

Ecological fidelity of open marine molluscan death assemblages: effects of post-mortem transportation, shelf health, and taphonomic inertia

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Based on 38 molluscan datasets from modern open shelf settings, disturbance from human activities – especially anthropogenic eutrophication (AE) – has the strongest negative effect on the fidelity of death assemblages to local living communities, suggesting that the composition of the death assemblage has lagged behind changes in the living community (taphonomic inertia). Fidelity is poorest where shelves are both AE and narrow (≤ 50 km from shore to the 200-m isobath), suggesting that cross-shelf post-mortem transportation might contribute bias, but this does not dominate and shelf width does not emerge as significant among non-AE shelves. Clear signatures of post-mortem transportation are present only in four shoreface datasets, all from wide shelves, that receive abundant allochthonous specimens from adjacent estuaries or rocky intertidal zones.

Shelves experiencing minimal human impact yield fidelity estimates that are most relevant for evaluating (paleo)ecological trends. There, death assemblages are on average 25% richer than a single census of the living molluscan community and show high similarity in taxonomic composition and species relative abundance that, based on a very limited number of studies, is comparable to or better than the agreement found among successive live censuses. Molluscan death assemblages on open shelves are thus generally good samplers of living community diversity and composition under natural conditions, and where the community is undergoing anthropogenic modification, retain a strong record of the precursor community. Taphonomic inertia will be strongest where the change in the community has been especially strong (outside the normal range of natural variability) and/or where the ‘new’ community has lower net rates of shell input than its precursor, so that input only slowly dilutes the time-averaged skeletal remains of the ‘old’ community. □ *Eutrophication, fidelity, molluscs, taphonomy, trawling.*

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Many factors are suspected to influence the fidelity of death assemblages to the local living community. These factors include post-mortem transportation, differential durability of species and age-classes (rapidity of post-mortem fading from time-averaged assemblages of a given taxon, and persistence of others), differential ‘productivity’ of species (contribution of dead individuals per unit time), and the duration and rigor of time-averaging in the environment of accumulation. ‘Live–dead’ comparisons of sedimentary death assemblages with their counterpart local living community are a widely used actualistic method of assessing death assemblage fidelity and identifying sources of bias (see review by Kidwell & Flessa 1996, plus recent discussions by Vermeij & Herbert 2004; Zuschin & Oliver 2003).

However, extrapolating the results of live–dead analyses to the fossil record has several caveats. One is the difficulty of assessing post-depositional alteration.

The living community is compared only to dead material accumulating in the surficial ‘mixed layer’ of the sedimentary column. This is still a useful value to know, however, because it indicates the maximum fidelity that is possible in underlying ‘historic layers’, including lithified record. A second caveat is that most live–dead studies are based on only a single census of the living community. ‘Live data’ thus underestimate true living richness and provide only one snapshot of species relative abundances, which would almost certainly vary even in a steady-state community.

To these caveats can be added concern with the appropriateness of modern environments as analogues of past conditions. For example, two recent *Lethaia* seminars (Donovan 2002; Dominici & Zuschin 2005) have suggested that taphonomic bias in benthic marine records might be greater on narrow, steep continental shelves than on the wide shelves that are

typically studied, owing to the potential for post-mortem transportation. In addition, modern shelves might be appropriate analogues for transgressive, commonly sediment-starved systems tracts but be poor analogues for volumetrically more important highstand system tracts (or aggradational and progradational records in general, where the potential for environmental condensation is lower), and Holocene 'ice house' conditions might be poor analogues for the 'greenhouse' conditions that have existed over much of past time, for example owing to lower saturation states in overlying waters (Dominici & Zuschin 2005).

To this concern with modern environments as analogues can be added the growing evidence of anthropogenic modification of modern shelf ecosystems, via both eutrophication (Nixon 1995; Cloern 2001) and bottom-trawling for fin- and shell-fish (e.g., Kaiser 1998). To what extent do modern death assemblages diverge from living communities because human activities have recently shifted the composition of the living community outside the range of natural variability captured by earlier phases of time-averaging? Death assemblages might well have compositional inertia, the magnitude of which would depend on a number of factors, including the rate at which past cohorts of dead shells residing in local sediments are destroyed, the rate of production of shells from the 'new' community, and the relative preservation potential of those new shells. For example, if the rate of input (mortality rate) of the new community is low, and/or if the preservation potential of that new input is low (i.e. they fade faster than shells from the previous community; disharmonious time-averaging of Kowalewski 1996), then dilution of the pre-existing death assemblage may be very slow. Such 'taphonomic inertia' could result in low agreement in the composition of the death assemblage with a census of the living community for years or decades post-impact. This scenario for 'infidelity' might be a good analogue for environmental condensed fossil assemblages. However, if modern anthropogenic changes in communities are fundamentally more rapid than those in natural systems – and some recent changes are in fact thought to be unprecedented in rate – then actualistic estimates of death assemblage reliability will be overly conservative if drawn from human-modified study areas.

Community degradation from trawling and anthropogenic eutrophication (AE) has been postulated to explain poor live–dead agreement in several live–dead studies (e.g., Pandolfi & Greenstein 1997; Staff & Powell 1999), but is difficult to prove without the context of datasets from clearly unmodified settings. Here, I use a global database of molluscan

live–dead studies from 16 modern open shelves to assess relationships between the ecological fidelity of death assemblages and an array of methodological and extrinsic environmental factors, including recent anthropogenic modification of the living community ('shelf health', analogous to community health of Hewitt *et al.* 2005). Molluscs are a particularly important target for analysis: they are the most diverse metazoan phylum in modern seas (Bouchet *et al.* 2002), occur at all water depths and latitudes, constitute a large component of the post-Palaeozoic shelly record (Sepkoski 2002; Paleobiology Database paleodb.org), and have been the subject of a large number of actualistic 'live–dead' studies (described below). Ecological fidelity here concerns both the diversity and composition of communities, namely live–dead agreement in (1) species richness (does the death assemblage yield the same count of species as the living community?), (2) evenness (basically, does the most abundant taxon in the death assemblage have the same *proportional* abundance as the most abundant taxon alive, whatever its identity?), (3) taxonomic similarity (what proportion of species are present in both live and dead species lists?), and (4) species rank–order (when listed according to relative abundance, do taxa occur in the same order in the death assemblage as they do in the living community?).

Material and methods

Database composition

Thirty-eight habitat-level datasets where previous authors generated data on the numbers of live and dead individuals per species are included in analyses (Table 1). To supplement published information, many authors provided raw station-level data and details on methods and study areas. Shelf study areas range from 55°S to 54°N with most from the northern mid-latitudes. Substrata range from well-sorted sands to muds and a variety of shell and lithic gravels, plus one dataset from sandy patches within a rocky grassbed. With the exception of the pure carbonates of the Yucatan shelf (two datasets), all sediments are siliciclastic or mixed siliciclastic–carbonate in composition. Reefs and other continuously hard substrata are excluded, owing to the different challenges for sampling their live and dead fauna, and the different factors in post-mortem bias (for molluscs see Zuschin *et al.* 2000; Zuschin & Oliver 2003).

Shelves are operationally defined as euhaline subtidal settings where fair-weather open-ocean waves and currents impinge unimpeded upon the shore. Environments range from the shoreface (subtidal seafloor

Table 1. Open shelf study areas and habitat-level datasets. Shelf width in kilometre. If number of live censuses is > 1, duration of study is provided in parentheses. Mesh size in mm. AE = anthropogenic eutrophication; T = trawling. Live and dead numbers of individuals are for a single census. *Plus unpublished raw data or other information from the author.

