Mesh-size effects on the ecological fidelity of death assemblages: a meta-analysis of molluscan live–dead studies

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Abstract

Actualistic comparison of death assemblages with local living communities is a standard approach to estimating the quality of paleoecological data, but wide variation in methods of data collection and analysis undermines attempts to draw general conclusions. Here, I apply both standard and meta-analytic statistics to a stringently constructed database of 19 molluscan live–dead studies in order to isolate methodological artifacts from true taphonomic bias, focusing on three paleoecologically relevant aspects of live–dead agreement: (1) the preservation potential of shelled mollusks in their life habitat (percentage of live species that are represented among dead shell material), (2) the habitat-level spatial fidelity of skeletal remains (percentage of dead individuals that are from species also collected alive in the same habitat), and (3) the reliability of species dominance (similarity in the rank-order abundance of live and dead species). Overall, agreement for all three metrics is high, but results are sensitive to dataset size, sediment grain size, and, most importantly, sieve mesh size. Coarse-mesh (sieves ≥ 1.5 mm) datasets are composed of late juvenile and adult specimens and have significantly higher live–dead agreement than fine-mesh datasets (sieves ≤ 1 mm), which include, and are probably dominated numerically by, larvae and newly settled juveniles. Dataset-size effects are present but not significant, and sediment grain-size effects are significant only if datasets are first partitioned by mesh size (live–dead agreement is higher in muds than in sands/gravels). This previously unrecognized mesh-size effect makes sense both ecologically and taphonomically, and identifies a simple protocol for isolating the most reliable information in molluscan death assemblages (i.e., focus on specimens ≥ 1.5 mm). The pervasiveness and magnitude of the effect indicates that mesh size needs greater consideration in future taphonomic studies and in the collection and interpretation of (paleo)ecological data. A post-juvenile focus may also be key to isolating high-fidelity data among other metazoan groups. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

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1. Introduction

Over the past 40 years, the most common approach to estimating bias in paleoecological data (species composition, richness, relative abundances) has been to test agreement between living communities and the locally accumulating death assemblages in modern environments (for review, see Kidwell and Flessa, 1995). Such "live–dead" comparisons have yielded powerful guidelines for paleoecological reconstruction of some groups, most notably for pollen, where actualistic methods have been relatively standard (e.g., number of specimens or volume of sediment per sample; see Davis, 2000). However, for many important

groups in the fossil record, relevant actualistic data are either too scarce to generalize (about four live–dead studies each of reef scleractinians, land mammals, freshwater mollusks, and fouling communities on hardgrounds or dead shells, two studies of echinoids, one study each of decapods and reef mollusks, and none of brachiopods or bryozoans; studies reviewed by Kidwell and Flessa, 1995; Greenstein, 1993; Pandolfi and Minchin, 1995; Greenstein and Pandolfi, 1997; Zuschin et al., 2000) or data are impossible to acquire because of widespread extinction or ecological abandonment of important habitats (e.g., rarity of shelled cephalopods, absence of trilobites, and decline of stalked crinoids in shelf waters and of sessile shelled epifauna in general on muddy seafloors).

Marine bivalves and gastropods have been a happy exception, being the focus of many live–dead studies (for

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classic early studies, see Johnson, 1965; Cadée, 1968; Warme et al., 1976; for general reviews, see Kidwell and Bosence, 1991). However, it has been difficult to isolate true taphonomic bias from this wealth of information because of large among-study differences in sample types, sample treatment, dataset size (number of samples pooled), and analysis, as well as in the environments investigated. The quantitative effects of these methodological differences must be clearly identified before the effects of natural post mortem processes can be recognized.

Here, I summarize results from an ongoing project to assess true taphonomic bias in molluscan death assemblages by statistical synthesis of many individual live–dead studies. The aims of this project are to quantify molluscan death assemblage fidelity for use by paleoecologists and ecologists, and also to determine more general factors or procedures applicable to other groups. These results are based on a newly constructed database of 85 habitat-level datasets from muds, sands, and gravels in marine environments, and quantify the effects of dataset size, sieve mesh size (body size, ontogenetic age), and sediment grain size on three measures of interest to paleoecologists: (1) the preservation potential of shelled mollusks (percentage of live species that are represented among dead shell material), (2) the habitat-level spatial fidelity of skeletal remains (percentage of dead individuals that are from species also collected alive in the same habitat), and (3) live–dead agreement in species dominance (similarity in species rank-order numerical abundance). The latter point was first reported in Kidwell (2001a), but results from this database for the first two metrics are original to this paper.

For purposes of data synthesis, in the present paper, a "study" is a published article or archived thesis where an author reports numerical data for live and dead species from one or more habitats, i.e., one or more sedimentary facies. Most studies focus on only a single study area, but some contain information on several different areas (e.g., MacDonald's (1969) study of live and dead mollusk abundances from marsh and tidal creek habitats in 11 different estuaries along the Pacific coast of North America, versus Warme's (1971) study of three habitats (sandy intertidal flat, subtidal sand, and subtidal grassbed) in Mugu Lagoon). A "dataset" consists of live and dead data (species lists) based on pooling samples from a single habitat (sedimentary facies) within a single study area.

2. Data sources and methods

This project began informally ~ 10 years ago while writing a review article with Dan Bosence (Kidwell and Bosence, 1991). By going back to the raw data of 17 original studies and recalculating live–dead agreement in habitats using a standard set of metrics (including the first two listed above), we found that (a) studies yielded far more consistent answers than generally appreciated, (b) live–dead

agreement was very good for some metrics (i.e., taphonomic bias was low), and (c) the studies finding poor live–dead agreement generally suffered from low quantities of information on the live community (thus making it difficult to conclude that post mortem processes were necessarily responsible for live–dead disparities).

