Ecological fidelity of abundance data from time-averaged fossil assemblages:
Good news from the dead

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Relative abundance information for species is important for exploring many problems in community-level paleoecology, high-resolution evolution, and biogeography, and of course is an element of many biological definitions of diversity. However, this is a category of data that taphonomists have always been highly skeptical of extracting from the fossil record with accuracy, especially from time-averaged assemblages, because of the potential for bias from (1) exotic input from other habitats, (2) differential preservation of species, and (3) differential production, i.e. mortality rates of dead remains. The current challenge to taphonomy is determine the quantitative reliability of such data –be it very good or very poor– and, after establishing this for modern systems where causes might be understood, determine appropriate ways to evaluate ancient systems.

In actualistic tests of the accuracy of relative abundance in the fossil record, we need (a) the sum of dead input over the period of time-averaging represented by the youngest interval of the historic layer (not the time represented by the surficial mixed layer, up to and including today), and (b) the numerical abundance of species preserved in that historic layer, which is the youngest "permanent" part of the stratigraphic record. What we have available from "live-dead" studies are (1) the numerical abundance of species living today in a habitat; this is usually based on samples collected during a single visit (a census of live standing-crop), and (2) the numerical abundance of species present as dead remains within the mixed layer.

Although the content of historic layers (b) is easily determined, counterpart information integrating dead-input over some past interval (a) will never be available empirically, but can only be modeled. Thus our only options for *empirical* tests

of live-dead agreement are to compare live census data (or multi-year series of live censuses; 1) directly either to the historic layer (b; assumes that past communities did not differ from the present) or to dead material in the mixed layer (2). This latter comparison (1 → 2) has the advantage of overlapping in time, but completely ignores the issue of species' production rate: it simply asks "how closely does the composition of the presently accumulating death assemblage match the composition of the standing live community?". This is not an appropriate test for questions of energy flow in communities, such as concern many neo-ecologists. However, it *is* adequate for questions about community structure or standing abundance – that is, for the many issues for which standing crop data are used in biology. "Is Species X present, and if so is it rare or abundant?" "What is the relationship between a species' abundance and its evolutionary longevity?" "How are species packed into communities (is there a limit on the number of rare species, and does this vary with latitude/depth/nutrients)?" "What is the relationship between a species' abundance and the size of its geographic range, or its ability to cross provincial boundaries?"

In this talk I will summarize findings on the reliability of relative abundance data in death assemblages based on a meta-analysis of live-dead studies of marine shelled mollusks, and in particular will highlight results that should have relevance for evaluating – if not interpreting– the skeletal records of other groups. I have focused on mollusks because they have been the subject of far more live-dead studies than any other metazoan group, and also because they are widespread in modern environments and dominate the shelly macrobenthic communities of many post-Paleozoic marine facies.

DATABASE

The current database (2001) is based on 19 previously published or archived (thesis) studies, covering 30 different study areas in low to middle latitudes (0-54° N). An additional 26 live-dead studies, including many classics in the taphonomic literature, could not be included, usually because they had only presence-absence or occurrence data for species, listed only dominant species, or lacked sufficient information on field methods (e.g., mesh size) or environments to permit samples to be pooled into habitat-level datasets independently of faunal data. The 19 included studies have yielded 85 habitat-level datasets; each is based on pooling at least 2 samples (sites), and both live and dead data are derived from the same set of samples using the same known mesh size (ranges from 0.3 to 5 mm; median 1 mm).

AGREEMENT IN SPECIES RANK-ORDER

When ranked by their abundance in the death assemblage, species may occur in identical, random, or opposite order to their ranked abundance in the living com-
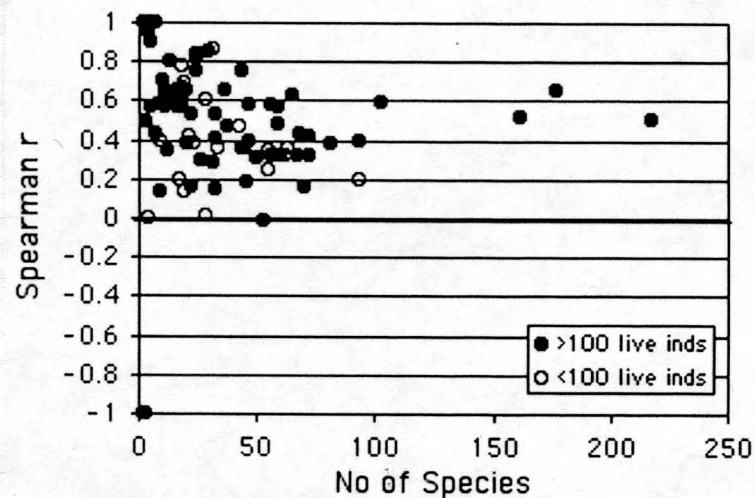
Figure 1. Funnel plot of rank-order correlation values for 85 live-dead datasets.