Study area	Latitude	Shelf width	Year sampled	No of censuses	Mesh size	Human impacts	Habitat	Live N	Dead N	Total species	Source
Eddystone, English Channel, UK	50°N	350	1931	1	1.5	T	Lithic gravel	54	672	24	Smith (1932)
Ditto	50°N	350	1931	2 (2 months)	1.5	T	Shell gravel	34	1322	22	Ditto
Ditto	50°N	350	1931	1	1.5	T	Sandy gravel	21	1067	23	Ditto
Ditto	50°N	350	1980–81	4 (6 months)	2	AE, T	Shell gravel	96	13543	62	Carthew & Bosence (1986)*
Stoke Point, English Channel, UK	50°N	350	1980–81	4 (6 months)	2	AE, T	Shell gravel	118	3466	59	Ditto
Plymouth Sound, UK	50°N	350	1980–81	4 (6 months)	2	AE, T	Shell gravel	4841	17847	72	Ditto
San Juan Islands, Washington, Pacific USA	48.5	30	2002	1	2.3	None	Shell gravel	1659	5232	86	Kowalewski <i>et al.</i> (2003)*
Livorno, Tuscany, Italy	43°N	50	pre-1978	1	1	AE, T	Rocky sand within grassbed	163	9093	140	Biagi & Corselli (1978), Corselli (1981)
Golfo Milazzo, Sicily	38°N	2.5	1985	1	0.5	AE, T	Sandy silt	85	1828	87	Giacobbe & Leonardi (1985)*
Ditto	38°N	2.5	1985	1	0.5	AE, T	Silty sand	56	415	56	Ditto
Brucoli, Golfo Catania, Sicily	37°N	5	1980	1	1	AE, T	Silt	98	5501	112	Di Geronimo & Giacobbe (1983)*
Brucoli, Capo Campolato, Sicily	37°N	3	1980	1	1	AE, T	Mobile sandy silt on rocky ground	54	2852	129	Ditto
Rhodes Island, Aegean Sea, Greece	36°N	3.5	1983–84	2 (9 months)	0.5	AE, T	Shell gravel	67	113	53	Pancucci-Papadopoulou <i>et al.</i> (1999); Zenetos & van Aartsen (1995)*
Ditto	36°N	3.5	1983–84	4 (9 months)	0.5	AE, T	Silty sand	157	509	121	Ditto
Chihama shelf, Pacific Japan	35°N	11	1958	1	1	T	Shoreface sand	167	496	80	Tsuchi (1959)
Oi River mouth, Suruga Gulf, Pacific Japan	35°N	5	1958	1	1	AE, T?	Offshore clayey mud	17	6	9	Tsuchi (1960)
Ditto	35°N	5	1958	1	1	AE, T?	Shoreface sand	21	28	12	Ditto
Tago-no-ura, Suruga Gulf, Pacific Japan	35°N	2	1958	1	1.2	AE, T?	Offshore mud	12	67	34	Tsuchi (1966)
Ditto	35°N	2	1958	1	1.2	AE, T?	Nearshore gravelly mud	43	29	18	Ditto
Sapelo Island, Georgia, Atlantic USA	31°N	130	pre-1986	1	1.5	None	Longshore channel shell gravel	15	24551	63	Henderson & Frey (1986)*
Ditto	31°N	130	pre-1986	1	1.5	None	Shoreface sand	19	1545	17	Ditto
Galveston, Texas, Gulf of Mexico, USA	29.5°N	180	1976–77	1	0.5	AE, T	Offshore mud	125	3145	57	White <i>et al.</i> (1985)*
Ditto	29.5°N	180	1976–77	1	0.5	AE, T	Shoreface sand	164	6962	63	Ditto
Ditto	29.5°N	180	1976–77	1	0.5	AE, T	Shelly muddy sand (relict)	286	40004	141	Ditto
Ditto	29.5°N	180	1976–77	1	0.5	AE, T	Shelly sandy mud (relict)	200	17836	117	Ditto
Corpus Christi, Texas, Gulf of Mexico, USA	27.5°N	110	1976–77	1	0.5	T	Offshore mud	104	2354	85	White <i>et al.</i> (1983)*
Ditto	27.5°N	110	1976–77	1	0.5	T	Shoreface sand	3602	41041	153	Ditto
Ditto	27.5°N	110	1976–77	1	0.5	T	Muddy sand	109	8218	84	Ditto
Ditto	27.5°N	110	1976–77	1	0.5	T	Sandy mud	77	3887	75	Ditto
Ditto	27.5°N	110	1986	8 (11 months)	1	T	Muddy sand/sandy mud	1785	18576	96	Staff & Powell (1999)*
Isla Contoy, Yucatan, Gulf of Mexico, MX	21°N	37	1971	1	3	None	High-energy strait	5099	75839	162	Ekdale (1972, 1977)*
Ditto	21°N	37	1971	1	3	None	'Open sea'	47	1070	93	Ditto
Amazon River mouth, Brazil	0–4°N	250	1989–91	4 (26 months)	0.3	None	Firm mud	69	29096	93	Aller (1995); Aller & Stupakoff (1996)*
Ditto	0–4°N	250	1989–91	4 (26 months)	0.3	None	Nearshore fluid mud	21	298	9	Ditto
Ditto	0–4°N	250	1989–91	4 (26 months)	0.3	None	Distal shelly sand (relict)	50	18520	70	Ditto
Beagle Channel proper, Chile	55°S	4	1994	1	0.3	T	Sandy mud	1909	815	63	Linse (1997, 1999); Linse & Brandt (1998)*
Beagle Channel mouth and southern Patagonian shelf, Atlantic Chile	55°S	280	1994	1	0.3	T	Offshore shell gravel	9317	15227	78	Ditto
Ditto	55°S	280	1994	1	0.3	T	Nearshore oozy mud	578	175	35	Ditto

down to fair-weather wave base) through the inner shelf (between fair-weather and normal storm wave base; 'transition zone') and outer shelf (below storm wave base to the shelf-slope break).

For inclusion, datasets were further required to: (1) be based on quantitative bulk samples, i.e. of a standardized sedimentary volume achieved by suction-excitation, remotely deployed grab apparatus (van Veen, Petersen, orange-peel), or subsampling of dredge hauls; (2) be based on at least two samples (generally this means a single grab from two or more physical stations), which were then (3) processed using a sieve of known mesh size; (4) provide counts of individuals from all taxa, not just dominant taxa; some studies focus on bivalves only, but most include gastropods, scaphopods, and chitons; (5) be drawn from un lithified substrata; and (6) provide basic information on sedimentary grain size for each sample, either from the original author or some other source, in order to group samples into habitat-level (facies-level) datasets. My groupings of samples into datasets in many cases diverge from those of the original author, who is more likely to have clustered samples on the basis of shared faunal composition. The study area of a single author thus might generate one or more habitat-level open-shelf datasets.

Counts of live and dead individuals are based on specimens sieved from the same set of samples. Exceptions are datasets from the Livorno, Rhodes Island, and Amazon study areas, where dead counts are from only a subset of the samples used to extract live specimens. Within each study area, a single person supervised taxonomic identification, so that names are applied consistently to both live and dead specimens.

Despite these restrictive criteria, datasets still differ in the number of spatial replicates pooled (range from two to 19 stations per habitat with median = 5), dataset size (either the number of live individuals or the number of dead individuals, whichever is smaller; this ranges from six to 9317 with median = 97; total individuals ranges from 623 to 80938 with median = 3088), ratio of dead:live individuals (0.3 to 1637 with median = 22), and the mesh size used to separate live and dead specimens from enclosing sediment (0.3 to 3 mm). Rather than exclude datasets arbitrarily, all are included in the analysis, and methodological variables are explored statistically.

In all datasets, the live species list reflects only a single census of the local community. For study areas where original authors made multiple censuses (Amazon shelf, English Channel, Plymouth Sound, Rhodes Island, Corpus Christi shelf; Table 1), I use as 'live data' the single census having the largest number of live individuals.

Characterization of shelves

Width. – Shelf width is operationally defined as the distance in kilometres from shoreline to the nearest 200 m isobath, and ranges from only a few kilometres to several hundred kilometres (Table 1). For binary tests of live–dead agreement, shelves ≤ 50 km wide are categorized as 'narrow' (16 datasets) and those ≥ 100 km as 'wide' (22 datasets). No shelves have intermediate widths.

Sediment type. – Seafloors are assigned to six ordinal categories of mud (oozy mud, firm mud; $< \sim 10\%$ sand), sandy mud ($< 50\%$ sand), muddy sand ($< 50\%$ mud), well-sorted sand ($< 10\%$ mud), gravel (gravelly sands, gravelly muds, shell gravels, lithic rubble), and grassbed. Datasets are fairly evenly divided among various fine-grained seafloors (23 datasets, of which 12 are dominated by mud and 11 by sand) and gravelly seafloors (15 datasets, of which one supports patches of *Posidonia*).

Shelf health. – For most study areas, original authors provided only qualitative information, at most, on anthropogenic modification of the environment. Categorization of bottom-trawling intensity and degree of AE at the time of sampling and estimating the date of onset of these impacts are thus based on a mixture of quantitative and qualitative information from general historical accounts of the region and from interviewing original authors when possible (for details, see SI-Table 2 in Kidwell (2007)).

Trawling intensity was difficult to quantify. Even when reports are available, metrics for effort vary over time and among regions, and fishing effort refers only to legal takes, whereas undocumented fishing can equal or exceed this in some areas. For this factor, 'trawled' means that, at the time of live–dead sampling, the shelf was already experiencing commercial bottom-trawling, dredging, or other disruptive methods of shell- or fin-fish extraction. In northern Europe and territorial waters of the USA, bottom-fishing has accelerated since the early 1970s, plowing many areas of the seafloor more than once a year (Kaiser 1998; NRC 2002). Coastal areas of the Mediterranean and Japan have had regulated fisheries for two millennia (extraction for market, not just local subsistence; Ruddle 1987; Zugarramurdi *et al.* 1995). There, operations at the time of live–dead sampling (1950s to 1980s) might not have used destructive methods or been of an industrial scale, but the cumulative historical impact of benthic harvesting for regional populations has probably been significant. 'Untrawled' indicates no local human exploitation or only artisanal extraction methods for local consumption.

For AE, shelves were assigned to several nested categories initially: areas of minimal human impact, which may be non-eutrophic or, when associated with upwelling, naturally eutrophic (e.g., Yucatan versus the Amazon and Patagonian shelves); areas of definite but diffuse human impact from coastal development and general population increase; shelves receiving runoff from areas of intensive agriculture using commercial fertilizers, animal husbandry, or land clearance (all of these shelves were either meso- or eutrophic); and shelves with a local point-source of pollution and/or known benthic dead zones (some bottom samples containing no live animals, for example the Tago-no-ura and Oi River shelves of the Suruga Gulf, adjacent to and down-coast from a pulp mill). Because of the limited number of datasets per category, this scale was collapsed to AE versus non-AE.

The effects of trawling are difficult to isolate because many shelves that are trawled are also affected by AE. Datasets were thus sorted into four categories of shelf health: neither trawling nor AE present (eight datasets, 'pristine' shelves), trawling present without AE (12 datasets), both trawling and AE present (14 datasets), and trawling uncertain but AE present (four datasets, all Suruga Bay). These subsets were combined for some tests: 'AE shelves' comprises the 18 datasets from shelves with AE ('non-AE shelves' comprise the other 20 datasets), 'trawled shelves' comprises the 26 datasets with known trawling, and 'non-pristine shelves' comprises the 30 datasets that are not pristine.