Contrary to expectation, we could not detect any clear differences in live–dead agreement among major environments (bathymetric zones: marsh versus intertidal versus subtidal coastal embayments versus open shelf). However, the studies we considered were very heterogeneous in terms of field methods and data type, including some studies for which only presence–absence data, occurrence data, or data on the dominant species were available. Subsequent tests on a slightly improved database (17 studies, 14 of which were retained from Kidwell and Bosence, 1991) suggested that high variance on the shelf was linked to sediment grain-size effects, and that, in general, studies with incomplete species lists (rare species omitted) produced inflated estimates of live–dead agreement ("1998 database"; Kidwell, 1999, 2001b). I also formally tested species rank-order agreement for the first time (16 habitat-level datasets from four studies; 87% had significant live–dead correlation). However, the studies in the database were still too methodologically heterogeneous—and too incompletely digitized—to test these and other effects with certainty.

Consequently, I began a concerted effort to upgrade the database by contacting original authors for supplementary information, and searched the fisheries and ecological literatures for additional studies to include. This brought the total to 45 molluscan live–dead studies, of which 19 (eight from the original set of 17) meet the stringent criteria for inclusion in the present (2001) database. The criteria were: (a) live and dead specimens were sieved from the uppermost part of the sedimentary column (usually the top 10–20 cm) using a single known mesh size (mesh sizes range from 0.3 to 5 mm), (b) numerical abundance data were available for both live and dead material, including rare species, and (c) faunal data for a given habitat were based on samples from at least two stations (that is, data for a facies were based on pooling information from at least two replicate samples of the facies, so that a mean could be calculated). The 19 studies meeting these criteria encompass 30 different study areas from tropical to temperate latitudes (0–56° N) and molluscan habitats ranging from salt marshes and tidal creeks to muds and relictual shell gravels of the outer shelf (Appendix A).

For each study area, I pooled individual samples into habitat-level datasets on the basis of sedimentary grain size, seafloor features (bedforms, vegetation, and mass properties, e.g., soft ground, firm ground), and salinity (when a strong gradient was reported). These features were the most commonly available environmental information for studies, and also are most likely to be reconstructed by paleontologists. The 19 studies yielded 85 habitat-level datasets meeting the criteria above (live and dead species lists for a

total 1386 samples; Appendix A). These habitats are comparable in spatial scale and distinctiveness to sedimentary facies in the stratigraphic record, and were defined independent of faunal data. For the purpose of testing sediment grain-size effects, "muds" include all mud-bearing sediments including sand–mud admixtures, and "sands" include gravels, shell-gravels, and sandy grassbeds as well as well-sorted sands.

Information on the living community ("live data") is usually based on only a single census (samples from a single visit), thus providing a very conservative estimate of true live diversity. For 12 of the 85 habitat-level datasets, multi-season time series of the live fauna are also available (Staff et al., 1986; Peterson, 1972; Miller, 1981; Carthew and Bosence, 1986a; Aller and Stupakoff, 1996) (1.75 years maximum duration of sampling program), providing a closer approximation of time-averaged input to the death assemblage. In the present analysis, these 12 datasets are each represented by only one single-census value (census with maximum number of live individuals) and one multi-census value (live data pooled from all seasons of sampling). In virtually all datasets (sets of samples pooled by habitat), live individuals are far less abundant than dead shells, and thus, "number of live individuals" is the most conservative (limiting) measure of dataset size. Datasets where live information is based on fewer than 100 live individuals are considered small because a single specimen would constitute > 1% of the "community"; consequently, the effects of various treatments and environments are tested both for the total database and for the subset of large datasets (each with > 100 live individuals).

The reliability of ecological information based on dead shell material is evaluated in this database (85 single-census datasets) using a combination of standard and meta-analytic statistical methods. (N.B. The 12 multi-season datasets are plotted for comparison, but omitted from statistical analysis.) *Standard statistics* include scatterplots of data, calculated grand mean and median values with 95% confidence intervals (CIs), and "vote-counting", i.e., determining the proportion of datasets that find a significant agreement between live and dead compositions ($P < 0.05$). Two results are considered significantly different if the mean value of one lies outside the 95% confidence intervals of the other.

Meta-analysis is a formal statistical method of weighting and combining the results of many independent studies ($n \gg 2$) of different sizes (different numbers of samples, etc.) in order to quantify an overall effect (Hedges and Olkin, 1985). For example, does the experimental treatment differ significantly from the control, and, more importantly, what is the average magnitude of the treatment effect (positive or negative? How positive? How negative?)? These methods were developed in the social sciences but are widely used in medicine and ecology (Gurevitch and Hedges, 2001; Osenberg et al., 1999), and are here applied to paleoecology for the first time (Kidwell, 2001a). Basically, a meta-analytic "effect magnitude" is a weighted

mean of all the individual effects observed in a set of studies (i.e., sum of weighted effects divided by the sum of weights); here, the number of species in a dataset is used to weight the effect (live–dead agreement) observed in a given dataset. Fundamentally, meta-analysis is a way to avoid two undesirable alternatives in standard data synthesis: (1) treating every dataset in the analysis equally, even though some are based on very small sample sizes and thus have low confidence, or (2) eliminating small datasets from the analysis a priori, thereby reducing overall statistical power. Importantly, in calculating meta-analytic confidence intervals (here, 95% CIs), variance is calculated as 1 over the sum of weights (here, 1 over the sum of species from all datasets). This is standard meta-analytic protocol: this is variance of the individual *weighted effects*, not variance of the original percentage values or correlation coefficients.

3. Results

3.1. Preservation potential of shelled mollusks in their life habitat

What proportion of the living molluscan community is represented in the local death assemblage (i.e., in the same sedimentary facies)? That is, what is the probability that a shelly species leaves a local sedimentary record?

