma$ PIE = PIE of summed collections,  $\mu$ PIE = mean PIE of individual collections,  $\sigma$ PIE = standard deviation of PIE.

|  | Live |     |     |              |           |              | Dead   |     |     |              |           |              |
|--|------|-----|-----|--------------|-----------|--------------|--------|-----|-----|--------------|-----------|--------------|
|  | $N$  | $S$ | $X$ | $\Sigma$ PIE | $\mu$ PIE | $\sigma$ PIE | $N$    | $S$ | $X$ | $\Sigma$ PIE | $\mu$ PIE | $\sigma$ PIE |
| Temporal Mixing                            |      |     |     |              |           |              |        |     |     |              |           |              |
| Texas Bays (Staff et al. 1986)             |      |     |     |              |           |              |        |     |     |              |           |              |
| Copano Bay                                 | 357  | 18  | 14  | 0.619        | 0.544     | 0.236        | 18,886 | 80  | 14  | 0.889        | 0.848     | 0.087        |
| Laguna Madre                               | 381  | 27  | 14  | 0.899        | 0.793     | 0.078        | 15,905 | 61  | 14  | 0.811        | 0.796     | 0.039        |
| California Lagoons (Peterson 1976, 1977)   |      |     |     |              |           |              |        |     |     |              |           |              |
| Mugu Lagoon                                | 9617 | 27  | 7   | 0.481        | 0.473     | 0.099        | 4628   | 46  | 1   | 0.758        | —         | —            |
| Tijuana Slough                             | 3161 | 27  | 7   | 0.679        | 0.665     | 0.061        | 1162   | 37  | 1   | 0.857        | —         | —            |
| English Channel (Carthew and Bosence 1986) |      |     |     |              |           |              |        |     |     |              |           |              |
| Plymouth Sound                             | 8465 | 19  | 4   | 0.176        | 0.152     | 0.145        | 46,850 | 87  | 2   | 0.579        | 0.578     | 0.012        |
| Stoke Point                                | 226  | 16  | 4   | 0.830        | 0.783     | 0.119        | 10,586 | 67  | 2   | 0.925        | 0.911     | 0.012        |
| Eddystone                                  | 190  | 14  | 4   | 0.865        | 0.805     | 0.080        | 35,280 | 67  | 2   | 0.914        | 0.913     | 0.004        |
| Spatial Mixing                             |      |     |     |              |           |              |        |     |     |              |           |              |
| Virgin Islands (Miller 1988)               |      |     |     |              |           |              |        |     |     |              |           |              |
| Smuggler's Cove                            | 535  | 22  | 29  | 0.648        | 0.569     | 0.261        | 43,059 | 79  | 37  | 0.846        | 0.829     | 0.042        |

measure cumulative richness as each subsequent sample in a series is added in succession. Richness is considered sufficiently sampled when the progressive increase in number of species begins to slow and approach an asymptote (Hayek and Buzas 1997).

Staff and Powell (1988) applied this approach to a compilation of 30 data sets of preservable marine benthos from soft-bottom habitats around the world (shelled molluscs, brachiopods, serpulid and spirorbid worms, calcitic sponges, hard bryozoans, barnacles, and echinoids). In their cumulative plots, the rate of living richness increase began to slow after 9–22 months of sampling (6–15 consecutive samples in any series), but many of their curves still showed increase even after two or three years of sampling.

However, because each consecutively added sample in a collector's curve increases the cumulative sample size, richness is expected to increase even if the taxonomic composition of the community being sampled does not change significantly. The critical issue when using collector's curves is thus the degree to which the observed increase in richness is simply a sample-size effect as opposed to a product of change in the taxonomic composition of the community. This is the fundamental difference between collector's curves and rarefaction curves—rarefaction curves display in-

crease in richness purely as a function of increase in sample size and do not account for differences in composition among particular subsamples (Gotelli and Colwell 2001). Thanks to three interrelated properties of PIE, namely additive partitioning, lack of sample-size bias, and a direct relationship to rarefaction (Lande 1996; Veech et al. 2002; Olszewski 2004), it can be used to recognize when collector's curves are increasing as a result of changing community composition rather than simply the addition of more individuals. Addition of random subsets from a stable community is not expected to change cumulative evenness, whereas combining samples that diverge significantly in taxonomic composition is expected to do so (Fürsich and Aberhan 1990; Lande 1996; Veech et al. 2002). When additional collections no longer influence cumulative evenness, the inference is that any additional increase in richness simply reflects an increase in sample size rather than change in the taxonomic composition of the habitat being sampled.