munity (i.e., Spearman rank-order correlation coefficients "r" may be +1, 0, or –1). I find wide scatter of values among the 85 datasets (individual Spearman tests), ranging from –1 to +1; Fig. 1). However, the vast majority show positive live-dead correlations in species rank-order (92% of all datasets, 97% of the 62 datasets based on a live sample of ≥100 individuals), with a median r of 0.48. When results from individual datasets are weighted according to dataset size (number of species), the meta-analytic average r is 0.45 ±0.03 (95% confidence interval, based on the sum of weights; Kidwell, 2001). That is, live-dead agreement in species' rank order is not perfect (identical), but is significantly non-random: species that are abundant in the death assemblage also tend to be abundant in a single sampling of the live community, and species that are rare dead are rare or absent alive.

Further partitioning of the large datasets (those based on ≥100 live individuals; #s of dead individuals are always greater) reveals a significant effect of sieve mesh size: datasets gathered using coarse mesh of 1.5 mm or larger, and thus consisting entirely of late juvenile and adult individuals, have an averaged (weighted) rank-order correlation of 0.54 ±0.05. This contrasts with an average weighted r of 0.38 ±0.06 for datasets based on mesh of 1 mm or finer, and thus including larval and early juvenile individuals (Kidwell, 2001). For both coarse-mesh and fine-mesh datasets, live-dead agreement in rank order is better in muddy substrata than in sand and gravel substrata (for coarse-mesh, average weighted r of 0.61 ±0.09 versus 0.50 ±0.06; op cit.).
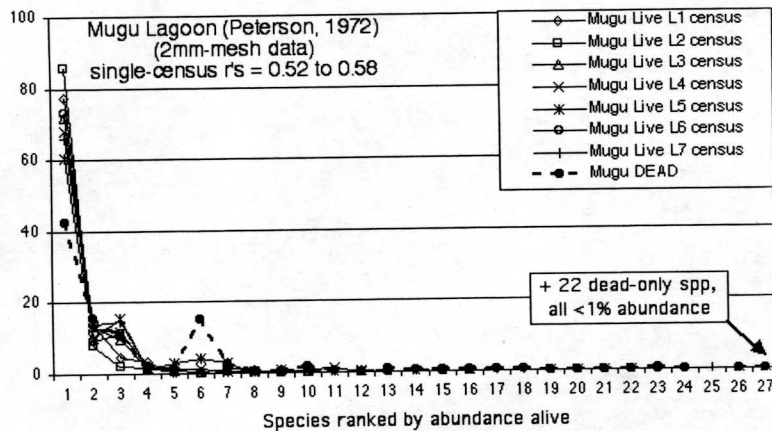
Figure 2. Agreement in species' rank-order numerical abundance at a rank-order correlation value of ~0.5, using the data of Peterson (1972) as an example.

Fig. 2 shows what these r-values mean in "real" terms. Species' relative abundances observed during 7 different censuses of the live community are plotted for Mugu Lagoon, California (unpublished 2mm-mesh data for subtidal sand from Peterson 1972, used with permission), and compared with the abundances of the same species in a single sampling of the death assemblage. Individual Spearman tests (7 tests of a single live census compared with the dead) range from 0.52 to 0.58. Note that, at this r-value, the taxon that is most abundant in each of the live censuses (species #1) is also most abundant in the death assemblage, and that the abundance of each species in the death assemblage lies within the cloud of points generated by its abundance alive, with only one exception (species #6, which is "over-abundant" in the dead). An additional 22 species occur dead-only (species too rare alive to have been sampled given the field program, or exotic to the habitat). This example (Fig. 2) illustrates the *average* live-dead rank-order agreement (r = 0.54) of coarse-mesh datasets in the database. At this r, the death assemblage clearly retains a great deal of information about the original relative abundances of species.