Nutrient level. – Direct measurements of chlorophyll-a were rarely available for study areas or, like satellite-based estimates, post-date live–dead sampling by decades and are relevant to surface rather than bottom-water conditions. As an indicator of organic loading at the sediment–water interface at the time of sampling, I thus used the composition of the living molluscan community itself, specifically the proportional abundance of 'organic-loving' molluscan species. Focusing on bivalves (ecological information for gastropods is of uneven quality, and many are opportunistic feeders, e.g. Cadée 1984a), this category includes all exclusively deposit-feeding species (most protobranch bivalves), all chemosymbiotic species (soleymid, thyasirid, and some lucinid bivalves), plus suspension-feeding species that are notably tolerant of episodic hypoxia (most lucinids, corbulid bivalves). Observed proportional abundance of these species in datasets ranges from 0 to ~90% of the live molluscan community, and both natural and human-modified shelves in the database occupy that entire range. For binary tests of live–dead agreement, the median observed value of 9% organic-loving individuals

was used to categorize datasets as either low organic or high organic.

Latitude. – With the exception of five tropical datasets from the Amazon and Yucatan shelves (2 and 21°N), datasets are exclusively from temperate, mostly northern mid-latitudes (Table 1). Given this relatively narrow distribution, and that both tropical shelves are from a single health category (non-AE, non-trawled), the database is inadequate for a rigorous test of latitudinal effects.

Ratio of dead:live individuals. – Where relevant to the fidelity metric, sample-size standardization can correct for differences in the numbers of living and dead individuals present. However, the ratio itself is an independent character of the environment, with high ratios expected to arise from time-averaging, input of allochthonous shells, or both. High values do not necessarily signify shell-rich sediments. Sands and muddy sands yield the highest average ratio of 241 (median = 41), whereas shell gravels and grassbeds have an average ratio of 43 (median = 26) and muds and sandy muds an average ratio of 22 (median = 18).

Metrics of live–dead agreement

Species richness. – Molluscan death assemblages from low to mid-latitudes typically contain two to three times more species than are sampled at the same set of stations in the living community (marsh to open shelf soft-sediment datasets in Kidwell 2002a). This excess is generally attributed to the effects of time-averaging skeletal remains from multiple generations. However, dead individuals typically outnumber live individuals in these same datasets, and thus 'excess dead richness' might arise simply from differences in live and dead sample size. To correct for this within each dataset, live and dead species lists were sample-size standardized by adjusting the larger sample (usually the dead) downward to the size of the smaller sample using two different procedures: (1) using the proportional abundance of taxa in the larger sample to calculate the number of species that would still be present (represented by > 0.99 individuals) at the smaller sample size (linear method used in Kidwell 2002a); and (2) rarefying the larger sample downward assuming a non-linear, hypergeometric distribution of occurrence probabilities; rarer taxa in the larger sample have a probability of < 1 occurring in the subsample, but will not be zero (method used in Olszewski & Kidwell 2007, 'Δ-S'). Rarefaction generally yields the same or slightly higher expected richness values in the subsampled list than does the linear method. Test outcomes are not affected by the

method of sample-size standardization; results using rarefied values are reported here.

Evenness. – Of the many metrics available to describe how evenly (uniformly) individuals are distributed among species in an assemblage, Hurlbert's Probability of Interspecific Encounter (PIE) is one of the least sensitive to variation in sample size and richness (Gotelli & Graves 1996; Olszewski 2004, and see Ess of Peters 2004, which yields values very similar to PIE). Owing to its sum-of-squares formulation, PIE is primarily an expression of dominance that is strongly and inversely correlated with the proportional abundance of the top taxon in the assemblage. Theoretically, it ranges from ~0 (virtually all individuals belong to a single taxon) to 1.0 (individuals uniformly distributed among taxa), and equals the slope of the steepest segment of a rarefaction curve (depicting richness as a function of number of individuals; Olszewski 2004). Live–dead agreement in evenness is quantified as the difference between the evenness of the death assemblage (dead PIE) and that of the living community (live PIE). This is 'Δ-PIE', following Olszewski & Kidwell (2007), and can range from +1 to –1.

Taxonomic similarity. – Taxonomic similarity is often expressed as the Jaccard index, which is simply the number of shared taxa divided by the total number of taxa observed in the two lists; it ranges from 0 to 1 (see reviews by Magurran 1988, 2004; Gotelli & Ellison 2004). However, if the compared samples differ strongly in size, the Jaccard (and most other indices, such as the commonly used Sorenson and Bray–Curtis indices, which double the weight of shared taxa) will underestimate similarity because of underestimated richness in the smaller sample. To correct for 'unseen species' in small samples, I use Chao *et al.*'s (2005) sample-adjusted Jaccard index, which incorporates information on the number of shared taxa that are known from only one or two individuals. Chao *et al.*'s (2005) sample-adjusted Sorenson index yields values ~0.1 units higher than the Jaccard–Chao index.

Rank–order abundance of taxa. – Following previous analyses (Kidwell 2001), live–dead agreement in species relative abundance is evaluated here using a Spearman rank–order test. Agreement can range from +1 (taxa occur in identical order in the two lists when ranked according to their relative abundance) to –1 (taxa in one list are reversed in order relative to the other list). The Spearman test is preferred to the Kendall and other tests because it places more stress on the top- and bottom-ranked taxa – that is, it minimizes

the impact of uncertainty about small differences in rank within each list (Sokal & Rohlf 1995).

Statistical analysis

The effects of eleven methodological and extrinsic environmental factors (independent variables) on these four metrics of live–dead agreement (dependent variables) were explored using: (1) differences in mean and median live–dead agreement among various partitions of the database, (2) bivariate linear regression, and (3) stepwise multiple linear regression. Variables that emerged as important by multiple methods were judged to be robust.

Mean and median values of live–dead agreement were calculated using raw (untransformed) data; 95% confidence intervals for means are based on the standard deviation of the population. If necessary to approximate a normal distribution, raw data were transformed before regression by a logarithmic (total number of samples, dataset size, ratio of dead:live individuals), square-root (shelf width, Δ-S), or angular transformation (proportional data such as the Jaccard–Chao Index and proportional abundance of organic-loving species). Spearman rho, mesh size, total species, latitude, sediment grain size, AE, and trawling intensity did not require transformation, and evenness was not transformable (Δ-PIE was bimodal).

Both forward and backward stepwise regressions were performed, focusing on the six independent variables that produced at least one significant relationship during bivariate regression. In the backward mode, all six independent variables were regressed against a given live–dead agreement metric simultaneously. Following Sokal & Rohlf's (1995) recommended routine, variables producing a $P < 0.05$ in the first round were retained permanently and those with $P > 0.2$ were removed; variables being retained permanently and those on hold were then regressed simultaneously in a second round and so on, until all variables were either retained permanently or deleted. In the final round, some variables retained from earlier rounds might have dropped in significance; only final coefficients and P -values are reported.

In the forward mode, the importance of each factor (percent of variation explained) was established by first regressing live–dead agreement against the independent variable having highest ranking in simple pairwise regressions; the residuals of that regression were then regressed against the next highest ranked factor, and so on, until the maximum variation had been explained. Freckleton (2002) argues that such residual regression does not truly control for the effects of other variables in the model, and thus the backward mode should be preferred.

However, *P*-values in both models are only approximate owing to the large number of independent variables (six) compared to the total number of observations (38 datasets). Ordinally scored variables such as sediment grain size, degree of AE, and trawling intensity were included in regression analyses: ordinal binning in this circumstance simply reflects the imposition of a coarse counting scheme on phenomena capable of yielding fundamentally continuous data (Sokal & Rohlf 1995; van Belle 2002, and see Case 1996 for an ecological application). For regression analyses, four datasets having unknown trawling intensity (all sampled from the Suruga Gulf in the 1950s) were given a score of 0.5.

Results

Mean and median fidelity of raw data

The fidelity of individual datasets varies widely: Δ -*S* ranges from 0.59 to 5.46, Δ -PIE from -0.39 to $+0.55$, taxonomic similarity from 0 to 1, and Spearman rho from -0.58 to $+0.71$ (Fig. 1). However, on average,

open-shelf death assemblages are richer (mean of raw Δ -*S* = 1.88 ± 0.34) and more even (mean of raw Δ -PIE = $+0.14 \pm 0.07$) than a single census of the counterpart living assemblages. Taxonomic similarity is relatively high (mean of raw Jaccard–Chao index = 0.70 ± 0.10) and rank–orders of live and dead species are positively correlated (mean of raw Spearman rho = 0.27 ± 0.09). Medians generally indicate the same or better live–dead agreement than do mean values, and mostly lie within the 95% confidence intervals of those means (Fig. 1).

