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Ecological Fidelity of Molluscan Death Assemblages

Susan M. Kidwell

Abstract: *Comparative analysis, still in progress, of marine molluscan faunas and their associated dead shells (so far comprising 80 habitat-level live-dead datasets from 17 study areas) indicates that sedimentary death assemblages are remarkably robust reflections of local community composition. Virtually all live species (mean 89% ±5) are present in the local death assemblage, dead individuals overwhelmingly belong to species found living in the same habitat (mean 82% ± 10), and the rank abundances of dead species do not diverge significantly from those of live species (80% of datasets tested; $p < 0.05$). Even small samples of the death assemblage thus capture basic dominance information and habitat preferences of the live fauna, with only slight differences in fidelity among environments (marshes and tidal creeks; intertidal flats; coastal embayments; open marine seafloors). This correspondence is especially striking given the number of post-mortem processes that might act to bias such a record. Because the species richness of a death assemblage is typically 2–3X greater than that of any single census of the local live community, inverse metrics such as "% dead species also present alive" suggest low live-dead agreement. However, the majority of dead-only species are rare and most of the discrepancy (excess dead species richness) is evidently due to undersampling of the live fauna. When limits imposed by sampling are considered, true post-mortem bias from the addition of exotic and relict shells is probably less than 25% of total dead species richness, and would have little effect on abundance-based diversity measures. Molluscan death assemblages thus provide a reliable—plus relatively rapid and inexpensive—means of assessing community composition, both for the purpose of establishing ecological baselines as well as for paleoecological analysis of ancient rocks.*

Introduction

Death assemblages of molluscan shells, sieved from the top few decimeters of sediment in marine habitats, might diverge in composition from the local live community for many reasons. Bias might derive from post-mortem transport of individuals, from differential destruction of species and age-classes (especially shells that are small, fragile, or chemically reactive), and from "time-averaging" of multiple generations and/or community states (because long-term sediment accumulation rates are generally slow compared to population turnover and mixing depths; for reviews, see Powell et al. 1989; Kidwell & Bosence 1991; Kidwell & Flessa 1995). But what are the net effects of these possible biases on the actual composition of death assemblages in modern benthic habitats: that is, to what degree do death assemblages diverge from the local live community? How does live-dead agreement vary among environments, and what are the causes of discrepancies? Quantitative assessment of the ecological fidelity of modern death assemblages is crucial to paleoecological reconstruction, because it indicates the extent to which fossil assemblages can be taken as proxies of original community structure and dynamics. Such tests also indicate the possible utility of death assemblages for environmental impact studies, most particularly their reliability as baselines of pre-impact community state(s). Because dead molluscan shells are typically many times more abundant than live individuals in benthic samples (see data below), they offer an extremely rapid and relatively inexpensive way to establish background conditions in habitats *if* they capture live patterns with sufficiently high fidelity.

Live-dead agreement has been tested in a series of individual studies, mostly by paleontologists during the 1970s and 1980s in response to R. G. Johnson's (1965) seminal study of Tomales Bay, California. The majority of authors reported high live-dead agreement at the habitat- or facies-scale (i.e., after pooling data from multiple samples of a single bottom type), but results were mixed and many were only qualitative (e.g., comparison of cluster analyses). A re-analysis of live-dead studies according to a set of standard metrics by Kidwell & Bosence (1991) indicated that the range in agreement of presence-absence data was largely an artifact of methodological differences among studies, compounded in many instances by undersampling of the live community.

Here I use a larger and more homogeneous collection of datasets to test the fidelity of both relative abundance and presence-absence data at the habitat scale, for environments ranging from vegetated marshes to muddy open shelves. Only half of these datasets are fully electronic (and another dozen are still in earlier stages of vetting and compilation), and so the present analysis is only a progress report (December 1998).

Materials and Methods

Table 1 lists the 17 molluscan datasets used in this analysis. Most studies examined more than a single habitat, and provide either sample-by-sample data on live and dead species or species lists already pooled by habitat. The numbers of samples per habitat range from one to more than 100, and species range from a few to several hundred. In pooling samples, "habitat" is defined operationally as a sedimentary environment that might be recognized as a distinct facies in the rock record. These groupings in almost all cases correspond to clusters based on the composition of the live fauna. A wide variety of bottom-sampling methods were used in the original studies: can cores and trenches in marshes and intertidal flats, and various grab, dredge, and SCUBA-operated suction methods in the subtidal. Samples thus vary widely in volume, depth of penetration (but generally no deeper than 20 cm), bias toward epifauna or deep infauna, and total numbers of specimens (in virtually all studies, live fauna and dead shells come from the same samples). Sieve size also varies (Table 1) along with methods of counting bivalve individuals.

The minimum requirement for a dataset in this re-analysis is unambiguous information on whether species occur alive, dead, or both alive and dead within a habitat. The most common shortcoming in candidate datasets, especially older benthic surveys that were not conducted for the purpose of live-dead comparison, is the failure to indicate whether dead material is present when a species occurs alive: authors commonly note when a species is known only from dead material, but do not always stipulate the opposite in published lists. Whenever possible, original authors have been contacted to clarify these and other ambiguities in the composition or mapping of samples. In this same way some published presence-absence datasets have also been amended with relative abundance information and some truncated lists have been expanded to include rare species. Several commonly cited live-dead studies have had to be excluded because insufficient data survive for habitat-level tests (Parker 1963; Johnson 1965), because the original tallies mixed live and dead specimens (Straaten 1960), or because live and dead were retrieved from sieves of different sizes (e.g., central bay habitat of Lingwood 1976a but not other habitats from the same study area). Two other studies are excluded from this analysis (although included in the analysis of Kidwell & Bosence 1991) because the environment is known to have changed significantly through human intervention in the recent past. This includes Mevagissey Bay, England, which is changing from a muddy to a shell-gravel bottom following cessation of China clay waste water input in the 1970s (Knight 1988), and Canso Bay, Nova Scotia, where construction of a causeway in 1954 changed water circulation significantly (Wagner 1975). Live-dead agreement is tested using five different metrics, described with the results below.

Results

RESULTS OF TEST I: PERCENT OF LIVE SPECIES CONTRIBUTING DEAD MATERIAL

Almost all species sampled alive in a habitat are also present in the death assemblage (grand mean 89% ± 5, based on 80 habitat-level measures of live-dead agreement): 91% of live species in vegetated marshes and their tidal creeks, 86% in intertidal flat habitats, 95% in subtidal habitats of coastal embayments, and 85% in open marine sediments (Fig. 1). Restated, this is the percent of known live species richness captured by the local death assemblage. Means do not differ significantly among broad environmental groupings.

