

**Supplemental Table 1.** Fidelity of molluscan death assemblages (DAs) to living assemblages (LAs) for selected biological attributes, based on statistical syntheses of multiple datasets from subtidal seabeds in tropical and temperate areas. Unless otherwise noted, all study areas had minimal human activities at the time of sampling. Only significant results are reported. The capacity of time-averaging to explain observed levels of live-dead discordance is evaluated by modeling, which uses LA data to produce an “expected” DA by time-averaging alone (no taphonomic bias); the expected DA can then be compared with the observed DA. Point-scale = the set of living and dead individuals extracted from sediment taken at a single point or site on the seafloor. Habitat-scale = specimens from two or more points within a relatively narrow depth zone and bottom-type are pooled before living and dead lists are compared. Regional dataset = LA and DA data from multiple habitats are available. All analyses summarized here are based on habitat-level datasets and have been corrected for differences in living and dead sample sizes (numbers of individuals) within datasets, unless otherwise noted. DL = DA/LA ratio or DA-LA difference. From Kidwell 2013.

Biological attribute	Observed death assemblage (habitat-scale)	Source	Variance & mechanisms
<b>DIVERSITY</b>			
Raw species richness (presence-absence)	Larger count of species on average (median raw DL ratio of species = 2.6), owing to larger number of dead than living individuals in most sediment samples (median raw DL ratio of individuals = 8).	85 mostly pristine datasets (Kidwell 2002a)	Raw DL ratios of individuals and species are smaller in cold temperate and boreal provinces based on preliminary data; suggests less time-averaging (lower preservation rates), lower productivity, and/or less beta diversity in molluscan LAs (unpub. obs.)
Sample-size standardized species richness	Larger count of species on average regardless of standardization method: median DL ratio of species richness is 1.22 based on subsampling with replacement, 1.52 based on subsampling without replacement (40 datasets; 1.3 at habitat-scale and 1.8 at point-scale using 31 datasets).	85 mostly pristine datasets (Kidwell 2002a); 40 (Kidwell 2009) and 31 exclusively pristine datasets (Tomasovych & Kidwell 2010a).	Modeling shows that time-averaging alone can increase DA richness by 1.6 (2.1 at point-scale); richness always increases with time-averaging, even holding sample-size constant and with no change in environmental conditions, and the increase is always greater at point- than at habitat-scales (Tomasovych & Kidwell 2010a).
Shape of rank-abundance distribution (RAD)	RADs of DAs are on average flatter (lower dominance by a single species) and have longer tails of rare species (represented by singleton or doubleton individuals) than LAs, resulting in greater average richness and evenness in size-standardized samples. See same effect at point scale.	31 datasets (Tomasovych & Kidwell 2010a); anticipated by conceptual models of Fürsich & Aberhan (1990).	Modeling of within-habitat metacommunity dynamics shows that (1) stochastic switching in the identity of the most abundant species in the LA over time (a few decades to centuries) decreases their proportional abundances in the DA, thereby reducing the initial steepness of the RAD, and (2) rare metacommunity species are temporally short-lived in local communities, fostering accumulation of many rare species in the DA.
Estimated size of regional species pool (gamma richness)	The DA sampled at a point in space or time (DA alpha richness) captures more of the total (gamma) richness of a region or time-series than does the LA sampled at a point (DA alpha = median 0.8 of DA gamma versus LA alpha = median 0.6 of LA gamma).	9 regional datasets, each including several habitats, and 2 time-series in a single habitat (Tomasovych and Kidwell 2009a).	Modeling indicates that DA alpha richness increases rapidly in the initial decades to centuries of time-averaging, owing to chance colonization by patchy and/or ephemeral species; this effect occurs even when samples are size standardized (Tomasovych & Kidwell 2010a).
<b>TAXONOMIC COMPOSITION</b>			