Using raw data, fidelity of community diversity (richness, evenness) is sensitive to several variables: it is higher among wide shelves, non-AE shelves (outlined by rectangle), non-trawled shelves, and among datasets having high ratios of dead:live individuals (Fig. 1A, B). Fidelity of *community composition* (taxonomic similarity, species rank–order) is sensitive to most of the variables tested (Fig. 1C, D). It is higher among large datasets, wide shelves, non-AE shelves, low nutrient levels, and high ratios of dead:live individuals. Mesh size and sediment grain size have no effect on any of the four ecological metrics, although there is the suggestion of greater variance and/or

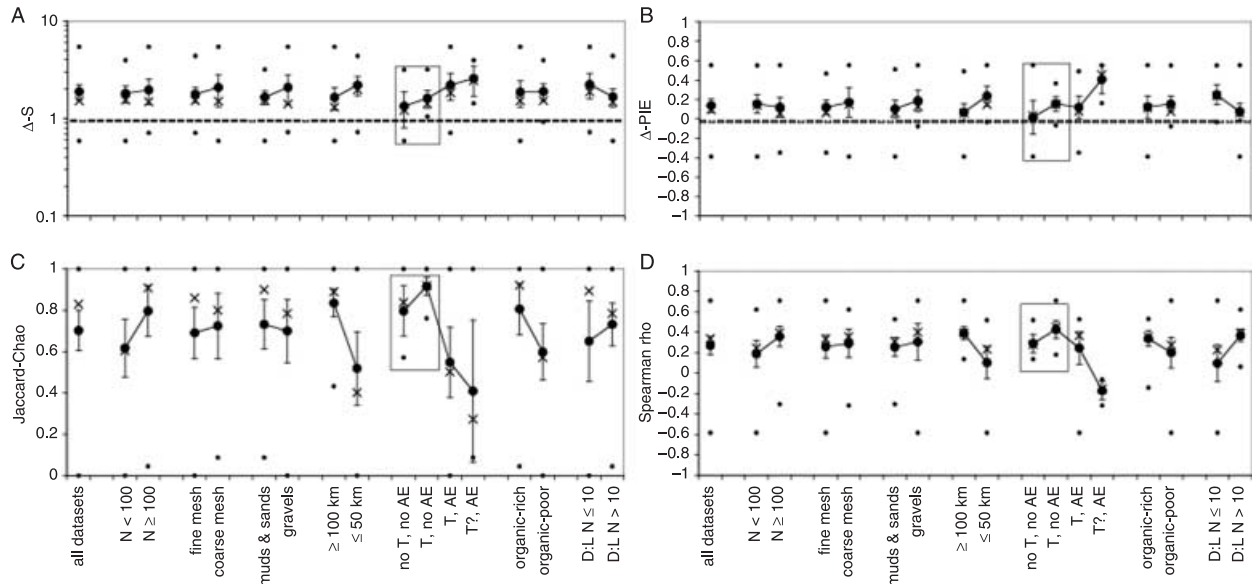


Fig. 1. Differences in mean (large black circles with 95% confidence intervals on the standard error) and median (x icon) values for various binary partitions of the open shelf database. Small black circles are maximum and minimum values. □A. Ratio of species richness of the death assemblage versus the richness of a single census of the local living community, using a hypergeometric rarefaction routine to standardize live and dead sample sizes; log scale. Perfect fidelity = 1 (dashed line). □B. Difference between the evenness of the death assemblage and the local living community, using Hurlbert's PIE. Perfect fidelity = 0 (dashed line). □C. Taxonomic similarity of dead and live species lists, using a sample-size corrected Jaccard–Chao index. Perfect fidelity = 1. □D. Agreement in the order of species in live and dead species lists when ranked by their relative abundance, using a Spearman test. Perfect fidelity = +1. Database partitioned by dataset size (large = at least 100 live and 100 dead individuals), mesh size (fine = ≤ 1 mm), sediment grain size, shelf width, shelf health (anthropogenic eutrophication (AE) and/or bottom trawling (T)), nutrient level as measured by the proportion of organic-loving species in the living molluscan community, and ratio of dead individuals to live individuals (D: L N). Rectangles enclose values from shelves lacking AE: for most metrics, this partition shows the highest average fidelity and least dispersion.

poorer average fidelity among gravels compared to (aggradational) sands and muds (Fig. 1). Non-AE shelves generally yield the highest fidelity values, and this partition of the database is generally also the most effective in narrowing the range of maximum and minimum values (enclosed by rectangles in Fig. 1).

Bivariate regression

Linear regression of normalized data finds that the fidelity of richness (Δ -S) and evenness (Δ -PIE) are significantly positively correlated with each other (Table 2). Datasets with strong live–dead differences in richness also tend to have strong live–dead differences in evenness, with the richer species list (usually the dead list) usually having the greatest evenness (and see Olszewski & Kidwell 2007 for this relationship among a larger array of datasets that includes these open-shelf studies). This relationship is expected from the need for individuals to be spread among more species in rich assemblages, thus reducing the maximum possible proportional abundance of any single species. Δ -S is also significantly but negatively correlated with taxonomic similarity, as expected: as the number of species in one list becomes large relative to the second list, then the proportion of species shared by the two lists must decrease.

In contrast, taxonomic similarity and species rank–order abundance are significantly and positively correlated (Table 2). However, this is not required and thus suggests control by some independent variable. Two species lists may be identical in species composition but have those species in any order including opposite rank order. Moreover, although rank–order agreement must be low when taxonomic similarity is zero, good rank–order agreement may be preserved even at relatively low taxonomic similarity as long as shared species are mostly high ranked or low ranked in both lists. Rank–order agreement is also significantly negatively correlated with Δ -PIE (Table 2), which is apparently a signature of independent variables because no constraints on these values should exist. Low Δ -PIE can arise when both living and death assemblages have high evenness; rank–order agreement should tend to be low to zero because species can shift positions within lists relatively easy. Low Δ -PIE can also arise when both assemblages have low evenness: rank–order agreement can have any value from -1 to $+1$, as it should also when Δ -PIE is high (one assemblage is uneven and the other even). The expected pattern of variation in Δ -PIE and Spearman rho is thus a wide scatter of values, with the greatest density around neutrality.

Table 2. Correlation matrix (multiple- r values) of transformed data; critical r for $*P < 0.05 = 0.321$, r for $**P < 0.01 = 0.413$, for $v = 36$.

	Delta-S	Delta-PIE	Jaccard-Chao	Spearman rho	Shelf width	Organic-loving	AE	Trawling	Grain size	Latitude	Mesh size	Total samples	Total species	Dataset size	Dead:live N
Delta-S	1	0.780**	-0.484**	-0.291	-0.16	0.11	0.380*	0.213	0.109	0.19	0.196	0.028	0.186	0.171	-0.27
Delta-PIE		1	-0.3	-0.325*	-0.264	0.21	0.188	0.131	0.058	0.166	0.18	0.01	0.045	0.135	-0.509**
Jaccard-Chao			1	0.633**	0.390*	-0.233	-0.534**	-0.107	-0.114	0.044	0.036	0.035	0.1	0.222	0.05
Spearman rho				1	0.521**	-0.296	-0.398*	0.167	0.058	0.108	0.09	0.126	0.287	0.442**	0.437**
Shelf width					1	0.041	-0.334*	0.028	0.279	0.042	0.049	0.058	0.162	0.218	0.355*
% Organic-loving N						1	0.142	0.076	0.209	0.232	-0.387*	0.244	0.136	0.0429	0.309
AE							1	0.352*	0	0.188	0.078	0.118	0.048	0.257	0.051
Trawling								1	0.104	0.565**	-0.367*	0.343*	0.067	0.013	0.204
Grain size									1	0.227	0.470**	0.036	0.157	0.213	0.219
Latitude										1	0.201	0.088	0.177	0.037	0.294
Mesh size											1	0.28	0.033	0.008	0.136
Total samples												1	0.594**	0.378*	0.129
Total species													1	0.577**	0.338*
Dataset size														1	0.143
Dead:live N															1

AE, anthropogenic eutrophication; PIE, Probability of Interspecific Encounter.

Table 3. Multiple regression models of live–dead fidelity for 38 open shelf datasets using the six independent variables having significant correlations in bivariate analyses (Table 2). Values are partial coefficients from backward modelling, with the r^2 value of the final round: ‘ns’ indicates the variable was discarded from the model as not significant during the modelling process; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; values lacking a P -value were significant during the modelling process, but by the final round had a P -value ≥ 0.05 . Values in parentheses are multiple- r values from forward modelling; no metric advanced beyond the first round.

	Delta-S	Delta-PIE	Jaccard–Chao	Spearman rho
r^2 (%)	19.6	32.2	35.2	59.1
Dataset size	NS	NS	NS	0.14**
Mesh size	0.11	0.08	NS	NS
Shelf width	NS	NS	NS	NS (0.52***)
AE	0.28* (0.38*)	NS	-0.41** (-0.53***)	-0.21**
Trawling	NS	NS	NS	0.20*
Dead: live N	NS	-0.14*** (-0.51**)	NS	0.16***

AE, anthropogenic eutrophication; PIE, Probability of Interspecific Encounter; NS, not significant.

Simple regression yields few statistically significant relationships between fidelity metrics and extrinsic environmental and methodological variables (Table 2). Of the community diversity metrics, Δ -S varies significantly only with AE, and Δ -PIE only with the ratio of dead:live individuals. Taxonomic similarity and rank–order agreement vary significantly with both shelf width and AE. In addition, rank–order agreement covaries significantly with dataset size and ratio of dead:live individuals.

Several environmental and methodological variables covary significantly (Table 2). The most important of these, given the relationships mentioned above, are that AE is more prevalent on narrow shelves, narrow shelves tend to have lower ratios of dead:live individuals, and AE and trawling tend to co-occur. Sediment grain size and nutrient level are both significantly negatively correlated with mesh size: muddy substrata are processed almost exclusively using fine mesh, and thus high-organic datasets (both AE and non-AE) tend to have been processed using fine mesh. However, none of these factors emerge as significant for fidelity. Notably, nutrient level shows no significant relationship to AE – upwelling creates high-nutrient conditions on some non-AE shelves – permitting the effects of AE to be isolated. Finally, the significant relationships observed among measures of study size (total species, dataset size) are expected from sampling theory, as is the relationship between total species and the ratio of dead:live individuals.