Species that are not present in the death assemblage ("live-only" species) are virtually all numerically rare and, in addition, tend to be small-bodied, exceptionally thin-shelled, composed of organic-rich shell types (such as nacreous aragonite), or all of these (e.g., species among small fragile ericynacean bivalves and rissoid and opisthobranch gastropods, and among fragile pinnid, anomiid, and solenid bivalves). These biases match those found by Valentine (1989) in his province-level comparison of living and Pleistocene molluscan faunas from the Californian Province.

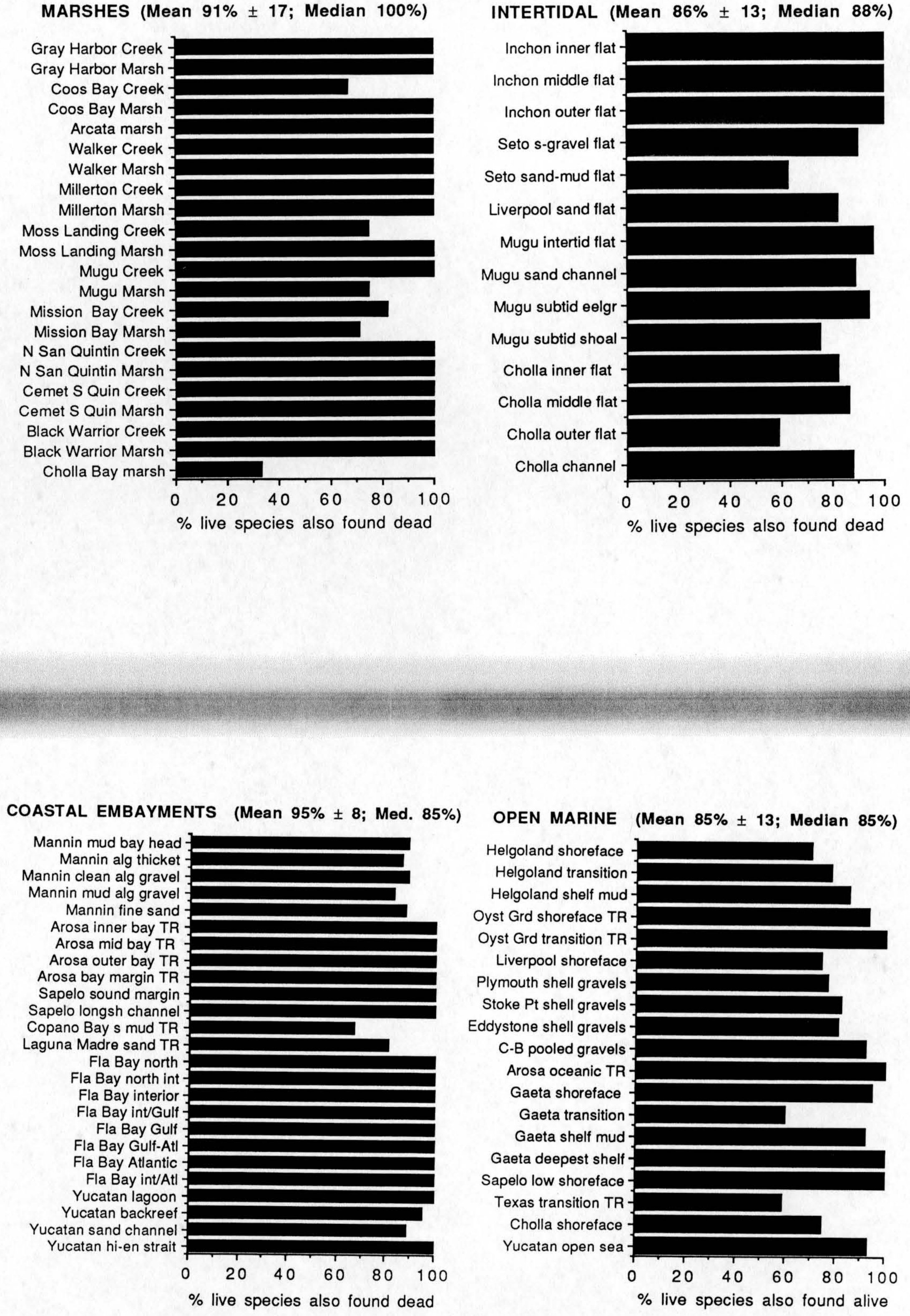
RESULTS OF TEST II: FIDELITY OF DEAD INDIVIDUALS TO SPECIES' LIFE HABITATS

Although death assemblages typically contain 2–3X more species than are found alive in the same set of samples, most dead *individuals* in these death assemblages belong to species documented alive in the same habitat (82% ± 10 grand mean of 67 habitat-level measures). Ninety-three percent of dead individuals in marshes and creeks are from species that were also found alive, 76% in intertidal habitats (83% if the Inchon inner flat data point is excluded; live in this habitat consisted of a single specimen), 88% in coastal subtidal habitats, and 72% in open marine habitats (Fig. 2). Restated, this is the percent of the local death assemblage (dead individuals) that could be generated by the local live community based on the current composition of the live community, and shows that death assemblages are preferentially composed of species that are known to live locally.

The remaining dead individuals (from "dead-only" species) may have several explanations. Some are possible exotics, that is, specimens imported from other habitats after death, or possible relicts exhumed from older deposits. Intertidal and open marine environments contain the largest proportional numbers of suspect dead individuals (16% and 23%, respectively). A significant

Table 1. Datasets used in analysis of live-dead agreement, indicating data source and number of habitats (bottom types) sampled.