3.1.1. Standard statistics

Values from individual single-census datasets range from 42% to 100%, but the median value is very high (median 100% of live species are represented by dead material in the life habitat; grand mean 91 ± 3%; $n = 85$ datasets (Fig. 1)). These values are similar to those derived from earlier databases (grand mean 88% in Kidwell and Bosence, 1991; grand mean 89 ± 5% in the 1998 database of Kidwell, 2001b). This estimate of preservation potential is thus quite robust to composition of the database: the overwhelming majority of shelled molluscan benthic species leave a skeletal record in their original life habitat.

Scatterplots (Fig. 1) show that some of this variance is a function of dataset size, in that larger datasets (i.e., habitat-level lists based on larger numbers of live individuals) show slightly less scatter in values and overall higher estimates of species preservation potential (datapoints in Fig. 1(A) and (B) must be combined to visualize scatter in total database). However, this dataset-size effect is too small to change median and grand mean values significantly (e.g., if one were to compare the mean or median value of all fine- and coarse-mesh datasets composed of < 100 live individuals against the mean or median of all datasets based on >100 live individuals).

Sieve mesh size also has an effect. Coarse-mesh datasets (sieve mesh openings ≥ 1.5 mm, that is, mesh sizes of 1.5, 2.0, etc.) yield overall higher values of live–dead agreement

A. Fine-mesh datasets (≤1 mm sieve)

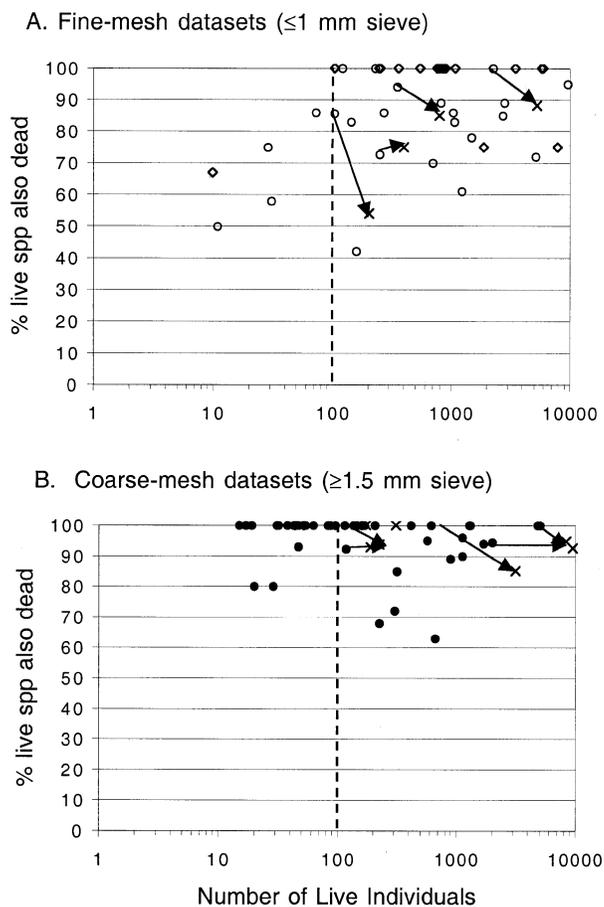## B. Coarse-mesh datasets (≥1.5 mm sieve)

Fig. 1. Preservation potential of shelled mollusks is tested by the metric "what proportion of species sampled alive in a habitat are also present dead?" Each polygon-point on these scatterplots is the raw, unweighted result for a habitat-level dataset, based on a single census of live and dead fauna (diamond = marsh or tidal creek dataset; circle = intertidal, subtidal coastal embayment, or open shelf dataset; total $n = 85$ datasets). For 12 of these habitats, data from multiple seasons of collecting live fauna can be pooled ("×"; arrows connect with single-census results for the same habitat; some arrows overlap). The number of live individuals in a dataset is used as a measure of dataset size (horizontal axis, log scale). (A) Results for datasets generated using a fine-mesh sieve ≤ 1 mm ($n = 43$ single-census datasets). (B) Results for datasets generated using a coarse-mesh sieve ≥ 1.5 mm, and thus only including late juvenile and adult individuals ($n = 42$ single-census datasets). Overall, species in coarse-mesh datasets (i.e., known to be alive as late juveniles or adults) have higher probability of occurring in the local death assemblage than species collected using fine mesh.

(a higher, tighter cluster of values; Fig. 1(B)) than do fine-mesh datasets (≤ 1 mm, i.e., mesh openings of 1.0, 0.8, 0.5, 0.3 mm, etc.; Fig. 1(A)). Coarse-mesh datasets are composed exclusively of late juvenile and adult individuals (body sizes ≥ ~ 1.5 mm), whereas fine-mesh datasets include, and are probably numerically dominated by, larvae and newly settled juveniles (body sizes up to ~ 1 mm).

Multi-season datasets underscore the differing "behaviors" of fine- and coarse-mesh datasets. Pooling samples over time (thereby increasing the known live fauna) tends to decrease the proportion of live species known dead in

fine-mesh datasets more strongly (Fig. 1(A); perhaps because new live species are rare as well as small-bodied) than it does in coarse-mesh datasets (Fig. 1(B)). In both cases, the multi-season values lie within the range of the single-census datasets.

These plots indicate that species present alive as late juveniles or adults have a higher probability of leaving a skeletal record than species present alive primarily (or perhaps only) as larvae or newly settled juveniles. Most paleontologists and taphonomists would intuitively expect this result, and this plot demonstrates how strong this effect can be.

3.1.2. Meta-statistics

Meta-analysis permits the mesh-size effect to be quantified. The percentage of live species also dead from each dataset is weighted (i.e., multiplied) by the number of live species in the dataset, reasoning that a result based on a study containing many species is more reliable than a result from a dataset with only a few species (because the behavior of any single species in a species-rich dataset has proportionately less effect on the outcome for that dataset). The sum of weighted percentage values is then divided by the sum of weights (total number of species, from all datasets) to get the average weighted percentage value, and 95% CIs are calculated using variance as the reciprocal of the sum of weights. Because raw percentage values do not form a normal frequency distribution (note in Fig. 1 that the density of points is skewed toward 100%), the calculated average weighted percentage values will be conservative (low) estimates of the true effect.