Stepwise multiple regression

Because several fidelity metrics vary with more than one independent variable and because some of these independent variables are linked to each other (Table 2), multiple regression was used to assess their

relative importance (Table 3). None of the metrics advanced beyond the first round of forward modelling, and thus the only variables identified as significant are those with the highest multiple- r values in Table 2. The backward model identified only AE as significant for Δ -S and Jaccard–Chao, explaining 20 and 35% of variation, respectively, and only the ratio of dead:live individuals emerged as significant for Δ -PIE (32% of variation; Table 3). The backward model identified four significant independent variables for Spearman rho, namely AE, trawling, the ratio of dead:live individuals, and dataset size in that order (ranked by coefficients), and these together explain 59% of variation. Variation in Spearman rho with trawling has the opposite sign to that expected (live: dead agreement is higher on trawled shelves than on non-trawled shelves).

Means of partitioned data

Among the eleven independent variables tested, AE, trawling, and shelf width emerge most strongly and consistently as factors influencing live–dead agreement (Table 4). Partitioning data using these variables and testing differences in means using transformed (normalized) data reveal that, for all four metrics, fidelity is poorest on narrow AE shelves (Fig. 2). Shelf width does not have a significant effect among non-AE datasets, and fidelity on wide AE shelves is not significantly poorer than on any width of non-AE shelves. Trawling either has no significant effect on fidelity when it is tested among non-AE shelves (community diversity metrics), or has an effect opposite to expectation (community composition metrics). Shelves that are ‘pristine’ – neither AE nor trawling at the time of sampling ($n = 8$ datasets) – yield the highest fidelity death assemblages (values summarized in Table 4; Fig. 2). AE shelves – which are also all

Table 4. Summary of statistically significant factors in ecological fidelity (from Figs 1 and 2, Tables 2 and 3). All analyses were performed on transformed data unless otherwise noted. Reported mean values of ecological fidelity for pristine (non-AE, non-trawled) shelves have been back-transformed to a linear scale. Delta-S value in parentheses is where live and dead sample sizes are standardized using a linear model rather than by hypergeometric rarefaction. When 'trawling' is in parentheses, variation in fidelity is significant but has a sign opposite to that expected.

Test	Delta-S	Delta-PIE	Jaccard-Chao	Spearman rho
Difference in means (raw data)	Width, AE, trawling, dead:live <i>N</i>	Width, AE, trawling, dead:live <i>N</i>	Width, AE, nutrient level, <i>N</i>	Width, AE, (trawling), nutrient level, <i>N</i>
Bivariate regression	AE	Dead:live <i>N</i>	AE, Width	Width, AE, <i>N</i> , dead:live <i>N</i>
Forward multiple regression	AE	Dead:live <i>N</i>		Width
Backward multiple regression	AE (20%)	Dead:live <i>N</i> (32%)	AE (35%)	AE, (trawling), dead:live <i>N</i> , <i>N</i> (59%)
Difference in means of partitioned data	Narrow AE shelves	Narrow AE shelves	Narrow AE shelves, (trawling)	Narrow AE shelves, (trawling)
Mean values on pristine shelves	1.25 ± 0.48 (0.92 ± 0.40)	0.02 ± 0.17	0.84 ± 0.12	0.29 ± 0.09

AE, anthropogenic eutrophication; PIE, Probability of Interspecific Encounter.

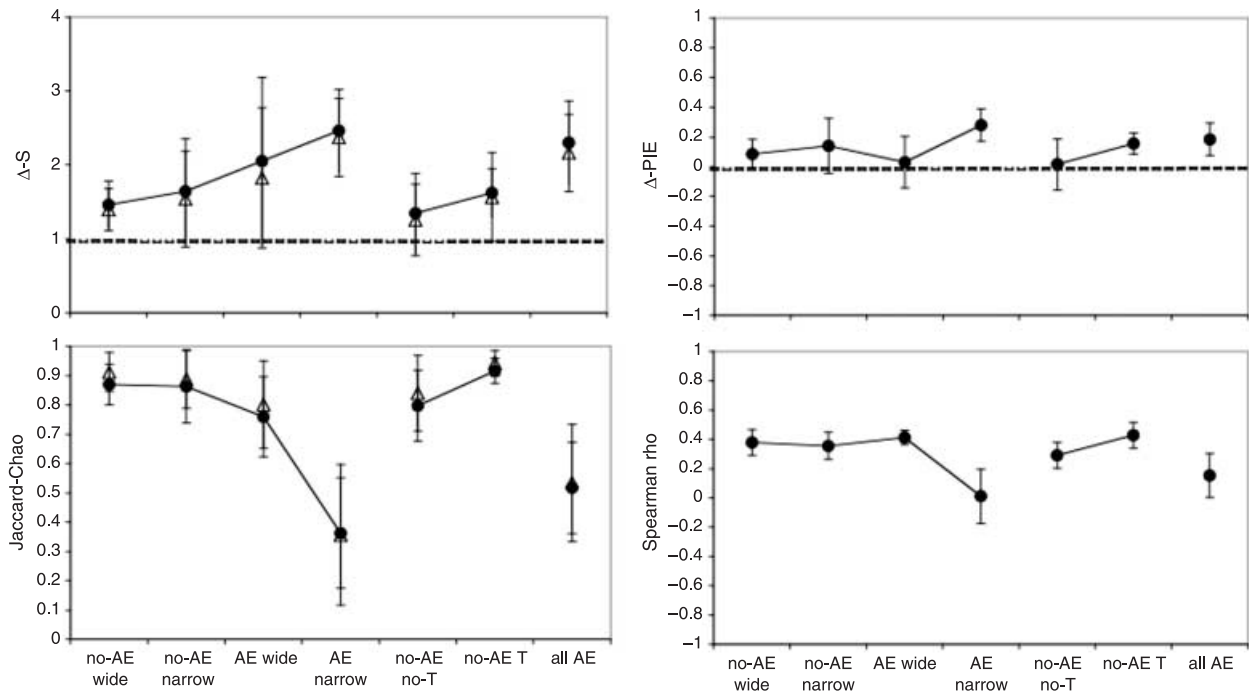


Fig. 2. Mean fidelity with 95% confidence intervals for datasets grouped by anthropogenic eutrophication (AE), shelf width, and trawling (T). Black circles = means of raw data; open triangles = means of normalized data, back-transformed to linear values. The poorest average fidelity is found among AE shelves, and in particular narrow AE shelves. Death assemblages from 'pristine' shelves (neither AE nor trawled) have the highest fidelity. Dashed lines denote perfect fidelity values for ΔS (1) and ΔPIE (0).

trawled or suspected to be trawled, and span all widths ($n = 18$ datasets) – yield the poorest fidelity death assemblages (Fig. 2). These results are robust to using both raw and transformed data.

Scatterplots of raw values highlight the polygonal distribution of fidelity values, especially for community composition, as a function of both shelf health and shelf width (Fig. 3).

Discussion

Robustness of results

Variation in ecological fidelity is multifactorial for each of the four metrics (Table 4). Significant differences in means identify shelf health – AE and trawling – and shelf width as factors significant to all metrics,

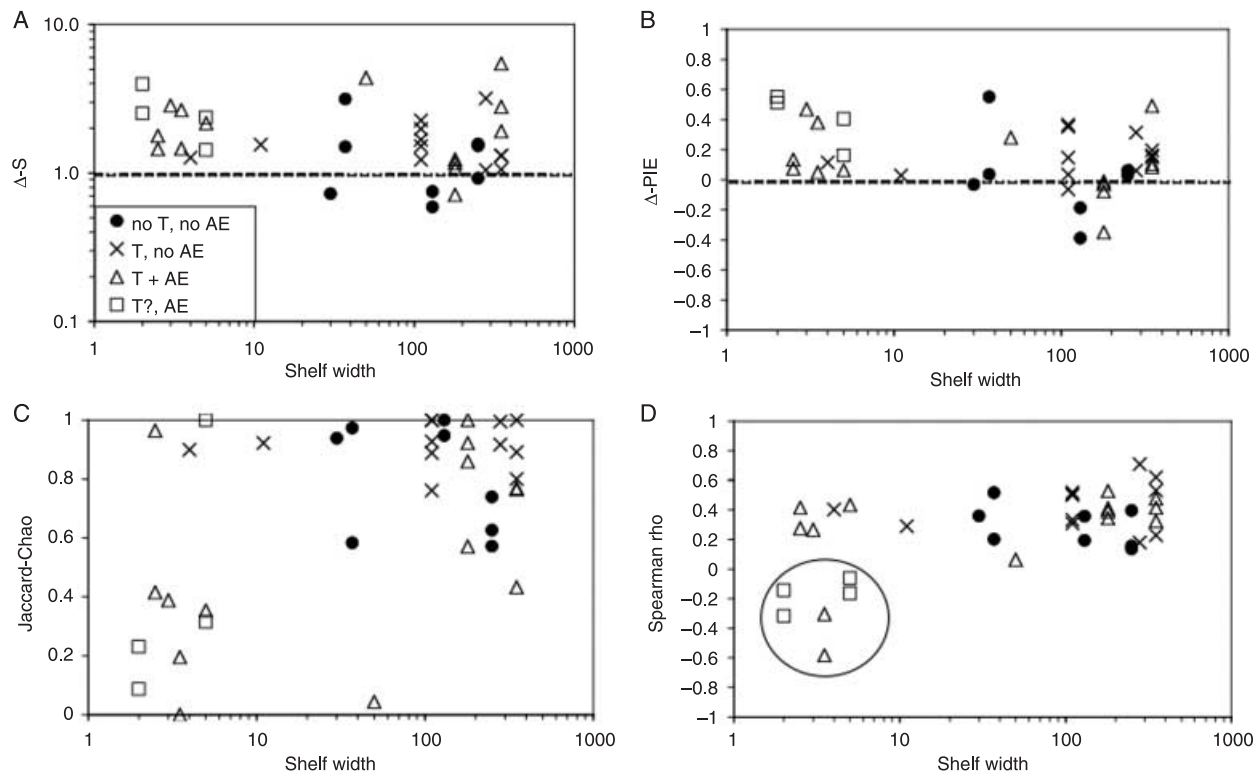


Fig. 3. Fidelity as a function of shelf width. The fidelity of richness (A) and evenness (B) does not vary with shelf width nor shelf health. The exceptions are three wide-shelf datasets that have $\Delta\text{-PIE} < 0$: these are shoreface sands that were sampled near tidal inlets and whose death assemblages contain abundant allochthonous specimens of the opportunistic estuarine bivalve *Mulinia lateralis*. Fidelity in taxonomic composition (C) and species rank-order (D) show polygonal distributions, with higher variance and lower average fidelity on narrow shelves and among shelves experiencing anthropogenic eutrophication (AE), especially in Suruga Bay and Rhodes Island (circled in D). Black circles = pristine, neither trawling nor AE. X = trawling but no AE. Open triangle = both trawling and AE. Open square = uncertain trawling, definite AE. Dashed lines denote perfect fidelity values for ΔS (1) and ΔPIE (0).