The shortest time series in the database in terms of both temporal duration (six months) and number of points (four) come from Carthew and Bosence's study in the English Channel (1986) (Fig. 9). Each point in the three time series reflects pooling of three to four stations from within a 1 km radius sampled us-

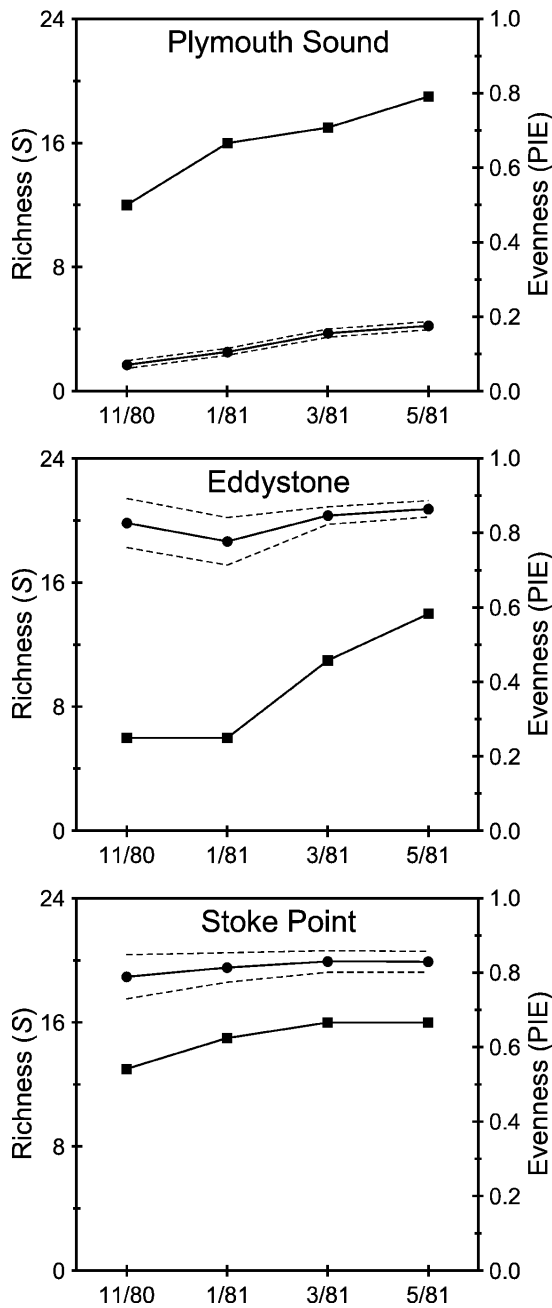


FIGURE 9. Time series of cumulative live richness (squares) and PIE (circles) from Carthew and Bosence's (1986) English Channel study areas. Dashed lines are 95% confidence intervals around PIE.

ing 2 mm mesh. At Plymouth Sound, monotonic increase in cumulative live richness over six months is accompanied by a slight but significant increase in cumulative live PIE, suggesting that the living community was chang-