This procedure is used to calculate the average weighted effect both for the total database ($n = 85$) and for various subsets of the database (Table 1). *Dataset size* has a slight, but insignificant, effect: values in cells from rows 1 to 3 (total database) are within the confidence limits of counterpart values in rows 4 to 6 (large datasets only). However, *sieve mesh size*, which determines whether the death assemblage is dominated by adults and late juveniles (coarse mesh ≥ 1.5 mm) or larvae and newly settled juveniles (≤ 1 mm), does have a significant effect. Focusing on results from large datasets (> 100 live individuals, all habitats, because fundamentally, these should be the most reliable pictures of the source live community), on average, 93% of live species are present dead in coarse-mesh death assemblages, whereas the average drops to 84% for fine-mesh datasets. (For comparison, these values are 95% and 87%, respectively, if averages are calculated without meta-analytic weighting; Kidwell, 2001a.) Finally, species representation does not vary significantly with sediment grain size (compare mud and sand columns within rows; mean of sand is within confidence interval of mean of mud). That is, species living in sands and gravels are as likely to be represented locally by dead remains as species that live in muds.

Table 1

Average weighted percentage of live species also collected dead, weighted by number of live species, ± 95% confidence intervals. Number of datasets analyzed is within square brackets. N.B. Maximum percent-agreement is 100%

	A	B	C
	All facies	Muds	Sands
Total database			
1. All datasets	88 ± 6 [85]	89 ± 9 [50]	88 ± 8 [35]
2. ≤ 1 mm mesh	83 ± 9 [43]	86 ± 12 [31]	79 ± 13 [12]
3. ≥ 1.5 mm mesh	94 ± 8 [42]	92 ± 13 [19]	94 ± 10 [23]
Datasets with >100 live individuals			
4. All datasets	88 ± 6 [62]	97 ± 9 [39]	89 ± 9 [23]
5. ≤ 1 mm mesh	84 ± 9 [38]	85 ± 12 [29]	81 ± 14 [9]
6. ≥ 1.5 mm mesh	93 ± 9 [24]	91 ± 15 [10]	94 ± 12 [14]

3.2. Habitat-level spatial fidelity of skeletal remains

What proportion of dead specimens in a habitat (facies) are from species known to live locally? That is, to what extent is a molluscan death assemblage dominated by indigenous species?

3.2.1. Standard statistics

Fidelities of individual datasets vary widely from 10% to 100% (Fig. 2), but the median value is quite high (median 86% of dead individuals are from species also sampled alive in the habitat; grand mean 78 ± 5%; *n* = 85 single-census datasets). These values are similar to those from earlier mixed-quality databases (grand mean 83% in Kidwell and Bosence, 1991; grand mean 82 ± 10% based on the 1998 database of Kidwell, 2001b).

As in the analysis of the percentage of live species found dead, scatterplots of raw unweighted values (Fig. 2) show that datasets having the lowest live–dead agreement are small (< 100 or 200 live individuals)—that is, the live fauna that the dead material is being compared with is based on a small number of live individuals and thus is not well known. As datasets with better-known live faunas are considered, there is less scatter in values, and overall live–dead agreement increases.

Segregated by sieve mesh size (Fig. 2(A) versus (B)), fine-mesh and coarse-mesh datasets show similar ranges of live–dead agreement. Coarse-mesh datasets are clustered more tightly and at higher values than the fine-mesh datasets, and they also differ in outliers. Fine-mesh datasets show two dramatic outliers among the largest datasets (Fig. 2(A)): (1) a shoreface sand dataset from the Italian Gulf of Gaeta that is overwhelmed by exotic specimens of the brackish-water bivalve *Lentidium mediterraneum* and freshwater species (imported by seasonal floodwaters), and (2) a sandy mud dataset from brackish Copano Bay, TX, dominated by the dead shells of species with strongly seasonal life-cycles. Multi-season live data are available for Copano Bay (Staff et al., 1986), and live–dead agreement improves from 27% to 77% if these live data are used (arrow connects single-census datapoint to multi-season datapoint). In contrast, the only outlier among the largest coarse-mesh datasets (Fig. 2(B)) is from a shallow subtidal shell gravel in

A. Fine-mesh datasets (≤1 mm sieve)

B. Coarse-mesh datasets (≥1.5 mm sieve)
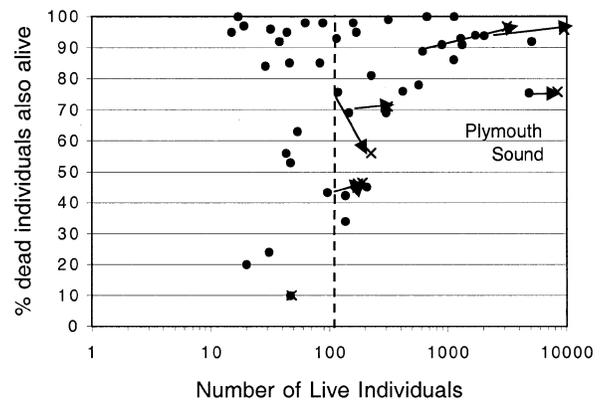
Number of Live Individuals
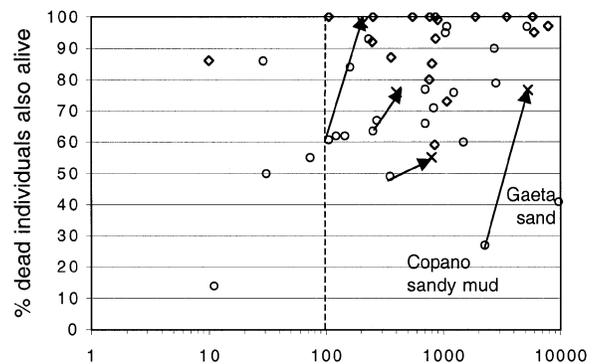
Fig. 2. The spatial fidelity of molluscan skeletal remains is tested by the metric "what proportion of dead individuals are from species also collected alive in the habitat?" That is, what proportion of the death assemblage is demonstrably indigenous to the sedimentary facies? Datapoints are coded as in Fig. 1. As dataset size increases, coarse-mesh datasets funnel rapidly to high live–dead agreement (one outlier). Fine-mesh datasets show greater scatter, but strong improvement if multi-season live data are applied (arrows).