with poorest fidelity on narrow AE shelves; these results are robust to using both raw and transformed data. Regression analyses identify this same subset of environmental factors as important for all metrics except $\Delta\text{-PIE}$, which covaries significantly only with the ratio of dead:live individuals (degree of time-averaging and allochthonous input). This ratio also contributes to the fidelity of species rank-order. The explanatory power of these variables ranges from 20–35% for community diversity and taxonomic composition, to 59% for species rank-order (Table 3).

These results are qualitatively robust to alternative binning of shelf health scores and to updating of the database. The same patterns emerged in an earlier analysis when AE was subdivided more finely (four-category scale of minimal human impact, versus coastal urbanization and general population growth, versus land clearance and commercial agriculture with industrial fertilizers, versus point-source polluters and known dead zones). In addition, the previous database included three datasets now omitted because they lack data for rare species (shoreface sand of Bahia

la Choya (Fürsich & Flessa 1991), shoreface sand and inner shelf of Oyster Ground (Cadée 1984b)), and lacked five datasets that are now included (newly available data from the San Juan Islands (Kowalewski *et al.* 2003) and from Staff & Powell's (1999) study of the Corpus Christi shelf; plus three datasets from Smith's (1932) Eddystone study; Table 1). Re-inclusion of the Bahia la Choya (wide non-AE shelf; study area onshore of trawling grounds) and Oyster Ground datasets (wide AE shelf, trawled) would not change the results for the fidelity metrics that can be calculated.

Taphonomic inertia to recent anthropogenic changes

The negative correlation of ecological fidelity with shelf width seen for all four metrics (Fig. 3, Table 4) is consistent with the expectation that post-mortem transportation is more severe on steep, narrow shelves (e.g., Donovan 2002; Dominici & Zuschin 2005). However, differences in the taxonomic composition

of live and dead species lists indicate that AE, which is correlated with shelf width and just as strongly and negatively correlated with fidelity (Table 2), is the actual cause of poor fidelity.

For example, two datasets having some of the lowest compositional fidelities – Jaccard–Chao < 0.5 and Spearman $\rho < 0$ – are from Rhodes Island, Greece (Fig. 3). Living molluscan communities there are dominated by organic-loving species (58% and 42% of individuals, respectively; *Solemya* and *Nuculana* are the most abundant of these taxa), whereas this category constitutes a much smaller proportion of counterpart death assemblages (13 and 9% respectively). In addition, these death assemblages, even after sample-size standardization (linear method) include infaunal and epifaunal suspension feeders and mixed suspension–deposit feeders that are absent in the living community (*Astarte*, *Glans*, *Azorinus*, *Pitar*, several cardiids; *Flexopecten*, *Lima*, *Pseudamussium*, *Arca*; *Tellina*). These compositional differences are contrary to those expected from the input of allochthonous shells: most ‘dead-only’ species have large and/or robust shells that are unlikely to have been transported, and are moreover ecologically consistent with the grain size they are associated with. Instead, the differences suggest that an increase in organic input has shifted the composition of the benthic community, with the composition of the death assemblage lagging behind owing to the diluting effect of existing dead shells and/or the lower preservation potential or otherwise lower input rates of the new community. The death assemblage is thus most likely the time-averaged accumulation of local populations, but has compositionally lagged behind strong recent changes in the community, a phenomenon here termed ‘taphonomic inertia’.

The dominance of living assemblages on the Rhodes shelf by organic-loving species is contrary to the oligotrophic chlorophyll-*a* values measured by *in situ* analyses of surface waters (Ignatiades *et al.* 1995). Thus organics are apparently being supplied laterally along the seafloor, presumably from coastal pollution sources such as Rhodes Harbor, rather than from surface production. Krönke *et al.* (2003) invoked just this kind of significant lateral transport of nearshore organics to explain significant benthic deposit-feeding on the deep (basinal) seafloors beneath the oligotrophic surface waters of the eastern Mediterranean. Taking a broader regional view, Caddy *et al.* (1995) argued that the continuing high catches of fish in the generally oligotrophic Mediterranean derive from diffuse AE: fish populations should otherwise be declining, given intensified fishing effort.

The other datasets yielding both low Jaccard–Chao and negative Spearman ρ values are from the Suruga Gulf, immediately adjacent to or alongshore from a then-active pulp mill (Tago-no-uro and Oi River shelves, respectively; Fig. 3D). All of these datasets are quite small, but the pattern is similar to that of the Rhodes shelf. Living communities are dominated by organic-loving protobranch, corbulid, and/or lucinid bivalves, usually with similarly abundant mixed-feeding tellinids, whereas death assemblages generally include these taxa plus dead-only specimens of suspension feeders typical of lower organic conditions (e.g., *Glycymeris*, *Dosinia*, *Bathyarca*). Again, although post-mortem transport might be suspected given the narrowness of the shelf in the Suruga Gulf (Table 1), taphonomic inertia to recent (anthropogenic) eutrophication is a more likely explanation for the observed live–dead differences.

Datasets having low Jaccard–Chao values (< 0.5) but *positive* Spearman values are mostly from Mediterranean shelves that are narrow and AE, with one exception (wide-AE Eddystone dataset of Carthew & Bosence 1986; Fig. 3). Examination of these species lists suggests a variety of causative factors, but significant cross-shelf transportation of dead shells is not one of them. For example, datasets from the Brucoli shelf of Sicily suggest taphonomic inertia to AE: living assemblages are strongly dominated by deposit-feeding protobranchs, whereas death assemblages include these species but also organic-tolerant corbulids, dead-only mixed-feeding *Turritella*, and suspension feeding infaunal and epifaunal bivalves (venerids, anomids, pectinids). Undersampling of small-scale heterogeneity of habitats is indicated for the Livorno dataset, which was sampled from patches of sand among *Posidonia* grassbeds and has near-zero taxonomic similarity of live and dead species lists. The Livorno death assemblage includes a large number of epiphytic gastropods that were, understandably, either entirely absent or rare among the living community of the loose sand, which was dominated by donacid bivalves. This low fidelity would be unrelated to the narrow width or possibly degraded health of the Livorno shelf. Clear mixtures of rock-dwelling and sand-dwelling species occur in the death assemblages of sand pockets in many rocky areas (e.g., Bosence 1979; Russell 1991; Zuschin & Oliver 2003), leading to poor live–dead agreement when, owing to logistical challenges, the living community of one patch type is better sampled.

Finally, the death assemblage of the Eddystone shelf (wide, AE, trawled, as sampled in 1980; Jaccard–Chao < 0.5 but Spearman > 0) diverges from the living assemblage in a way suggesting taphonomic inertia to trawling rather than to AE. The death

assemblage includes all of the primarily suspension-feeding species found in the living community, but contains a much higher proportion of epifaunal individuals, especially the pectinid *Palliolium* and various anomiid (these all occur dead-only). When the same area was sampled in 1931 by Smith (1932), using virtually the same mesh size, live–dead fidelity was better by all metrics but the death assemblage was still enriched in epifaunal species, consistent with disruption from trawling (anomiid, pectinid, modiolid, limid, byssate arcoids, almost all occurring dead-only).

These AE, primarily narrow-shelf datasets that have both low taxonomic similarity and low to negative rank–order agreement also have some of the poorest fidelity of richness and evenness (Fig. 3). This is also consistent with a scenario of taphonomic inertia to AE, trawling, or both: the death assemblage not only contains some individuals from the ‘new’ community, but retains a time-averaged memory of the pre-impact community. It thus tends to have greater dead:live disparity in richness (and evenness) than in situations where the community has been stable or has fluctuated around a stable mean composition.

The narrow-shelf AE syndrome is intriguing. Is fidelity lower owing to (1) *chance* (narrow shelves have received higher anthropogenic nutrient loads than wide shelves for reasons unrelated to shelf width); (2) *ease of nutrient dispersion* (the coastal injection of nutrients more readily pervades a narrow shelf, perhaps because of the smaller surface area or steeper bathymetric gradient); (3) *severity* (benthic communities on narrow shelves suffer greater consequences for a given change in nutrient input, perhaps because narrow shelves tend to be rockier or otherwise more heterogeneous at a fine scale, and thus have more biological diversity to lose); (4) *taphonomic inertia* (narrow-shelf death assemblages respond more slowly to a given ecological change than their counterparts on wide shelves); or (5) causal interactions (a combination of both post-mortem transportation and taphonomic inertia, not simply one acting alone, is required to disconnect living and death assemblages significantly)?