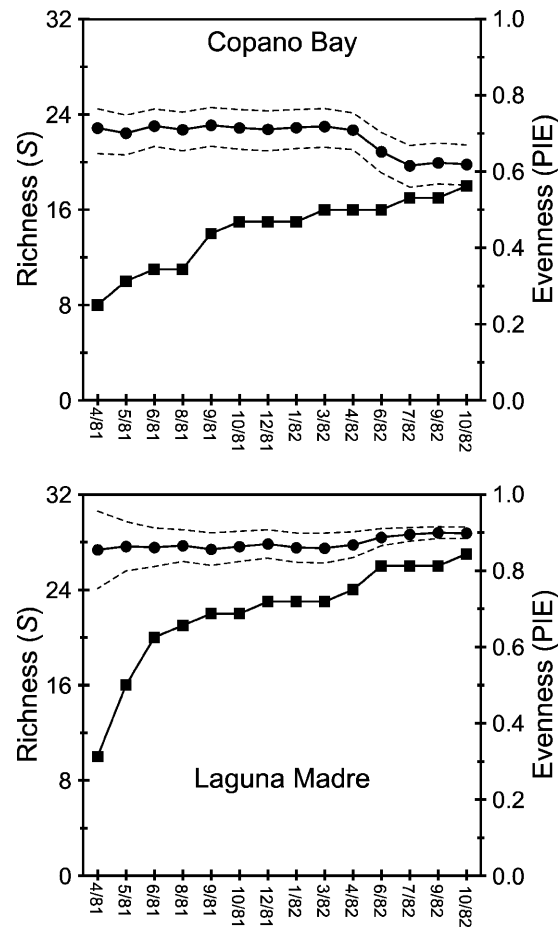


FIGURE 10. Time series of cumulative live richness (squares) and PIE (circles) from Staff et al.'s (1986) Texas bay study areas. Dashed lines are 95% confidence intervals around PIE.

ing during the period of sampling and that the full range of variation possible in the habitat was not caught in this series. The absence of significant change in cumulative live PIE at Eddystone and Stoke Point (Fig. 9) indicates little change in the living community, with cumulative increases in live richness simply due to increasing sample size.

The most densely sampled time series (14 points) come from two Texas bays sampled by Staff et al. (1986) over a period of 18 months (Fig. 10) using 0.5 mm mesh. Each census represents the combination of two sampling stations chosen randomly along a 100 m shore-parallel sampling line (Powell et al. 1982). Copano Bay shows a monotonic increase in richness with a jump between 8/81 and 9/81

(time between consecutive samples was six weeks). However, this step in richness is not accompanied by a change in evenness, implying that it reflects an artifact of sampling. A drop in cumulative live evenness in the time series between 4/82 and 7/82 reflects addition of several large samples dominated by a previously present taxon (possibly larval spat-falls of a single species), which is why richness does not change very much at this point. Laguna Madre shows a dramatic initial increase in richness, then a slowdown until there is a step up between 4/82 and 6/82. The initial richness increase is not accompanied by any significant change in evenness, but the later step is (evenness values from the first year of sampling are all below the lower 95% boundary of the last three points). This suggests that the living community changed in taxonomic composition in the spring of 1982.

The last two time series come from multiple pooled stations (several dozen sites per census) in two California lagoons sampled seven times by Peterson (1976, 1977) over two years using 2 mm mesh (Fig. 11). Mugu Lagoon shows a constantly rising cumulative live richness, and this trend apparently continued for another year (Peterson 1976: Fig. 1). Cumulative live evenness initially drops but then rises until late fall of 1970, stabilizing thereafter, suggesting that some proportion of the early rise in cumulative richness reflects a change in the living community's taxonomic composition. Tijuana Slough shows a rapid initial increase in cumulative live richness from the first to the second census, then a slow rise from late fall 1969 to early spring 1971, after which no new species were observed. Richness did not increase for the rest of Peterson's study, which lasted until early spring 1972 (Peterson 1976: Fig. 1). The initial rise in richness coincides with a significant sharp rise in evenness, indicating a change in the taxonomic composition between the first sample and the second. After peaking in late fall 1969, evenness shows a significant, progressive drop to a stable lower value, suggesting that any observed increase in richness in this interval is actually slower than would be expected for a static community that was simply being increasingly sampled (i.e., the commu-