Plymouth Sound that contains large numbers of a minute rissoid gastropod washed in from adjacent rocky intertidal areas: 75% of the dead individuals are indigenous using single-census live data for comparison, and 77% are indigenous if one uses multi-season live data, suggesting that these rissoids are truly exotic to the subtidal habitat (data of Carthew and Bosence, 1986a).

Table 2
Average weighted percentage of dead individuals from species also collected alive, weighted by number of dead species. Other conventions as in Table 1

	A	B	C
	All facies	Muds	Sands
Total database			
1. All datasets	73 ± 3 [85]	72 ± 5 [50]	73 ± 4 [35]
2. ≤ 1 mm mesh	67 ± 5 [43]	65 ± 7 [31]	70 ± 8 [12]
3. ≥ 1.5 mm mesh	76 ± 4 [42]	80 ± 7 [19]	74 ± 5 [23]
Datasets with >100 live individuals			
4. All datasets	76 ± 3 [62]	75 ± 6 [39]	76 ± 5 [23]
5. ≤ 1 mm mesh	68 ± 6 [38]	67 ± 7 [29]	70 ± 9 [9]
6. ≥ 1.5 mm mesh	81 ± 5 [24]	87 ± 9 [10]	79 ± 6 [14]

Again, in general, pooling multiple seasons of live data has a stronger effect in fine-mesh datasets than in coarse-mesh datasets (Fig. 2), and the effect is to increase apparent live–dead agreement (as the live fauna becomes better known, more dead individuals become demonstrably indigenous to the local habitat).

3.2.2. Meta-statistics

For meta-analysis, each dataset was weighted by the number of dead species. This is analogous to weighting by the number of dead individuals, but limits the range in weight sizes to two orders of magnitude (two to 215 dead species per dataset) rather than an unreasonable five orders of magnitude (five to 240 000 dead individuals per dataset). Results are summarized in Table 2. Live–dead agreement by this metric (percentage of dead individuals from species known alive) does increase if only large datasets are considered, but not significantly: in Table 2, values in cells from rows 1 to 3 (total database) lie within the confidence intervals of counterpart values in rows 4 to 6 (large datasets only).

However, as in the preceding section, mesh size clearly does have a significant effect (in Table 2, compare row 2 with row 3, or row 5 with row 6). Focusing on results from large datasets, 82 ± 5% of dead individuals in coarse-mesh death assemblages are from species also sampled alive in that habitat, whereas in fine-mesh datasets, an average 67 ± 6% of dead individuals are indigenous (≤ 1 mm; cell 6A versus 5A). (For comparison, these values are 82% and 68%, respectively, if averages are calculated without meta-analytic weighting; Kidwell, 2001a.) The low live–dead agreement in fine-mesh datasets has two sources. First, the two outlying datasets with low agreement (Gaeta sand and Copano sandy mud in Fig. 2(A)) contain relatively large numbers of dead species compared to other fine-mesh datasets (67 and 81, respectively; median number of dead species per fine-mesh dataset is 16), and thus are relatively heavily weighted. Second, the fine-mesh datasets having 100% live–dead agreement in Fig. 2(A) are all from marshes and tidal creeks. These supratidal datasets contain large numbers of live and dead individuals but low numbers of dead (and live) species (2–18 dead species; median = 5), and thus are weighted only slightly in calculating meta-

analytic averages. (N.B. There are no coarse-mesh datasets from comparable marsh and creek environments.)

Among coarse-mesh datasets, live–dead agreement also varies with sediment grain size: death assemblages in muddy habitats contain a larger percentage of indigenous dead individuals than death assemblages in sandy/gravelly habitats (88 ± 9% versus 79 ± 6%; Table 2, cell 6B versus 6C). That is, death assemblages in sands tend to contain a significantly larger percentage of potentially exotic dead shells than death assemblages in muds. Again, this fits our expectations: sands and gravels tend to be higher-energy settings, and thus should be more likely to receive exotic debris from adjacent rocky shores. Meta-analysis permits the difference in fidelity to be quantified. In contrast, fidelity in fine-mesh datasets does not vary significantly with sediment grain size: in both substrate types, live–dead agreement is ~ 68% (in Table 2, compare cells 5B and 5C). This is ~ 10 percentage points lower than the quality of coarse-mesh datasets in sands, and ~20 percentage points lower than the quality of coarse-mesh datasets in muds.

The phrase "potentially exotic shells" refers to the fact that these values are maximum estimates of exotic content—as information on the composition of the local live community increases, then more and more dead species are known alive, and thus, more and more dead individuals become demonstrably indigenous. However, all datasets should show increases in live–dead agreement with increasing live data, and so, I suspect that, although the absolute values should be higher if live data were universally better, the magnitude of the difference between coarse- and fine-mesh death assemblages and between mud and sand substrata would probably remain unchanged (i.e., ~10%).

3.3. Live–dead agreement in species dominance

Death assemblages clearly share many species with the local live community, and the large majority of dead individuals are drawn from those species (results of the two tests above). But how similar are the relative abundances of species in live and dead assemblages? The simplest approach is to compare the rank order of live and dead species. That is, are the top dead species also the top live species,

and are species that are rare (represented by few individuals) in the death assemblage also rare alive?