Univariate similarity indices	Median similarity of DA and LA is 0.90 using Chao's sample-size corrected version of the Jaccard index (presence-absence data); median 0.92 in estuaries & lagoons, 0.84 on shelves.	18 shelf datasets (Kidwell 2008), 27 estuarine datasets (Kidwell 2007)	In hard-seafloor settings, DL differences in richness owe to rare/singleton species that occur dead-only or live-only; capture of LA presence/absence is otherwise good (Zuschin et al. 2000).
Multivariate analysis of taxonomic dissimilarity	Using presence-absence data, median DL difference is 0.4 (Jaccard dissimilarity, thus a similarity of 0.6); using relative abundance data, median DL difference is 0.35 (Horn-Morista dissimilarity).	31 datasets (Tomasovych & Kidwell 2010a).	Despite a shift from mean LA composition, the mean point-scale DA composition frequently lies within the cloud of replicate point-scale LA samples; such dissimilarity can be generated largely or entirely by time-averaging of random variability in LAs.
Similarity in species rank-order abundance	Median Spearman rank correlation rho of raw DA & LA species lists is 0.58 in estuaries & lagoons (69% of DL correlations are significantly positive) and 0.38 on shelves (61% significantly positive).	18 shelf datasets (Kidwell 2008), 27 estuarine datasets (Kidwell 2007).	Similar results from 85 datasets from mostly pristine areas; rho is higher if exclude juvenile individuals (Kidwell 2001, 2002b). Rho <1.0 in pristine settings arises from within-habitat time-averaging of natural LA variability, natural environmental condensation, and taphonomic bias.
Proportional abundances of species	A given species can be more or less abundant in the DA than in the LA (observed DL differences range from -0.51 to +0.47) but the median difference is quite small (-0.001; IQR is 0.02). In each dataset, only a few species are responsible for DL differences in proportional abundance – most species are rare both alive and dead.	193 species occurrences from 7 pristine habitats (Kidwell and Rothfus 2010); 31 datasets (Tomasovych & Kidwell 2011)	DL differences in proportional abundance are not significantly correlated with either lifespan or adult body size, because neither variable correlates with abundance in LA. Most DL differences arise from within-habitat time-averaging of LA variability; residual “unexplained” DL differences in 25-65% of datasets must owe to taphonomic bias and/or environmental condensation (between-habitat time-averaging).
Estimating species identities and abundances in the species pool at broader spatial scales	The species composition and rank-abundance distribution of the DA at a point approaches that of the source metacommunity given time-averaging of LAs on decadal to centennial scales, using neutral and non-neutral, dispersal-limited dynamics of species colonization.	Model parameterized using 31 datasets and compared with data in 12 datasets (Tomasovych and Kidwell 2010a); direct tests of 2 time-series with known time-averaging (Tomasovych and Kidwell 2010b)	DAs collected at a point (and especially at a habitat) level are an efficient means of generating a regional species list and estimating species' relative abundances at a regional scale, data that are difficult to acquire from live-sampling alone. Can assume that species do not differ in shell preservation and individual lifespan.
<b>SPATIAL PATTERNS</b>			
Beta diversity	DAs show less turnover in species composition among points than do LAs (lower beta diversity): in 9 of 11 datasets, between-point dissimilarity of DAs is positively correlated with that of LAs but is damped by ~25% (fewer compositionally distinct communities). DAs thus tend to under-estimate the true spatial variability of LAs at both point and habitat scales.	9 regional datasets and 2 time-series in a single habitat (Tomasovych and Kidwell 2009a); 31 datasets (Tomasovych and Kidwell 2010b).	Modeling shows that reduced beta diversity can largely be explained by within-habitat time-averaging of natural temporal variability in colonization, without recourse to significant environmental condensation or postmortem spatial mixing. Reduced beta anticipated by early models (e.g., Miller and Cummins 1990). Temporal, down-core variability should also be damped (Tomasovych and Kidwell 2010b).
Variation in community composition along environmental gradients	DAs detect a significant gradient where LAs detect a gradient in 6 of 7 datasets using presence-absence data (5/7 using proportional abundance data), and the DA gradient is as strong or stronger than the LA gradient. Environment explains about the same proportion of between-point compositional variation among DAs as it does among LAs.	9 regional datasets (Tomasovych and Kidwell 2009b). And see powerful single-region tests by A.I. Miller (1988, Miller et al. 1992, Ferguson & Miller 2007)	Variation along gradients persists despite the potential for spatial mixing and is commonly strengthened by within-habitat time-averaging. The environmental resolution of DAs supports paleoenvironmental analysis using mollusks as well as paleoecological discrimination of species-sorting and mass-effects models of meta-community structure.