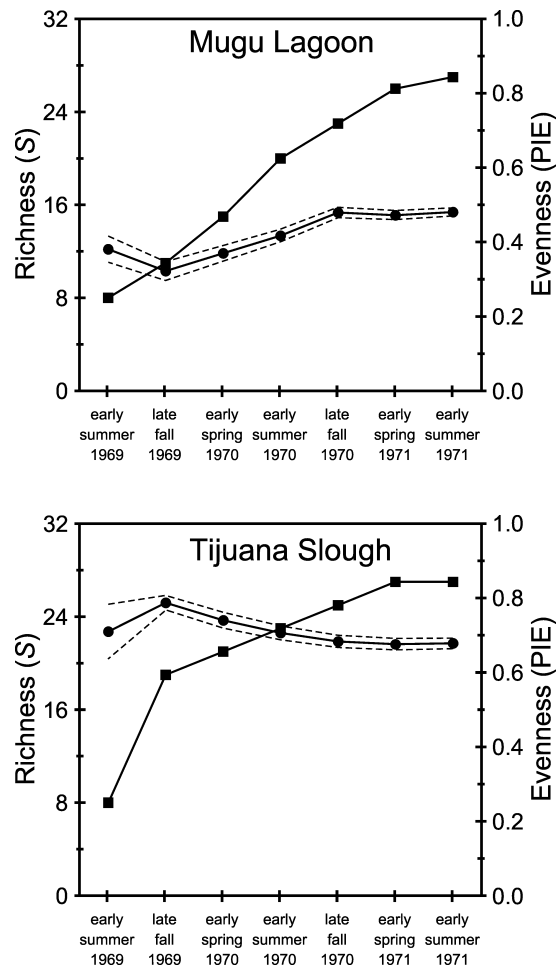


FIGURE 11. Time series of cumulative live richness (squares) and PIE (circles) from Peterson's (1976, 1977) California lagoon study areas.

nity is experiencing an increase in dominance by a species that was present initially).

These few time series of live data provide several important observations about the diversity of accumulating death assemblages. First, *cumulative* live evenness can remain quite stable for as long as a year and then change relatively suddenly, either upward or downward, as in the Texas lagoons. Alternatively, live evenness can increase or decrease continuously without showing evidence for reaching a steady state over 6 to 24 months, as in Plymouth Sound and the California lagoons. These few studies hint at the temporal scale of volatility in living communities and the degree to which it can influence the diversity of an accumulating death assemblage if

time-averaging is sufficient to incorporate such temporal change. Longer time series are needed to assess how long it takes for living communities to show their full range of variation and whether their cumulative evenness (presumably that of the habitat) ever reaches a steady state.

*Comparing Cumulative Live and Dead Diversity: Can Observed Living Variability Account for Dead Diversity?*—The single-census comparisons described earlier indicate that passive accumulation from a static living community (the naïve model) cannot generally account for diversity differences between live and dead assemblages. However, the volatility of living assemblages, even over a few years (Figs. 9–11), suggests that the large variation in  $\Delta$ PIE observed among the single-census live-dead comparisons (Figs. 2, 3) may simply reflect the state of a particular community when it was censused. Can the additional variation contributed by differences among repeated surveys of the living community explain death assemblage diversity? To answer this question, it is necessary to compare the cumulative live results to the corresponding death assemblages.

First, what can be said about the volatility of death assemblage evenness relative to live? Using the additive property of PIE, the difference between the summed evenness ( $\Sigma$ PIE) of death assemblages (i.e., the evenness of all the individual censuses pooled into a single composite sample) and the average per-census evenness ( $\mu$ PIE) reveals how much evenness is inherent in individual censuses and how much evenness in the total is due to differences among censuses (Lande 1996; Veech et al. 2002). In the five available cases from Texas lagoons and the English Channel (the California lagoons have only one dead census each), dead  $\Sigma$ PIE is greater than dead  $\mu$ PIE but never significantly so (Table 2). This suggests that compositional differences among dead samples are within the expected range of variation had they all come from a single accumulation of dead mollusc shells.

Despite the apparent stability of death assemblage evenness in these examples, cumulative live evenness mostly falls short of that of the corresponding death assemblages (Ta-

ble 2). In all cases except Laguna Madre, the evenness of individual and cumulative death assemblages is significantly higher than the cumulative live assemblage. This would require some form of temporal or spatial mixing outside the range of the samples in the available live time series, selective destruction of common live species, or differences in the mortality and life history among species. In the case of Laguna Madre, the  $\mu$ PIE values of both live and dead assemblages are virtually identical, whereas live  $\Sigma$ PIE is substantially greater than dead. The similar  $\mu$ PIE values of live and dead might suggest that the dead are snapshot assemblages, but if this were the case, live and dead  $\Sigma$ PIE values would also be expected to be similar (i.e., they would accumulate new species at the same rate). Thus, Laguna Madre appears to have a fairly stable death assemblage but not one that can be explained by the variability of the living community during the sampling period.

Although the data described here are frustratingly few, they consistently indicate that single censuses of death assemblages are random samples of a stable dead pool. The observed stability and the near equality of dead  $\Sigma$ PIE and  $\mu$ PIE are much more constrained than the corresponding variation in the estimates of live evenness. This suggests that much of the variability in  $\Delta$ PIE in the single-census database could be due to volatility in the sampled evenness of the living communities. However, combining live samples from time series of six to 24 months still does not account for the observed, stable death assemblage evenness.