3.3.1. Standard statistics

This question was addressed using the non-parametric Spearman rank-order test. I found (Kidwell, 2001a) that individual datasets yield a wide scatter in *P*-levels (statistical significance of results) that can largely be explained by dataset-size and mesh-size effects (Fig. 3). Datasets composed of specimens exclusively ≥ 1.5 mm yield more significant live–dead agreements (*P* < 0.05) than those generated using fine (≤ 1 mm) mesh sizes, especially if datasets based on extremely small numbers of specimens (< 100 live individuals) are excluded; only 60% of fine-mesh datasets with > 100 live individuals show a significant correlation between live and dead rank orders (23 out of 38 Spearman rank tests, individual *P* < 0.05; Fig. 3(A)). In contrast, live and dead species rank orders are significantly correlated in 92% of coarse-mesh datasets exceeding a threshold size of 100 live individuals (22 out of 24 Spearman rank tests, individual *P* < 0.05; Fig. 3(B)). If the threshold mesh size is set at ≥ 2 mm, then 100% of the datasets show a significant correlation.
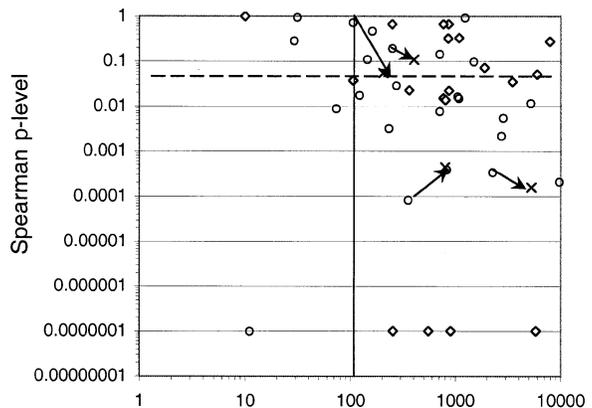
With increasing quantities of live data, live–dead correlations in coarse-mesh datasets become more significant, whether data are increased by larger single-census collections or (less consistently) by pooling time-series data (Fig. 3(B)). Agreement in fine-mesh datasets does not increase with increasing single-census data, but only in response to pooling time-replicate samples (three of four cases; Fig. 3(A)), and these increases are smaller than in coarse-mesh datasets. Overall, discrepancies between live and dead species rank order in fine-mesh datasets appear to reflect a more fundamental methodological or taphonomic problem than inadequate dataset size (e.g., temporal variability in larval settlement).

Hypothetically, in any dataset, the rank orders of live and dead species may be exactly the same (# 1 top species dead is also # 1 top live, # 2 dead is # 2 live, etc.; Spearman correlation coefficient "*r*" of +1), or live species may be in random order relative to dead species (Spearman *r* = 0), or live and dead may occur in exactly opposite order (# 1 species dead is rarest species live, etc.; Spearman *r* = – 1). It is thus highly meaningful that Spearman *r*-values are positive in 92% of the total 85 datasets, and in 97% of the 62 datasets with >100 live individuals. Thus, although not all comparisons are significant at *P* < 0.05 (Fig. 3), coarse- and fine-mesh death assemblages are qualitatively consistent: species that are numerically dominant in a single census of the live fauna tend to be among the most abundant dead in the same set of pooled samples, and species that are rare or absent alive are usually rare among the dead.

3.3.2. Meta-statistics

Meta-analytic synthesis of individual Spearman *r*-values quantifies the strength of this positive result (each *r*-value is
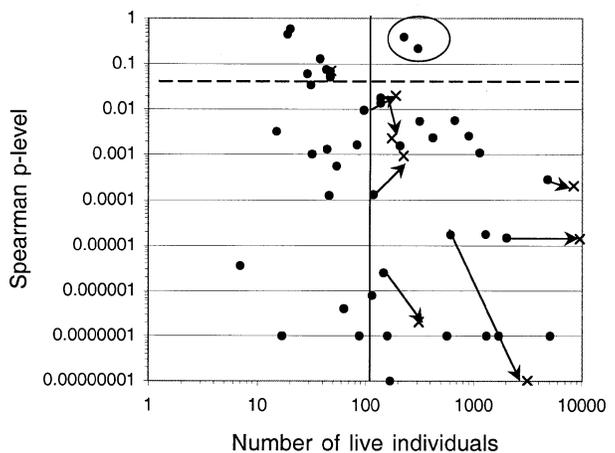

Fig. 3. Live–dead agreement in species relative abundance is tested by the non-parametric Spearman rank-order test. Each point on these scatterplots is the statistical significance (*P*-level) of the Spearman test for a dataset. Datapoints are coded as in Fig. 1. In datasets below the dashed line (*P*-level 0.5), the rank-order abundance of dead species is significantly correlated with the rank order of the live fauna. Virtually all coarse-mesh datasets (B) above a threshold size of 100 live individuals show significant correlations in the rank orders of live and dead species (22 of 24 datasets), whereas fine-mesh datasets (A) show a wide scatter regardless of dataset size.

weighted by the total number of species in that dataset; Kidwell, 2001a). The average weighted *r* for the complete 85 datasets is 0.45 ± 0.03 (Table 3). Eliminating extremely small datasets (< 100 live individuals) increases the estimate slightly but not significantly (average weighted *r* of 0.47 ± 0.04 for the 62 large datasets).

As with other metrics, segregating datasets by sieve mesh size has a large, previously unrecognized, effect: for datasets with >100 live individuals, the average weighted *r* is 0.54 ± 0.05 for coarse-mesh death assemblages (24 datasets) versus 0.38 ± 0.06 for fine-mesh (38 datasets).

Meta-analysis also reveals clear differences in live–dead rank-order correlation as a function of substratum type. For both coarse- and fine-mesh death assemblages, species rank-order correlations are significantly higher in muddy habitats than in sandy habitats (Table 3).