Ongoing analysis of the database indicates that this level of live-dead correlation is very similar to that when two successive coarse-mesh live censuses are compared (median r = 0.55 from live-live correlations; graphs to be presented in talk), demonstrating the ecological stability of the late juvenile/adult component of benthic communities *and* the ability of death assemblages to capture that composition. In contrast, live-live rank-order correlations for fine-mesh datasets (including larvae and early juvenile individuals) are highly volatile and commonly negative to zero (species in opposite or random order; r's of -0.7 to +0.8, median 0.00). Live-dead

agreement in fine-mesh datasets, averaging ~0.4, is thus actually *better* than what one would observe through successive sampling of the live fauna alone.

BROADER SIGNIFICANCE OF BODY SIZE EFFECTS

Cummins et al. (1986) recognized in their fine-mesh (0.5 mm) dataset from Copano Bay, Texas, low agreement in species numerical abundances (as here), but better agreement if species were ranked instead on their biomass. This biomass transformation is the same as moving to a coarser mesh, that is, shifting the focus to the species composition of larger late-juvenile and adult individuals. This Texas study is unique in having body sizes and thus biomasses for individual specimens, both live and dead. The meta-analysis of a global database described here, partitioned by mesh-size, demonstrates the broader effect on live-dead agreement of the body-size and ontogenetic phase of the community that is actually tested. I am finding that differences in live-dead agreement among habitat types (muds versus sands, gravels, grassbeds) and environments (marshes, tidal flats, estuaries, open shelf) are in fact completely masked if data are not first sorted by mesh-size (Kidwell, 2001), and that mesh-size also has a strong influence on live-dead agreement in other ecological metrics, such as species richness and spatial fidelity (Kidwell, in review).

Body-size effects are also likely to appear among other metazoan groups owing to the smaller total mass, higher surface-area-to-mass ratio, and more fragile skeletal structures that typify ontogenetically young individuals compared to adults. Behrensmeyer and Dechant Boaz (1980), for example, found a significant effect on preservation potential (presence-absence & abundance) among land mammals based simply on adult body weight, suggesting that body size differences between juveniles and adults would probably have an effect. The magnitude of a body-size effect among non-molluscan metazoans– and outside soft-sedimentary habitats –requires testing, of course, because of the wealth of other biological and environmental factors that determine ultimate live-dead agreement. But it is clear that, although live-dead studies are extremely laborious and only a substitute for difficult-to-acquire mortality data mentioned in the introduction, a strong signal of the living community can be captured in the initial, death-assemblage stage of accumulating a fossil record. This reliability of mixed-layer skeletal material should be of practical value to biologists in assessing recent ecological change (Holocene), regardless of our ultimate discoveries concerning bias in the transformation of death assemblages into a permanent fossil record.

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The stratigraphy of skeletal concentrations: Testing for broad-scale trends

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Concentrations of macroscopic skeletal material – whether invertebrate or vertebrate in composition – come in many forms and have diverse origins, ranging from small lenses created by predators to large clinoforms of current-swept debris and thin widespread beds punctuating transgressive-regressive cycles. This array has significance both to paleontologists (as sources of biological and biostratigraphic information) and to sedimentary geologists (e.g., as reservoirs and conduits of fluids). "Bone beds" and "shell lags" also have a long and primarily anecdotal use as marker beds for within-basin correlation and as criteria for unconformities. Moreover, among European geologists, diagenetically and paleontologically complex horizons are well-accepted clues to significant condensation.

To extract full value from such concentrations, however, including understanding their significance in terms of hardpart supply (biological productivity) and hardpart destruction (biogeochemical recycling), we need a more systematic and *quantitative* characterization of their distribution in the stratigraphic record, which will complement ongoing work on their genesis and reliability as archives of biological information. Examples of large-scale issues include:

THEME I

Concerning the most simple, objective aspects of skeletal concentrations that guide fossil prospecting and the exploration of bioclastic facies: How do the abundance (i.e., stratigraphic frequency, raw numbers) and physical scale (dimensions) of skeletal concentrations vary through the stratigraphic record? That is, along environmental gradients within basins, among major depositional systems, along latitu-

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Turritella terebralis (MPV 75 GF1) from Eocene of France, placed over a spanish mesozoic
ammonite (Collection of the Natural Sciences Museum of Valencia, Spain)
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