	Vegetated Marsh, Tidal Creek	Intertidal Flats, Channels	Coastal Bay, Ria, Lagoon	Open Marine Shoreface, Shelf	Sieve Size	Limits on Numerical Abundance Data
Washington State to Baja California (MacDonald 1969)	11 paired sets				0.5 mm marsh, 1 mm creeks	
Inchon, Korea (Frey et al. 1988)		3			not specified	
Seto Sea, Japan (Tanabe et al. 1986)		2			5 mm	
Mugu Lagoon, California (Warme 1971 & unpubl. data)		4			3mm	
Choya Bay, Mexico (Fürsich & Flessa 1991)	1	4		1	3 mm	no data for rare dead taxa (≤1%)
Liverpool Bay, United Kingdom (Lingwood 1976a,b)		1		1	5 mm	presence–absence data only
Copano Bay & Laguna Madre, Texas (Staff et al. 1986)			2		0.5 mm	no data for rare taxa (≤1%)
Florida Bay, Florida (Turney & Perkins 1972)			8		1 mm	presence–absence data only
Mannin Bay, Ireland (Bosence 1979 & unpubl. data)			5		< 2mm	
Ria de Arosa, Spain (Cadée 1968 & unpubl. data)			4	1	2 mm	no data for rare taxa (≤1%)
Sapelo Island, Georgia (Henderson & Frey 1986)			2	1	1.5 mm	
Yucatan, Mexico (Ekdale 1972)			3	4	3 mm	
Gulf of Mexico, Texas (Staff & Powell 1999)				1	1 mm	no data for rare taxa (≤1%)
Oyster Ground, SE North Sea, Netherlands (Cadée 1984 & unpubl. data)				2	1mm	no data for rare taxa (≤1%)
Helgoland Bight, North Sea, Germany (Reineck et al. 1971)				3	6.3 mm	digitized from spindle diagrams
English Channel, SE United Kingdom (Carthew & Bosence 1986 & unpubl. data)				3 sets of shell gravels	2 mm	
Gulf of Gaeta, Italy (Dörjes 1971; Hertweck 1971)				3	8 mm	digitized from spindle diagrams



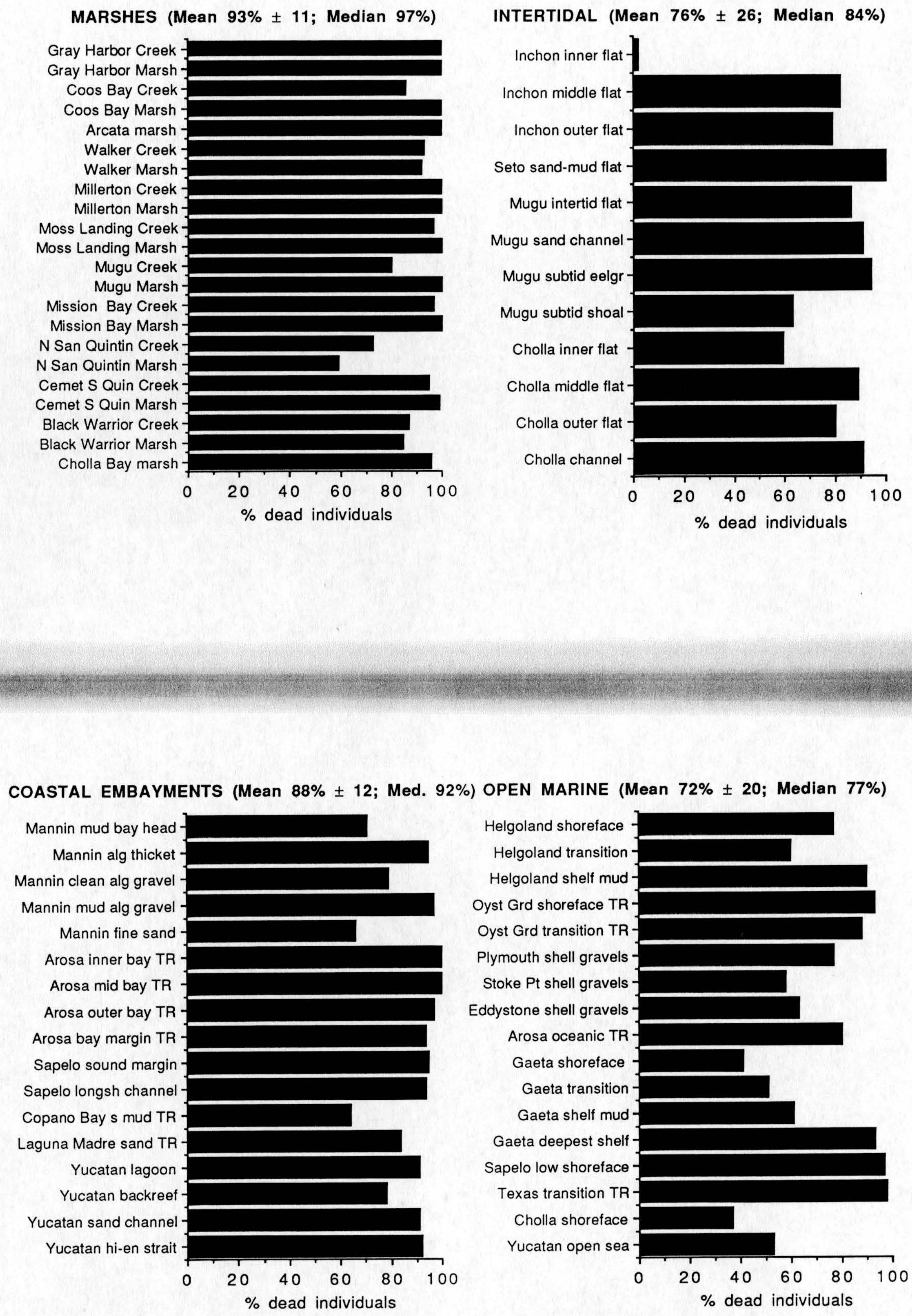
MARSHES (Mean 91% ± 17; Median 100%)

INTERTIDAL (Mean 86% ± 13; Median 88%)

COASTAL EMBAYMENTS (Mean 95% ± 8; Med. 85%)

OPEN MARINE (Mean 85% ± 13; Median 85%)

Fig. 1. Live-dead agreement as measured by the percent of live species that were also sampled dead in the same habitat ("% live species also present dead"). Each bar reflects a habitat-level dataset within a study area. Study areas are listed from north (top) to south (bottom), with habitats arrayed onshore to offshore within each study area. TR = truncated dataset lacking data on rare species, usually defined as <1% of individuals. The vast majority of mollusk species leave a record in the local death assemblage (grand mean of all habitat-level datasets is 89% ± 5; n = 80).