*A Transect of Live and Dead Evenness: How Uniform Are Habitats?*—Determining the degree to which ergodic, within-habitat mixing can contribute to the diversity of death assemblages requires knowing the spatial variability among patches in a habitat. Although all the single-census comparisons of evenness incorporate at least two sampling stations, Miller's (1988) study of molluscs in a back-reef lagoon provides an exceptional opportunity to assess the variability of diversity along a particularly well constrained and densely sampled environmental gradient. Both living and death assemblages were sampled using a 4 mm mesh

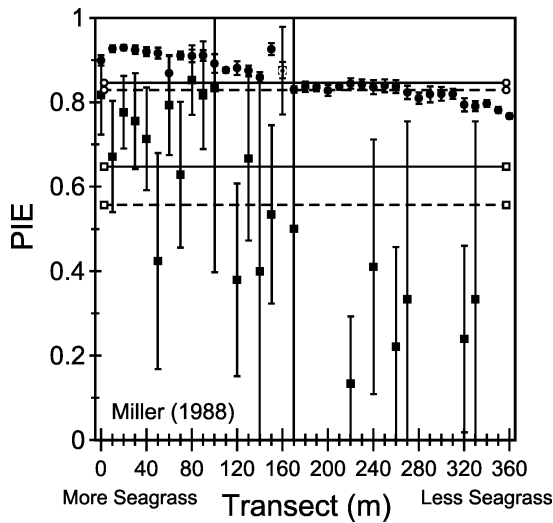


FIGURE 12. Death assemblage evenness along an environmental gradient from Miller's (1988) study of Smuggler's Cove, Virgin Islands. Note that the live evenness gradient is preserved in the dead data, although dead PIE values are consistently higher and show a smaller range than live PIE values. Circles = dead data, squares = live data, solid symbols = individual samples, dashed lines with open symbols = mean PIE ( $\mu$ PIE), and solid line with open symbols = cumulative PIE ( $\Sigma$ PIE).

every 10 m along a 360 m transect from an area of dense seagrass cover to one of sparse seagrass cover in Smuggler's Cove, U.S. Virgin Islands. Using a variety of multivariate techniques, Miller (1988) demonstrated that live faunal composition changed along this gradient and that this change was preserved in the death assemblage.

Miller's data reveal that evenness also changes along the transect: both live and dead PIE values increase with seagrass cover (Fig. 12). Consistent with his earlier findings (Miller 1988), this indicates that dead shells are not homogenized along the entire length of the transect—i.e., samples maintain some degree of faunal distinctiveness despite any postmortem transportation or past habitat shifting that may have occurred. The  $\Sigma$ PIE values of both living assemblages and death assemblages lie within the range of variation of the individual samples and are not significantly greater than the corresponding live and dead  $\mu$ PIE values (Table 2). At every sample site, however, the dead PIE value is greater than the live value, significantly so in all but eight cases (Fig. 12). In addition, the live  $\Sigma$ PIE is less than any in-

dividual dead PIE value, which means that even when all local live assemblages along the gradient are combined, they cannot account for the observed evenness of any local death assemblage.

The higher evenness of the dead than the live at individual stations indicates that these are not snapshot assemblages, yet the preservation of the evenness gradient even at a 10 m scale of resolution indicates that the influence of the living assemblage in the immediate vicinity is significant. This preservation of an environmental gradient could result from younger shells having less time to be dispersed than older shells, thereby allowing more recently added dead material to maintain differences among local patches in species composition and abundances, while still allowing dead diversity to accrue to higher values than observed live. In other words, death assemblages at different patches in a habitat share a similar older core of material that has had time to be mixed over a wider area, via either postmortem transportation or time-averaging of migration of living populations, but they differ because of the imprint of the most recently added material, which has not yet been dispersed (Olszewski and West 1997; Kidwell 2002a). Similar patterns of heterogeneous species distribution in time-averaged death and fossil assemblages have also been reported by Cummins et al. (1986b), Bennington (2003), and Zuschin et al. (2006).

This explanation is consistent with more recent work by Ferguson and Miller (2003), who resampled Miller's (1988) transect 20 years after the original study. They found that the distinctiveness of live and dead species composition along the gradient has remained significant but that the species composition of both live and dead has changed during that time. This finding suggests that it is the most recent dead material—i.e., that portion that most closely reflects recent volatility in the living community—that maintains differences among single-census dead samples. It may also explain why time-averaged fossil samples from the same bed are not statistically identical (Bennington 2002; Zuschin et al. 2006)—they represent additions of material from slightly different times and places (i.e., different living

community states within a habitat) as well as vagaries of shell concentration during the accumulation of the fossil bed.