Table 3
Average weighted Spearman rank-order correlation coefficients (r-values), weighted by total number of species. N.B. Maximum possible r = + 1, minimum possible r = – 1. Other conventions as in Table 1

	A	B	C
	All facies	Muds	Sands
Total database			
1. All datasets	0.45 ± 0.03 [85]		
2. ≤ 1 mm mesh	0.37 ± 0.06 [43]		
3. ≥ 1.5 mm mesh	0.50 ± 0.04 [42]		
Datasets with >100 live individuals			
4. All datasets	0.47 ± 0.04 [62]	0.51 ± 0.06 [39]	0.44 ± 0.05 [23]
5. ≤ 1 mm mesh	0.38 ± 0.06 [38]	0.44 ± 0.08 [29]	0.31 ± 0.09 [9]
6. ≥ 1.5 mm mesh	0.54 ± 0.05 [24]	0.61 ± 0.09 [10]	0.50 ± 0.06 [14]

The high rank-order agreement among coarse-mesh death assemblages from muddy substrata (average weighted r of 0.61 ± 0.09) is very encouraging: live–dead agreement apparently prevails despite the high rates of carbonate dissolution documented in many marine muds (linked to microbial decomposition of organic matter; Green et al., 1993; Walter and Burton, 1990) and the potential for exotic (out-of-habitat) shells to be introduced via rafting vegetation and storms (reviewed in Kidwell and Bosence, 1991). Although still strong, the lower rank-order agreement in sand-hosted death assemblages (average weighted r of 0.50 ± 0.06) is expected and probably reflects multiple taphonomic factors, including higher rates of physical destruction and bioerosion, greater hydraulic import/export of shells, and greater time-averaging (especially in "relict" shell gravels and amalgamated sand bodies).

4. Discussion

4.1. Overall agreement levels

All of the metrics of live–dead agreement tested here yield strongly positive results overall, and the broad agreement with earlier results from smaller and less homogeneous databases (Kidwell and Bosence, 1991; 1998 database of Kidwell, 2001b) is encouraging. Based on the present meta-analysis of studies across a wide range of latitudes, bathymetric environments, and non-reefal substrata (Appendix A), on average, ~90% of live species can be expected to be captured by the sedimentary record of their life habitat, three-quarters of dead individuals are produced by species indigenous to the environment of accumulation, and the rank-order abundances of live and dead species are positively correlated (average weighted r of 0.45). These reliabilities can be improved by focusing on particular subsets of the death assemblage and on particular sedimentary habitats (see below).

4.2. Sources of variation

Variation among datasets reflects both methodological artifacts and natural taphonomic factors.

4.2.1. Dataset size

Dataset size—or, more precisely, the quantity of information on live fauna—affects most metrics positively (see trends in Figs. 1–3), but not as strongly as expected from previous work (e.g., Kidwell and Bosence, 1991). In fact, using a threshold of 100 live individuals, differences in live–dead agreement between small datasets and large datasets are present but not statistically significant (column 3, Table 4). Given the trends in Figs. 1–3, the effect probably does exist, but the present database contains too few really large datasets to quantify a significant effect.

Kidwell and Bosence (1991) did not actually test the statistical significance of dataset size, and, moreover, found the strongest qualitative effect where death assemblages were compared against live data pooled from multiple seasons of sampling, rather than the single-census live data used in the present analysis. In the present analysis, the effects of pooling multi-season live data are neutral to positive for coarse-mesh data (which dominated the Kidwell and Bosence, 1991, review), and highly varied for fine-mesh data.

4.2.2. Mesh size

Mesh size, i.e., the body size—and, indirectly, the ontogenetic stage of live and dead individuals—has a strong, consistent, and previously unrecognized effect on all three metrics: coarse-mesh data show higher live–dead agreement (column 4, Table 4). This methodological decision affects live–dead agreement for a series of underlying ecological and taphonomic reasons (Kidwell, 2001a). Ecologically, any census of mollusks based on ≤ 1 mm sieves will capture, and often be numerically dominated by, larvae and newly settled juveniles. Most molluscan recruits die before reaching adult sizes of ≥ ~ 2 mm, and thus, the species composition and abundance of live data generated by fine sieves are especially sensitive to the timing of the live census (as demonstrated by census-to-census variation in the fine-mesh multi-season live data of Staff et al., 1986; Aller and Stupakoff, 1996). Taphonomically, shells smaller than 1.5–2 mm are especially prone to out-of-habitat transport (e.g., Aller, 1995) and can have extremely low persistence in the surficial mixed zone of the seafloor (e.g., half-lives < 100 d, versus immeasurably long persistence of

Table 4

Summary of the effects of dataset size, mesh size, and sediment grain size on ecological information in molluscan death assemblages, based on meta-analysis of live–dead studies

Metric of live–dead agreement [a]	Overall result	Agreement increases as data on live fauna increases?	Agreement higher in coarse-mesh than in fine-mesh datasets?[b]	Agreement varies with sediment grain size?
Number of datasets	85	85	62 large datasets	62 large datasets
Percentage of live species also present dead	88 ± 6%	N.S.	Yes (93% versus 84%)	N.S.
Percentage of dead individuals from species also present alive	73 ± 3%	Yes but N.S.	Yes (81% versus 68%)	Yes for coarse-mesh data (87% in muds, 79% in sands)
Similarity in rank-order abundance	Strong positive correlation ($r = 0.45$)	Yes but N.S.	Yes ($r = 0.54$ versus 0.38)	Yes ($r = 0.51$ versus 0.44)

"Large datasets" are those containing >100 live individuals. N.S. = effect not significant at $P < 0.05$.

[a] All ecological metrics of live–dead agreement are for data pooled at the scale of a sedimentary habitat (facies); live data are based on a single census of living community.