 MARSHES (Mean 93% ± 11; Median 97%)

INTERTIDAL (Mean 76% ± 26; Median 84%)

COASTAL EMBAYMENTS (Mean 88% ± 12; Med. 92%)

OPEN MARINE (Mean 72% ± 20; Median 77%)

Fig. 2. Live-dead agreement and spatial fidelity as measured by the percent of dead individuals in the death assemblage that are from species also sampled alive in that habitat ("% dead individuals"). The vast majority of dead specimens are from species known to occur in the same habitat (grand mean of all habitat-level datasets is 82% ± 10; n = 67).

number of these might in fact be exotics or relicts, since these environments include the highest energy, most erosive, and most sediment-starved habitats (intertidal flat margins, various tidal channels, foreshore and shoreface sands, starved offshore shell gravels; cf. Cadée 1984). However, dead-only species might also result from undersampling of the live community: most live datasets are based on a single census of the local community and thus are almost certainly incomplete measures of actual live diversity. Single censuses are unlikely to sample all rare live species, especially those that are patchy or seasonal in occurrence within the habitat (cf. Peterson 1976). Opportunistic species, in particular, can depress live-dead agreement by this metric: they can contribute large numbers of dead shells both to local and to exotic habitats, since these shells tend to be small and relatively transportable, and even multiple censuses can fail to encounter live specimens (cf. Levinton 1970). In fact, large numbers of dead opportunistic bivalves flood a few of the habitat-level datasets included in this analysis (e.g., *Lentidium* transported into Gaeta shoreface, transition, and shelf mud facies; Hertweck 1971).

Even taken at face value, these results indicate that habitat preferences are far from obliterated by post-mortem transport. Most death assemblages are overwhelmingly dominated by demonstrably indigenous specimens (40 of 67 habitats measured have ≥ 85% indigenous dead individuals; Fig. 2). In addition to almost always being rare, species not sampled alive tend to be small-bodied, epifaunal or epiphytic (thus raft-able), derived from shallower water habitats (including rocky shores and subtidal outcrops), or all of the above (e.g., seaweed-dwelling rissoid and other small gastropods; freshwater and land gastropods). The shared attributes of dead-only species provide further evidence for selective rather than wholesale post-mortem transport of individuals out of and into habitats. Thus, the most abundant species in a death assemblage are generally meaningful indicators of habitat preferences during life, with potential exceptions being predictable from species and/or habitat characteristics.

Results of Test III: Fidelity of Dead Rank Order to the Local Live Community

Species rank abundances in death assemblages are strongly correlated with census data from the local live community: in 13 of 16 habitat-level datasets tested so far, the null assumption that live and dead rank orders are mutually independent is rejected at $p < 0.05$ (Spearman rank test; Conover 1980; Fig. 3). Species that dominate the live community (in a single census) usually also dominate the dead; and species that are numerically rare alive are usually also rare dead. The three datasets with poor rank-order agreement have poorly known live faunas based on fewer than 50 live individuals (and pooling of only a few samples from the habitat), in contrast to the other datasets where live rank-order is based on hundreds to thousands of live individuals.

Results of (Inverse) Test IV: Percent of Dead Species Also Present Alive

The species richness of a death assemblage is generally 2–3X that of live fauna collected in the same sedimentary volume. Consequently, an impression of relatively poor live-dead agreement results if the metric is "% of dead species also present alive" (grand mean 46% ± 10, 80 habitat-level measures; Fig. 4). Marsh and creek habitats show the best live-dead agreement by this metric (mean 61%), probably because the numbers of species are so low (most datasets have < 10 species). However, the 95% C.I. is so large that this does not differ significantly from the situation in other environments: 42% of dead species are also found alive in intertidal habitats, 38% in coastal subtidal habitats, and 45% in open marine habitats (Fig. 4).

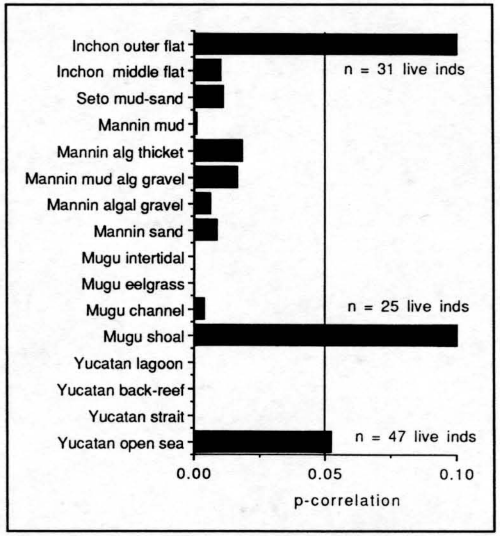


Fig. 3. Live-dead agreement in species' rank order: 13 of the 16 habitat-level datasets tested show no significant difference between live and dead species' rank order, indicating that death assemblages capture dominance information from the live community. The three exceptions have poorly known faunas based on fewer than 50 live individuals.