Other factors in live–dead agreement

Sources of variation that are *not* explained by the methodological and extrinsic environmental factors considered in the present analyses still need to be fully explored. These sources would include:

1. Undersampling of temporal variation in living community composition. The present analyses compare time-averaged death assemblages to

only a single snapshot census of the living community. This should tend to inflate Δ -S and Δ -PIE (see Olszewski & Kidwell 2007) and depress Jaccard–Chao and Spearman rho. For example, the few molluscan live–dead studies that include two or more seasons of replicate sampling indicate that a single census typically captures only ~30% of living species that would be recorded by pooling census data from additional seasons, and similar values emerge from live time-series of complete macrobenthic communities (e.g., raw data plotted by Staff & Powell 1986).

2. Undersampling of spatial patchiness in the habitat. Collection of living fauna from only one patch type on a finely heterogeneous seafloor – for example, small patches of loose sand within a grassbed, or soft seafloors with patches of hard substrata – should decrease fidelity. Death assemblages from the sampled patch are likely to include specimens from nearby ecologically discordant patches, as well as time-averaged specimens from previous states (e.g., when the sand was more homogeneously vegetated or rocks less completely blanketed).
3. Differences among species in their intrinsic rates of shell production, and thus their absolute contribution of dead individuals over the period of time-averaging. These ‘supply-side’ issues have been raised by Van Valen (1964), Powell (1992), and Vermeij & Herbert (2004), and are a function of several life-history attributes, including lifespan (= ‘mortality bias’ of Rothfus & Kidwell 2006), and the average age at first reproduction, frequency of reproduction, and clutch size, which together create a ‘fecundity bias’. Species having short lifespans, especially if combined with high fecundity, should become disproportionately abundant in time-averaged death assemblages relative to their standing abundance, all else being equal, affecting the fidelity of diversity but not necessarily presence–absence composition.
4. Differences among species in their intrinsic preservation potential, owing to such factors as body size, shell mineralogy, and life habit. This could affect the magnitude of bias and even its polarity, especially given the potential for cross-correlation with supply-side issues of point 3 above (Kidwell 2002a; Tomasovych & Rothfus 2005).

Information on intrinsic characteristics of molluscan species are presently being compiled to explore these issues, but initial results suggest that mortality bias is not a significant factor, despite intuition (e.g., Rothfus & Kidwell 2006). On the other hand, intrinsic

preservation potential almost certainly does play a significant role, at least in some circumstances. For example, organic-loving species have proportionately lower abundances dead than alive in virtually all AE datasets that are nutrient-rich (11 out of 12 datasets where organic-loving species constitute > 9% of individuals), but also in all five of the datasets from nutrient-rich pristine shelves (Amazon and Patagonia), suggesting that these species have intrinsically lower *per capita* preservation potential. This might owe to many having small, thin shells, which in some key cases are composed of organic-rich aragonitic microstructures (e.g. protobranch bivalves). The death assemblages of nutrient-rich communities are still, on average, enriched in organic-loving species compared to other datasets – that is, the qualitative pattern is preserved. However, such intrinsic bias against preservation of organic-loving species would magnify taphonomic inertia in AE settings. Dead individuals from the ‘new’ community would only slowly dilute the existing death assemblage, unless their population sizes and turnover rates were much higher than those of species in the precursor community.

Bias from post-mortem transportation

The discovery that shelf health rather than shelf width determines first-order variation in ecological fidelity does not negate the reality of post-mortem transportation of individuals and entire assemblages, nor its importance in some circumstances. Modern environments and stratigraphic records provide many unambiguous examples of allochthonous assemblages, as re-emphasized by Dominici & Zuschin (2005; and see Kidwell & Bosence 1991 and Kidwell 1991 for reviews). Formal live–dead studies of settings prone to strong allochthony – such as washover fans, cheniers, turbiditic fans, and seabird middens – are essentially non-existent because the results would be obvious. Instead, existing live–dead studies permit analysis of the taphonomically more subtle situations mentioned by Donovan (2002) and Dominici & Zuschin (2005), namely whether death assemblages from steep narrow shelves and gravelly seafloors where considerable out-of-habitat transport *should* occur actually *do* exhibit significant assemblage-level bias consistent with post-mortem transportation. On such shelves, out-of-habitat movement may be diffuse rather than directional, and may act on a subset of species or size-classes rather than *en masse*, producing little corroboratory physical evidence (graded bedding, high-energy bedforms, distinctive shell orientations) because of the continuous nature of the process or because of overprinting by fair-weather conditions.

The present database indicates that ecological fidelity of time-averaged molluscan death assemblages is strongly multifactorial, and that poor live–dead agreement is restricted to shelves that are both narrow *and* anthropogenically eutrophied. This suggests that both post-mortem transportation *and* taphonomic inertia to human insults are required for death assemblages to diverge significantly in composition from the local living community. (Shell) gravels tend to yield lower fidelity death assemblages than fine-grained substrata but not significantly; this is consistent with both transportation (some shellgravels arise via sediment starvation rather than bypass and winnowing, but higher energy is common to many) and taphonomic inertia (gravel communities are more likely to be trawled and degraded by trawling, and typically have few organic-loving taxa before eutrophication).

In the present database, post-mortem transportation is unambiguous in only a few datasets, all from wide shelves. Three datasets from shoreface sands near a major tidal inlet contain abundant allochthonous specimens of a single estuarine species (the small, opportunistic bivalve *Mulinia lateralis*). In two of these (shoreface sand and longshore channel of Sapelo shelf), allochthonous shells drive Δ -PIE to negative values (low-evenness death assemblage) and Δ -S to < 1 (sample-size standardized death assemblage is less rich than the living community). In contrast, Δ -S and Δ -PIE values are ‘normal’ (both positive) for the Corpus Christi shoreface dataset: allochthonous *Mulinia* actually increase the evenness of the death assemblage, which is otherwise strongly dominated by dead specimens of the indigenous shelf species *Abra aequalis*. Other shoreface sands in the database were sampled at a distance from tidal inlets and lack significant allochthonous estuarine species: their fidelity values fall within the scatter produced by other shelf environments.

The death assemblage of the Plymouth Sound shell gravel, collected nearshore in only 13–16 m water depth on a wide AE shelf, clearly receives considerable allochthonous input from adjacent intertidal habitats. However, the allochthonous components include a variety of dead-only epiphytic and intertidal gastropods and the fragile infaunal bivalve *Ensis*, rather than a single dominant species, and are combined with the effects of trawling-related taphonomic inertia (death assemblage includes dead-only subtidal epifauna and shell-gravel specialist infauna, such as *Glycymeris*). The net effect is an increase in death assemblage diversity (Δ -S and Δ -PIE of 5.5 and 0.4, respectively; Fig. 3), rather than the decrease observed when allochthonous shells are from a single species.

Why no substratum or mesh-size effects?

The failure of fidelity to vary significantly with substratum type is remarkable, given actualistic evidence that taphonomic damage and processes vary in intensity among environments. However, sediment grain size does not emerge as significant by any test, nor does it emerge if only pristine shelves or non-AE shelves are analysed (in fact, P values are all > 0.15). This is consistent with previous meta-analyses: as the molluscan database has grown, sediment grain size has wobbled in and out of significance depending on the metric and the datasets used (Kidwell 2001, 2002b, this paper; Olszewski & Kidwell 2007), suggesting that it is not a first-order factor. Apparently, although habitats differ in their types or relative intensities of taphonomic processes, their overall capacity to destroy shells or otherwise render them taxonomically unidentifiable is comparable, or is perhaps counter-balanced by variation in the intrinsic durability of local molluscan fauna, so that no net trends result.

In contrast, mesh size has consistently emerged along with dataset-size as a significant methodological factor in molluscan meta-analyses (Kidwell 2001, 2002b; Olszewski & Kidwell 2007). The absence of a mesh-size effect in the present analysis of open shelf datasets is probably because most original authors used fine mesh to process samples (25 of 38 were < 1.5 mm; Table 1), so that the coarse/fine differences found elsewhere are not manifest here.

Is death assemblage fidelity adequate for (palaeo)ecological analysis?

Using the eight shelf datasets where authors censused the living community more than twice, and focusing on taxonomic similarity and rank-order agreement, levels of live-dead agreement are generally comparable to (within the 95% confidence limits of) or better than agreement between successive live censuses within a habitat ('live-live' comparisons; Fig. 4). Live-live agreement itself varies greatly among these eight areas, and can clearly be poor even in pristine settings owing to temporal volatility in populations (e.g., the pristine Amazon shelf, which experiences strongly seasonal storms and upwelling). What is remarkable in Fig. 4 is the strong degree to which live-dead agreement tracks average live-live agreement across this array, despite the vagaries of sampling methods and local environmental circumstances. Live-dead agreement tends to match or exceed live-live agreement where conditions are natural (Amazon) or limited and diffuse (Corpus Christi shelf, English Channel), and declines where human

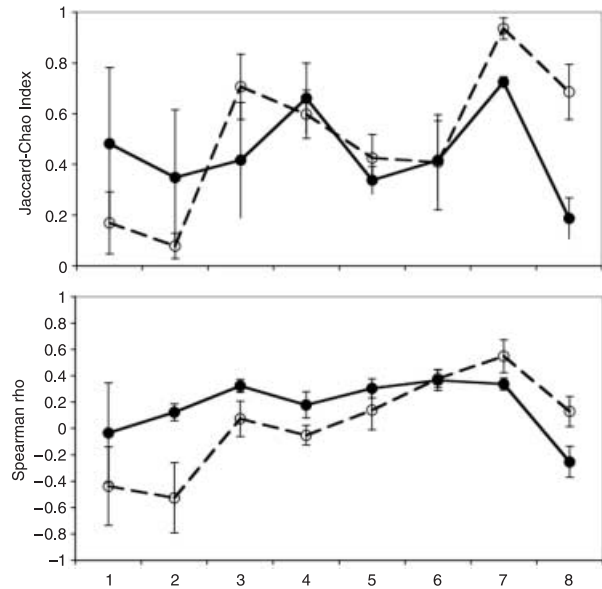


Fig. 4. Mean live-dead (black circles, solid lines) and 'live-live' agreement (white circles, dashed lines) in community composition, with 95% confidence intervals, for eight datasets where the living community was sampled more than twice by original authors. Means reflect all possible pairwise comparisons of live censuses with each other ('live-live') and with dead censuses within a habitat-level study area. Areas arrayed according to degree of human modification: Amazon shelf (1 = fluid mud, 2 = relictual shelly sand, 3 = firm mud, as sampled by Aller 1995), Corpus Christi inner shelf (4, as sampled by Staff & Powell 1999), shell gravels of Eddystone (5), Stoke Point (6) and Plymouth Sound (7), as sampled by Carthew & Bosence 1986), Rhodes Island silty sand (8), as sampled by Zenetos & Van Aartsen 1994.

disturbance is more intense (Plymouth Sound, Rhodes Island; post-mortem transportation also contributes in Plymouth Sound, and possibly on the narrow Rhodes shelf). The high degree of structure in this plot is very encouraging.