Habitat- (facies-) level preferences of species	Weighted meta-analytic mean $73 \pm 3\%$ (simple grand mean = 78%) of all individuals in the DA are drawn from species that are documented alive in that habitat (same set of samples).	85 datasets from mostly pristine settings (Kidwell 2002a).	Because LA information is based on a one-time survey and typically yields small numbers of individuals, this test provides a minimum estimate of the true spatial fidelity of DA individuals.
Variation in single-species abundance along environmental gradients	Species niche optima (positions of maximum living abundance and occupancy along environmental gradients) are detected in 7 of 9 of datasets; DAs do not detect optima where none are evident in the LA.	9 regional datasets (Tomasovych & Kidwell 2009b)	Median rank correlation between species optima in DAs and LAs are significantly positive regardless of data transformation; DAs have less ability to reflect niche breadth (blurred by time-averaging) and underestimate maximum abundance (carrying capacity).

**Supplemental Table 2.** Protocol to evaluate live-dead discordance. Analysis should focus on the subset of species that create the discordance, namely species (here, molluscs) that occur only in the living assemblage (live-only) or nearly so (their proportional abundance alive is much greater than their abundance dead) and species that occur only in the death assemblage (dead-only) or nearly so (dead abundance >> living abundance). Hypotheses (H1-5) to explain an observed live-dead discordance should be evaluated in sequence from left to right, but are not mutually exclusive. LA = living assemblage, DA = death assemblage. Modified from Kidwell 2013.

Observation	H1: Under-sampling	H2: Collection & other human bias	H3: Time-averaging	H4: Natural taphonomic bias	H5: Ecological change
Species is live-only and rare	Sample size DA small and < LA	Unlikely	DA reflects very little time-averaging	Species has intrinsically low preservation potential	New arrival to community
Species is live-only and is moderately or quite abundant	Unlikely	Unlikely	Unlikely	Species has extremely low preservation potential	Relatively new, highly successful arrival
Species is dead-only and is rare	Sample size LA << DA	Gear bias against LA; dumping of exotic DA	Most likely even if sample size LA is small	Postmortem exotic: most likely if consistently present in LA of adjacent habitat(s) or could be rafted	Waning; most likely if multiple dead-only species do not 'fit' with the LA
Species is dead-only and is moderately or quite abundant	Unlikely	Very strong gear bias; dumping of exotic DA	Unlikely	Postmortem exotic: most likely if abundant in LA of adjacent habitat(s) or could be rafted	Past dominant, now waning or extirpated

#### NOTES

Rare species: represented by only one or two specimens in an assemblage (low abundance) or present at only a few sites (low occupancy); the threshold percentage for abundance depends upon sample size but would typically be < or <<1% of all individuals in an assemblage.

H1 attributes strong live-dead discordance in a species solely to the small sample size of either the LA or the DA.

H2 attributes discordance to methodologic bias against collection or detection of a species in the LA, for example owing to gear that cannot acquire living individuals of deep-burrowing, cryptic, or highly mobile species, or species that attach to hard substrata or difficult-to-dislodge vegetation. H2 also includes "unnatural" bias of DA data, such as species that occur dead-only at a site because of beach replenishment, dredge-spoil dumping, or other human activities that deliver "exotic" dead shells.

H3 attributes discordance to the coarser temporal scale (natural time-averaging) of the DA compared to the LA. Time-averaging alters the number of rare species, etc in predictable ways because it subsumes natural, random variability in the LA (see Supplemental Table 1, main text Section 2), and thus a time-averaged DA is not expected to match the source nonaveraged LA even in the absence of taphonomic bias (H4) or of ecological change during the window of time-averaging (H5).

H4 attributes discordance to natural postmortem bias, e.g. long lifespan (few dead shells produced per unit time), low postmortem durability (e.g., small, thin, and/or high-organic microstructure; prone to being overgrown), and/or high potential for transportation (e.g., low-mass shell, epifaunal life habit).

H5 attributes discordance to a change in the LA within the window of time-averaging, for example from species invasion, extirpation, or a significant increase or decrease in its local population size; change may be driven by either natural or anthropogenic forces, and may reflect change in the biotic and/or abiotic environment. H5 is strengthened if the species that occurs live-only or dead-only does not 'fit' ecologically with species that occur both alive and dead, and is further strengthened if multiple species in the assemblage fit this description (e.g., an entire functional group is live-only or dead-only).

NB. There are some human modifications of habitats, for example dredge-spoil dumping, where human (as opposed to natural) transportation of dead shells modifies the local DA, augmenting it with "exotic", dead-only species. These dead shells can create a new habitat for living species, especially species that prefer or require substrata for attachment. The resulting live-only species signify a recent anthropogenic ecological change (H5). However, the dead-only species delivered by human agency do not signify either as H5 (ecological change) or as H4 (natural taphonomic bias), but rather should be categorized as H2, i.e. a human bias of the DA.