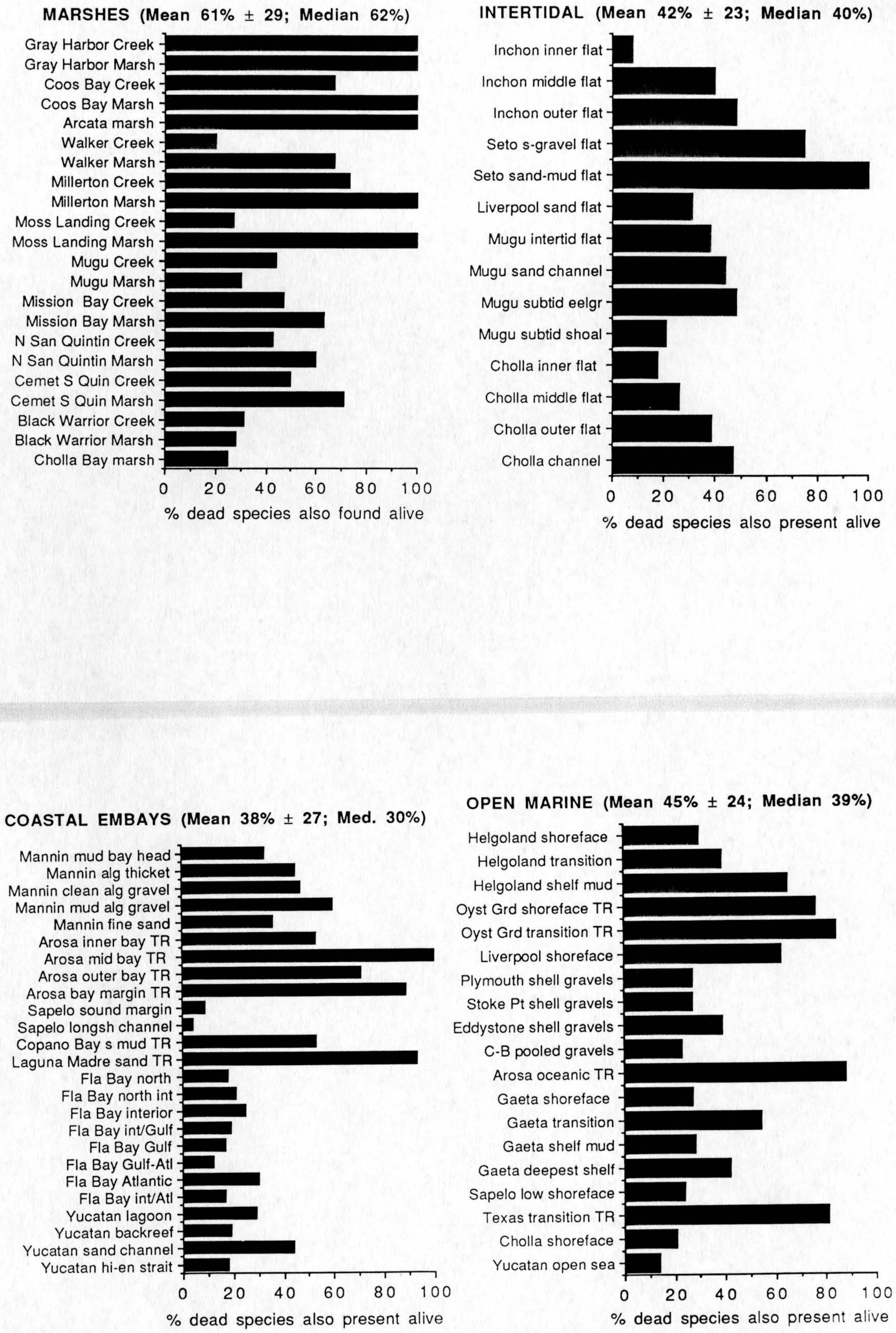
Across all environments, virtually all dead-only species are numerically rare (represented by only a few specimens and often in only a few samples from the habitat). This is consistent with the results of Test II above (grand mean 83% of dead individuals are from species that are also found alive). It also explains why truncated datasets, from which rare live and dead species have been excluded, usually yield significantly better live-dead agreement than full datasets by this same metric (note bars labeled TR in Fig. 4). For example, in the Ria de Arosa, Spain (Cadée 1968 and his unpublished data), the percentage of dead species also found alive in the open shelf habitat is 88% if rare species are excluded from the comparison but 30% using the full species lists. The same pattern holds for habitats inside the Ria (71% versus 37% in outer bay; 100% versus 25% in middle bay, 53% versus 22% in inner bay, 89% versus ~70% in bay margin; differences are plotted in Fig. 5).

There are many possible explanations for the large number of dead-only species in death assemblages ("excess dead richness"), and more than one may apply to a given dataset, as suggested by most of the original authors of these live-dead studies (references in Table 1). These factors include:

(1) undersampling of the live community. This is almost certainly a factor, since most live datasets in these studies are based on only a single census of the local community, and sediment samples typically yield far fewer live individuals than dead individuals (10–100X; see range in Fig. 6);

(2) enrichment of the death assemblage by exotics. This is almost certainly a factor near rocky substrata, which harbor distinctive fauna that are easily shed into adjacent soft-sediments, and in settings of high surge (e.g., along high-energy foreshores). Because a single exotic specimen adds a species, rare exotic specimens can have a large effect on dead richness but little effect on species relative abundance and rank-order; and

(3) enrichment of the death assemblage with relict shells of species that are now extinct locally. This is almost certainly a source of excess dead species richness in open marine sediments that are palimpsests of Holocene transgression (shelly sand and gravel veneers in shoreface and shelf waters). Relicts may be incorporated by exhumation from older deposits or by exceptionally



MARSHES (Mean 61% ± 29; Median 62%)

INTERTIDAL (Mean 42% ± 23; Median 40%)

COASTAL EMBAYS (Mean 38% ± 27; Med. 30%)

OPEN MARINE (Mean 45% ± 24; Median 39%)

Fig. 4. Live-dead agreement as measured by the percent of dead species that are also present alive in the same habitat ("% dead species also present alive). Bars as in Fig. 1. Death assemblages typically contain 2–3X the species richness of any single census of live fauna in the habitat, resulting in low live-dead agreement by this metric (grand mean of all habitat-level datasets is 46% ± 10; n = 80).

prolonged time-averaging of shell production, such as over periods of environmental change and local species extinction. Points 2 and 3 are probably part of the explanation why, among all open marine environments, shoreface sands and shell gravels consistently have greater excess dead species (lower % dead species found alive) than do fine-grained habitats (Fig. 5).

Before attributing live-dead discrepancies to taphonomic bias (points 2 and 3 above), the impact of possible undersampling of the live fauna must be evaluated. Pooling of data from replicate censuses of live communities over time, in order to capture indigenous but ephemeral species, is one method of improving species inventories. The few live-dead datasets where single study areas were subjected to replicate sampling programs do show a positive effect on live-dead agreement, supporting a hypothesis of sampling bias (Kidwell & Bosence 1991). In warm-temperate lagoons of southern California, for example, live-dead agreement by this metric (% of dead species also found alive) improved from 20% to 75% as live species richness accrued over 3 yr of successive benthic surveys (Peterson 1976), and a similar but smaller effect was found in open shelf habitats by successive pooling of three censuses over 17 yr (from 37% to 54%; Knight 1988) and of seven censuses over 90 yr (from 23% to 58%; Carthew & Bosence 1986) (calculations by Kidwell & Bosence 1991) . In all three studies, the pooled live data were compared with dead data from a single set of sediment samples. Longer-term sampling programs in more areas are needed to fully test this effect on live-dead agreement.

Increasing the number of samples per habitat also improves inventories of live species, and, thus, one might expect live-dead agreement to be higher among datasets based on dense sampling arrays. Within a habitat, live-dead agreement does increase with pooling of additional samples, up to the maximum number of samples available. However, the results are mixed when different habitat-level datasets are plotted on a single graph, probably because samples vary so much in type among studies and even among habitats in a single study (collecting gear, sieve size, etc.), yielding a large amount of scatter (Fig. 5). For example, marsh, intertidal, and open marine datasets show no correlation between live-dead agreement and sampling density. In coastal embayment habitats, datasets based on larger numbers of samples do have higher live-dead agreements when complete live and dead species lists are compared (truncated species lists consistently generate better live-dead agreement; Fig. 5). In open marine seafloors, shell gravels and shoreface sands generally exhibit lower live-dead agreement by this metric than do fine-grained open shelf substrata. This is consistent with their containing a significant number of relict shells, as mentioned above, but it may also be a consequence in part of shell gravels supporting fewer live individuals than adjacent soft substrata (e.g., Allen 1899), so that the live community is more difficult to inventory.