The subset of fidelity values that are most relevant to palaeoecology and to ecological analysis of modern death assemblages are those generated from pristine shelves (last row in Table 4). Such death assemblages, *on average*, are enriched by $\sim 25\%$ over a single census of the living molluscan community (Δ -S of 1.25 ± 0.48); their evenness is highly variable but centered near zero bias (Δ -PIE of $+0.02 \pm 0.17$); their taxonomic similarity is very high (Jaccard-Chao index of 0.84 ± 0.12); and their rank-order agreement with the local living community is significantly positive (Spearman rho $+0.29 \pm 0.09$). These values are relevant to 'natural' conditions, including the death assemblages that survive from precursor communities in areas subject to anthropogenic modification, and should be conservative given that the composition of the living community is based upon a single census. They are also conservative in that they are based upon analysis of complete species lists, including rare species: Zuschin & Oliver (2003)

have shown that most fidelity metrics improve significantly if only species comprising > 1% of the assemblage are considered.

Finally, these average values are appropriate only for judging the likely fidelity of *collections* of assemblages, such as might be used to compare the richness of one habitat to another or to establish general trends over time. They should not be applied to individual samples. For that, one would want to know the average live–dead agreement per collecting station or sample. This would generally be lower than the average *habitat*-level values presented here, where each value in the database was produced by pooling two to nineteen stations.

Magnitude of time-lag associated with taphonomic inertia

This statistical synthesis of live–dead studies suggests that molluscan death assemblages can have considerable value as ecological time-capsules, both in natural areas and in areas of anthropogenic stress. However, better information on the history of existing study areas, along with well-designed new studies, are needed to quantify the time-lag associated with taphonomic inertia. How much time is required for the composition of a death assemblage to ‘catch up’ with a directional shift in community composition, and how does this vary among communities and types of stress? For example, a decade appears to be required for corals killed by eutrophication and macroalgal overgrowth to acquire the *taphonomic* signature (bioerosion) of this change, which leaves no direct *taxonomic* signature (Aronson & Precht 1997; Wapnick *et al.* 2004). In contrast, death assemblages clearly can change rapidly in response to less profound changes in the living community – e.g., minor changes in rank–order within the species list rather than the introduction or extirpation of dominant taxa. Examples include the nearly instantaneous response of back-reef sediments to a hurricane (Perry 1996), local nutrient input (Ferguson 2006), and other variation (Ferguson & Miller 2003).

Lags are difficult to estimate for the open shelf datasets used here, in part because in most cases anthropogenic nutrients have diffuse sources that have intensified over time, as has disturbance from bottom-fishing. However, lags in composition are at least decadal in duration among datasets having the poorest agreements and discrete nutrient sources. For example, live–dead data collected from the Suruga shelf in 1958 shows strong disagreement, even though the pulp mill probably started operating in the late 1940s at least. The Rhodes shelf live–dead datasets sampled in 1983–84 show strong disagree-

ment even though eutrophication of Rhodes Harbour was by then already severe (‘loaded with sewage effluent’) from several decades of tourist development and surface waters of adjacent shelf areas clustered seasonally with harbor waters (Karydis & Coccossis 1990); anthropogenic nutrients were probably reaching the shelf by at least the 1970s. Shelves having more diffuse nutrient sources (various Sicilian and Galveston datasets, sampled in the early 1980s and late 1970s respectively) tend to have better live–dead agreement, but decadal lags are still implicit: globally, eutrophication of estuaries accelerated significantly in the 1950s (Lötze *et al.* 2006), and the eutrophication of shelves has probably accelerated synchronously (e.g. the growing Dead Zone of seafloor hypoxia east of Galveston, first reported in the 1970s (Rabalais & Turner 2001; Osterman *et al.* 2005). The Eddystone area of the English Channel exhibited quite good live–dead agreement when sampled in 1931 (Smith 1932), despite bottom-trawling, but only moderate agreement in 1980 (Carthew & Bosence 1986), by which time the area would have been considered AE (Micheli 1999) and, like most northern European shelves, was becoming intensely trawled by more destructive gear (Kaiser 1998).

Summary and conclusions

1. Thirty-eight molluscan live–dead datasets were scored for method of field collection, dataset size, habitat-level characteristics such as sediment grain size and organics, and shelf-level characteristics including the impact of humans on the benthic environment (disruption from bottom-trawling and increased nutrient loads from local populations, agriculture, and industry).
2. Of the eleven methodological and environmental variables tested as possible factors in live–dead agreement, shelf health and shelf width have the strongest explanatory power, with fidelity being poorest on narrow shelves undergoing AE.
3. Differences in the species composition of living communities and counterpart death assemblages indicate that anthropogenic modification of the living community – particularly increased nutrient loads – is the actual cause of low fidelity, and not post-mortem transportation, despite the association with narrow shelves. The composition of the death assemblage lags significantly behind changes the local community (taphonomic inertia), retaining a strong signal from the precursor community.
4. Trawling tends to co-occur with AE and thus is implicated in lower fidelity, but generally does

- not emerge as significant by itself; shelf width does not emerge as important among non-AE shelves; and fidelity is not sensitive to nutrient levels on non-AE shelves (some 'natural' shelves have high-organic loads from upwelling). All of these negative tests are consistent with anthropogenic modification of nutrient levels as the key variable in actualistic fidelity estimates on open shelves.
5. The ratio of dead:live individuals, which is a product of time-averaging and allochthonous input, is also a significant factor for some metrics (evenness, species rank-order).
 6. Together, the variables of shelf health, shelf width, and dead:live ratio explain 20–35% of variation in the fidelity of community diversity (Δ -S and Δ -PIE) and taxonomic similarity (Jaccard–Chao similarity), and ~60% of variation in species rank-order information (Spearman correlation coefficient). The remaining variation must have sources not investigated rigorously here, such as (1) temporal and spatial variability in community composition that is not captured by single-census live data, and (2) differences in the intrinsic preservation potential of species (shell form and composition, living abundance, mortality rate, rate of population turnover). Organic-loving species do appear to have intrinsically lower preservation potential than other species in high-nutrient settings (both natural and AE).
 7. Post-mortem transportation certainly occurs in modern and ancient shelf settings, but in the present database is unambiguous in only a few datasets, all from wide shelves where adjacent intertidal or estuarine habitats are the source area. Even then, allochthonous input affects live–dead agreement in diversity (richness and evenness) but not in the composition of the death assemblage, and affects diversity only under certain circumstances (when low-evenness exotic material is contributed to a high-evenness indigenous death assemblage).
 8. The observations (1) that the fidelity of some AE shelves ranges to values as high as found on non-AE shelves, with lowest fidelity restricted to shelves that are both AE and narrow, and (2) that organic-loving taxa may have fundamentally low intrinsic preservation potential regardless of setting, suggest that a combination of disadvantageous taphonomic and ecological factors are required to degrade fidelity to the lowest values observed in this database. The fidelity of molluscan death assemblages is remarkably resistant to modification by single methodological and extrinsic environmental factors.
 9. Live–dead comparisons on shelves that have suffered minimal human impact provide fidelity values most relevant to (paleo)ecological analysis. There, death assemblages are on average 25% richer than a single census of the living molluscan community (average Δ -S is 1.25 ± 0.48), average Δ -PIE is 0.02 ± 0.17 , taxonomic similarity is high (Jaccard–Chao index of 0.84 ± 0.13), and species relative abundances are positively correlated (0.29 ± 0.09). Based on a limited number of studies, live–dead agreement in composition is comparable to or better than the agreement found among successive live censuses.
 10. Because of taphonomic inertia, which may cause death assemblages to lag in composition for a decade or more behind significant anthropogenic changes in the living community, death assemblages probably provide reasonable time capsules of the average, pre-impact community.

Although many factors in death assemblage fidelity still require exploration, the human footprint on modern environments clearly deserves consideration in the design and interpretation of actualistic studies.

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Note added in proof. – Seventy-three molluscan data sets from estuaries and lagoons, analyzed to test the generality of patterns found here in open shelf settings, have also revealed significantly poorer average live–dead agreement in settings of documented anthropogenic eutrophication (AE) than in areas where AE and other human impacts are negligible (Kidwell 2007). Live–dead discordance thus might be widely useful as a conservative means of recognizing strong, recent change in ecological systems, given taphonomic inertia.

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