### Discussion and Conclusions

Comparing the postmortem richness and evenness of 132 marine molluscan death assemblages with the corresponding living assemblages reveals new insights into the preservability of species evenness and the processes that influence the fidelity of diversity. Dead evenness is accurately preserved *on average* in large collections of data sets processed using sieves of mesh size finer than 2 mm, but evenness in any single death assemblage can vary quite substantially in either direction from the corresponding single census. When time series of living censuses are summed, the difference between live and dead evenness is somewhat reduced but still significant. Where data have been collected using mesh  $\geq 2$  mm, average dead evenness is significantly and consistently higher than live evenness by an average PIE value of 0.2. Sediment grain size and depositional setting do not appear to influence the degree of bias of dead evenness. Dead richness is on average 1.45 times larger than live richness, regardless of rarefied sample size, although like evenness, it varies over a wide range. Also like evenness, coarse-mesh samples show greater differences between dead and live richness than fine-mesh.

Positive bias in both the evenness and rarefied richness of the coarser portion of marine, soft-bottom molluscan death assemblages indicates that they reflect a greater degree of non-ergodic mixing than the finer components due to longer environmental condensation—i.e., greater time-averaging. As discussed by Kidwell (2001, 2002b), the different degrees of live-dead discrepancy in fine- versus coarse-mesh collections can probably be explained by the expected greater taphonomic durability of large mollusc shells, the lower temporal volatility of late juvenile and adult components of living communities, or both. This bias, operating on classes within single collections, is likely inherited by fossil assemblages, influencing paleoecological interpretations (Kowalewski and Hoffmeister 2003). In terms of applying death assemblages to stud-

ies of modern ecological change (e.g., Powell et al. 1982; Kowalewski 2001; Kidwell 2001; Warwick and Light 2002; Warwick and Turk 2002; National Research Council 2005), it implies that different size classes carry information on different portions of a community's history.

Seven time series of live censuses show increasing richness as successive censuses are added, which is expected given the cumulative increase in sample size. Changes in cumulative evenness of these same series indicate that in several cases the observed increase in cumulative richness is due to real changes in taxonomic composition and not simply an increase in sample size. The final cumulative evenness of any live time series never approaches that of the corresponding death assemblages, which also show much less variance in evenness than the living censuses. It is important to note that these time series are almost certainly too short to capture all possible living community states within a habitat that contributed to the time-averaged death assemblage. Paleoecologists are in dire need of longer live time series and especially dead time series to evaluate this issue fully.

Just as change through time in the living community can lead to a cumulative increase in diversity, so can transportation among different patches within a habitat and among different habitats within a landscape. In the one available case study, an environmental transect only 360 m long showed a gradient in live evenness that was matched by dead evenness, despite the fact that dead evenness was significantly greater than live evenness at each individual station. This is very encouraging for paleoecological analyses focusing on the recognition of biotic gradients in the fossil record, but again, more studies of this type clearly are needed in modern settings. The elevated dead evenness despite preservation of the biotic gradient can be explained if older input cohorts in a death assemblage have had more time to be homogenized via postmortem transport whereas more recent influxes remain closer to the patches where they died. It also suggests an explanation for the surprising degree of compositional heterogeneity

among closely spaced replicate samples from fossil beds.

Because it is unlikely that fossilization of death assemblages would improve the accuracy of preserved evenness, the reliability of evenness from *individual* fossil collections as estimates of the evenness of local communities at a moment in time is questionable. Despite these concerns for comparisons based on single assemblages, comparisons of evenness based on *many* collections (e.g., Bambach 1977; Sepkoski 1988; Powell and Kowalewski 2002; Peters 2004; Bush and Bambach 2004) should provide reasonably accurate estimates of differences in average large-scale community structure.

Analysis of the existing legacy of live-dead studies provides a foundation for using death and fossil assemblages to understand recent and ancient change in ecological communities, but a deeper understanding will require field and experimental work on rates of loss, the effectiveness and rate of transport and mixing, and assessment of the long-term natural volatility of living communities and populations.

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