Live-dead agreement by this metric is correlated positively with the ratio of live to dead individuals, attaining 40–70% levels in datasets where the abundances of live and dead individuals are about equal (truncated datasets excluded from analysis; Fig. 6A). For datasets with larger numbers of live individuals, live-dead agreement rises to 70–100% (Fig. 6A). In contrast, the proportion of live and dead individuals within a dataset has no effect on the percent of live species found dead, which is consistently high (same metric as in Test I; Fig. 6B), showing that the correlation for percent dead species in Fig. 6A is informative. In future work, cumulative species curves will be generated to establish how well these numbers of live and dead individuals capture local or regional richness. But, even the bivariate plot presented here (Fig. 6A) shows the strong negative effect on live-dead agreement caused by undersampling live fauna.

These analyses indicate that the excess dead species richness (large numbers of dead-only species) observed in virtually all datasets are in many instances artifacts of undersampling of the local live community, rather than indicators of severe taphonomic bias in the death assemblage. Correlations between live-dead agreement and various measures of sampling intensity indicate that most dead species richness could accrue through normal time-averaging of spatially and temporally patchy populations indigenous to the habitat, such as might be sampled alive through an ambitious program of replicate censusing.

RESULTS OF (INVERSE) TEST V: OBSERVED LIVE-DEAD AGREEMENT COMPARED TO CALCULATED MAXIMUM POSSIBLE AGREEMENT

Given that so many datasets suffer from undersampling of live faunas, a more suitable method of estimating live-dead agreement might be to compare the observed "% dead species also found alive" (number of dead species also present alive, divided by total number of dead species) against the maximum agreement that is possible in the same dataset (total number of live species, divided by total number of dead species; assumes maximum overlap of the two lists). After all, if a total of only 10 live species are known from the habitat, and dead species richness is 20, then the maximum intersection of dead species with live species (the maximum possible % dead species also found alive) is 50%. A live-dead agreement of only 50% would, in this instance, coincide with the upper mathematical boundary for agreement (100% of maximum agreement possible). If only 40% of dead species are also known alive (that is, some species are live-only), then live-dead agreement is only 80% of the maximum possible, and so on.

Figure 7 plots observed live-dead agreements against their calculated maximum possible agreements; contour lines show how closely individual habitat-level datasets approach maximum possible agreement. In all environmental groupings, virtually all habitat-level datasets plot within 25% of their maximum possible agreement levels (grand mean 88%; graphs include values calculated from both full and truncated species lists where both are available). Live-dead agreement is nearly constant across the 80 habitat-level datasets by this metric, with very few outliers below 75% agreement values.

Conclusions

The tendency for live-dead agreement to rise to ~75% among several different metrics for presence-absence data suggests that 25% is a reasonable liberal estimate of the proportion of dead species richness that might be exotic or relict in origin. This would be a *maximum* estimate of taphonomic bias in death assemblage species richness, because it is possible that some portion of these 25% dead-only species are indeed indigenous but have simply not yet been encountered alive by the sampling program ("stubborn ecological noise"). Only programs of prolonged replicate sampling of the live community, comparable to scales of time-averaging in the death assemblage, will generate live species lists adequate to test this rigorously. However, some portion of this 25% excess dead species richness will comprise species that are truly exotic to the local habitat, and some portion will be relict, especially in habitats with slowly aggrading or erosive seafloors (see Kidwell & Bosence 1991 and Kidwell & Flessa 1995 for discussions of time-scales of faunal mixing in these various circumstances).

It should be realized that various inverse measures of live-dead agreement on species' presence-absence are the most pessimistic assessments of death assemblage fidelity. For example, truncated datasets that exclude rare species (species comprising < 1% of individuals) can yield ~75% or better live-dead agreement levels, even when based on small numbers of samples.

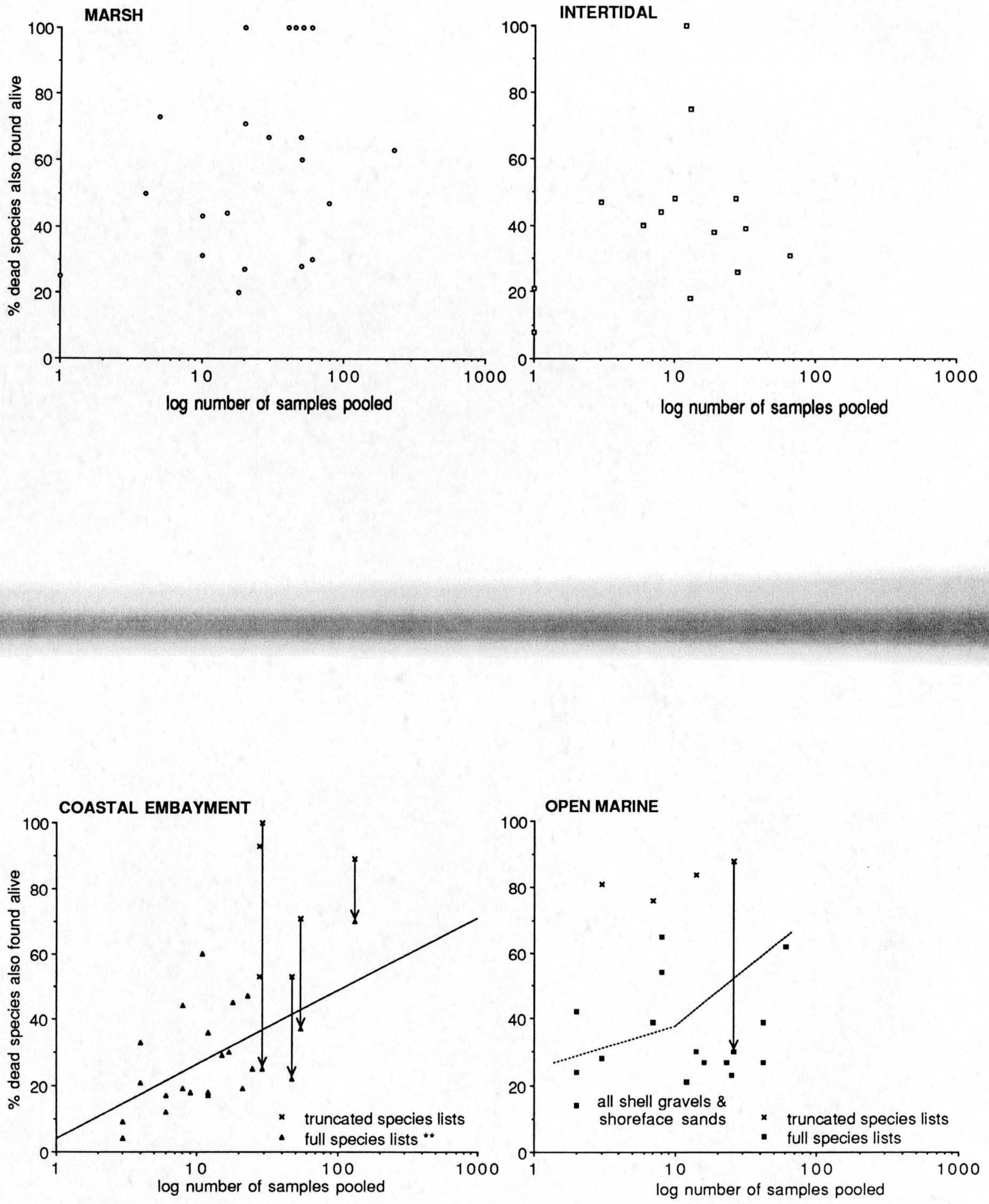


Fig. 5. The percentage of dead species also present alive shows no significant variation with number of samples except for habitats in coastal embayments (** significant at $p < 0.01$). Truncated datasets (x's) consistently have the highest live-dead agreements; arrows point to the lower values that are calculated when full (complete) species lists are used. Among open marine datasets, live-dead agreement is consistently lower in shell-gravels and shoreface sands (points below dashed line) than in the silty sands and muds of transition zone and offshore habitats.

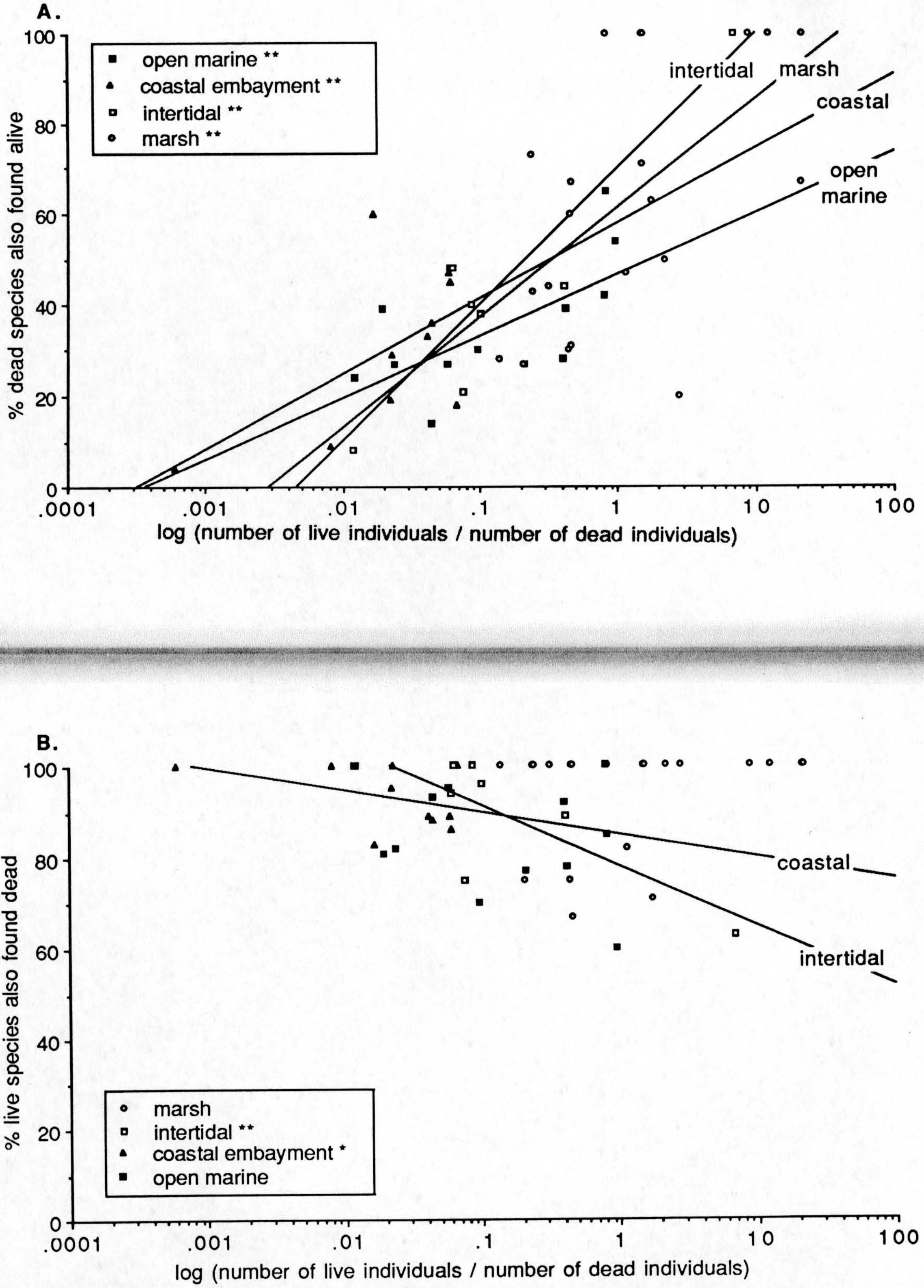


Fig. 6. A) Live-dead agreement as measured by the percent of dead species also found alive is correlated with the ratio of live to dead individuals in the dataset, indicating that much of the excess species richness in death assemblages is an artifact of undersampling of local live fauna. B) In contrast, the percent live species also found dead is unaffected by the proportion of live and dead individuals in the dataset. Truncated datasets not included in analysis. * significant at $p < 0.05$; ** significant at $p < 0.01$.

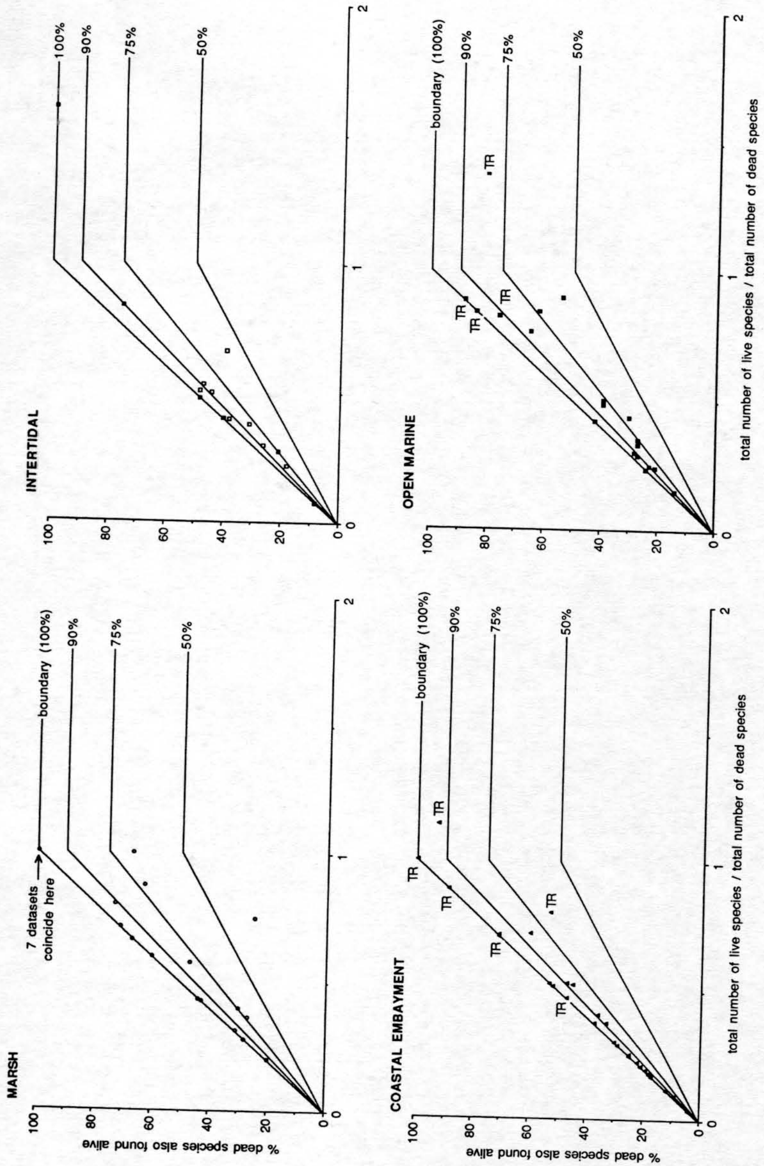


Fig. 7. To evaluate the effect on live-dead agreement of undersampling live fauna, observed values of percent dead species (number of dead species also present alive, divided by total number of dead species) are plotted against the maximum possible percent of dead species that can also be present alive (total number of live species, divided by total number of dead species in the same dataset). The majority of datasets have observed live-dead agreements that are within 75% of the calculated maximum agreement possible (grand mean of all habitat-level datasets is 8%; n = 71).

Table 2. Summary statistics by general environmental zone (mean and standard error, median in square brackets, and number of habitat-level datasets).

	marshes	intertidal flats	coastal embay-ments	open marine seafloors	grand means
I. % live species also present dead	91 ± 17 [100] (n = 22)	86 ± 13 [88] (n = 14)	95 ± 8 [100] (n = 25)	85 ± 13 [85] (n = 19)	89 ± 5 (n = 80)
II. % dead individuals from species also present alive	93 ± 11 [97] (n = 21)	76 ± 26 [84] (n = 12)	88 ± 12 [92] (n = 17)	72 ± 20 [77] (n = 17)	82 ± 10 (n = 67)
IV. % dead species also present alive	61 ± 29 [62] (n = 22)	42 ± 23 [40] (n = 14)	38 ± 27 [30] (n = 25)	45 ± 24 [39] (n = 19)	46 ± 10 (n = 80)
V. % dead species scaled to quality of live data	85 (n = 22)	87 (n = 14)	93 (n = 16)	85 (n = 19)	88 (n = 71)

Moreover, forward tests of the contribution of live faunas to death assemblages yield consistently very high live-dead agreement: across all tested habitats, the overwhelming majority of live species (grand mean 89%, Test I) leave identifiable dead material in the life habitat, and the majority of dead individuals (grand mean 82%, Test II) are from species that occur alive in the same habitat (Table 2). Live species thus do leave clear records of their presence in local death assemblages, and post-mortem processes do not homogenize the original habitat distribution of species. Although a more systematic investigation is required, live-only species are apparently not a random draw from the species pool but tend to be rare and exceptionally small or fragile, and thus most absences of species in death assemblages should be ecologically meaningful, especially if morphologically comparable species are present.

Because most dead-only species are rare, excess dead species richness does not compromise the reliability of rank abundance signals in death assemblages: rank orders of species do not differ significantly between live and dead ($p < 0.05$, Test III). Even a few samples from a death assemblage can apparently provide reliable dominance information on the local source live community, with taphonomic uncertainty focused on rare dead-only species. Thus in death assemblages, rank abundance data (and thus presumably the diversity indices based on them) typically show greater live-dead agreement than species richness measures based on presence-absence.

Based on available datasets, molluscan death assemblages thus capture both (1) dominance information, which is not significantly different from a snapshot census of the local community, and (2) information on the time-averaged species richness of the community, including indigenous species that are patchy, ephemeral, and/or sparse in occurrence and thus difficult to inventory in the live community without intense sampling programs. Whether such death assemblage data are deemed adequate depends on the ecological or paleoecologic question at hand—local needs will determine the degree of uncertainty that is acceptable in reconstructing the original biological signal. However, the outlook for practical applications is very good based on these provisional results: molluscan death assemblages show very high quantitative fidelity to the life habitats, taxonomic composition, and dominance structure of local live communities, and the ambiguity in species richness resides among the rare species, as it does even in ecological studies of live communities. Given the great abundance of dead shells compared to live individuals in sediments of most coastal and open marine settings, and the greater ease in processing and archiving such material, death assemblages are extremely promising as a rapid and relatively inexpensive method of benthic community assessment.

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