[b] Coarse-mesh data are from meshes ≥ 1.5 mm, fine-mesh data from meshes ≤ 1 mm. Coarse-mesh datasets are dominated by late juvenile and adult individuals, whereas fine-mesh datasets can include, and are probably numerically dominated, by larvae and early (newly settled) juveniles.

specimens $> \sim 2$–3 mm; Cummins et al., 1986). Thus, the composition and abundance of species collected dead in ≤ 1 mm sieves depends, like live data, upon the season of sampling, leading to a wide scatter in values of live–dead agreement among datasets based on a single census. Pooling data from multiple seasons or years should improve agreement, but there are too few such studies to test the effect rigorously (see 12 datasets in Figs. 1–3).

The stronger live–dead agreement found among single-census *coarse-mesh* datasets (body sizes ≥ 1.5 mm, and especially ≥ 2 mm) reflects (a) the relative ecological stability of the late juvenile and adult populations that constitute these size fractions, and (b) the greater taphonomic durability and resistance to transport of larger shells, which is supported by a wide range of experimental and field observations (reviewed by Kidwell and Bosence, 1991).

4.2.3. Sediment grain size

Sediment grain size affects different metrics to different degrees (column 5, Table 4).

It appears to have no significant effect on the short-term preservation potential of molluscan species (that is, preservation through early diagenesis): death assemblages in sandy/gravelly substrata capture the same high percentage of local living species as do death assemblages in muddy substrata. This is a bit surprising, but one explanation might be that the physically harsher post mortem conditions of sands and gravels are counterbalanced by the more robust shells of the species that live there. If so, the taxa missing from sandy death assemblages should consist primarily of species with more delicate shells (analysis in progress).

Sediment grain size affects the percentage of dead individuals that are indigenous, but only among coarse-mesh studies: of specimens ≥ 1.5 mm, death assemblages in sands/gravels contain a higher proportion of potentially exotic specimens than do muds, even when the effects of live-species sample size are taken into account. This finding is consistent with expectations: muddy habitats tend to be

farther (more distal) from the high-energy and/or high-topographic-relief habitats where dead shells are most likely to be mobilized.

Rank-order agreement of live and dead species is higher in muddy habitats than in sandy/gravelly habitats. This makes sense: sandy/gravelly habitats should be more likely to receive exotic shells from other habitats (test of percentage of indigenous specimens above), and also should be more likely to lose shells via in situ mechanical destruction and transport outward. It is interesting that rank-order agreement in muds is so high as it is, given geochemical evidence for post mortem dissolution of carbonate shells in many such settings (e.g., Walter and Burton, 1990; Green et al., 1993; Aller, 1995). These and other analyses (in progress) suggest that exotic import, although not a huge effect in absolute terms, may nonetheless be a more important source of bias than the within-habitat differential destruction of shells in determining live–dead agreement in species abundance.

4.3. Meta-analysis as a method

These are probably conservative estimates of live–dead agreement, because death assemblages are being compared to relatively small quantities of live data gathered during only a single census of the local community. However, these are probably "truer" conservative estimates of live–dead agreement than previously generated because (a) individual results are weighted according to data quantity, (b) datasets with artificially inflated agreement (incomplete species-list effect of the 1998 database; Kidwell, 2001b) have been eliminated, and (c) datasets constituting this 2001 database are more homogeneous in nature.

It should be noted that meta-analysis does not automatically yield stronger or more positive results than conventional methods of data synthesis. In fact, applied to this 2001 database, weighted averages of overall effects (first two metrics) are a few percentage points *lower* than standard unweighted averages (because many individual

datasets with extremely high live–dead agreement have low species richness (< ~ 10 species)). The value of meta-analytic methods appears in the analysis of variance, that is, in quantifying mesh-size and sediment grain-size effects from clouds of points and in doing this with far greater confidence than otherwise possible.

5. Conclusions

Shelled mollusks thus have quantitatively high preservation potentials in the surficial mixed zones of modern marine sedimentary habitats (top 10 or 20 cm), where death assemblages are generally dominated by specimens indigenous to the habitat. Moreover, dead species occur in statistically similar rank-order abundance to the local living community as measured by a single census. At least for coarse-mesh data (all specimens from sieves of ≥ 1.5 mm), live–dead agreement remains stable or improves as information on the composition of the living fauna increases through more prolonged or otherwise intensive sampling, indicating that these are conservative estimates. Further analysis is needed to determine the characteristics of molluscan species that fail to be preserved (are these primarily fragile shells? aragonitic shells? epifaunal species? rare during life?), how these selectivities in preservation vary, if at all, among environments, and the consequences for other aspects of community structure (e.g., evenness, preservation of trophic structure). Overall, however, these are extremely encouraging findings for paleoecologists, and also for ecologists interested in using death assemblages from sedimentary cores to build pre-historic time series on community composition.

The identification of mesh size as a large factor in live–dead agreement—more important than dataset size, and capable of masking variation linked to sediment grain size—is an important step in quantifying the sources and levels of true taphonomic bias. Meta-analysis of preservation potential and rank-order tests from a wide array of settings provides robust evidence that small-bodied individuals—presumably both those that are ontogenetically young and those that have reached adulthood at small size because of opportunistic strategies—are more prone to being under-represented or over-represented in local death assemblages. The analysis suggests both a specific protocol for practical application—(paleo)ecologists should focus on specimens ≥ 1.5 mm in molluscan death assemblages—and a quantitative estimate of the taphonomic reliability that is achieved by this protocol.

As to underlying cause, some of the live–dead discrepancy in fine-mesh datasets (death assemblages that include specimens ≤ 1 mm) may result from having only single-census live data, providing a too narrow picture of temporally heterogeneous larval and young juvenile populations. The magnitude of this methodologic effect could be tested by acquiring more fine-mesh datasets based on multi-season

sampling, especially if body sizes are tallied for specimens as in the unique field studies of Staff et al. (1986) (also see Staff and Powell, 1999). The effects of body size (and of describing species abundances in terms of biomass rather than numbers of individuals) could then be tested within a single study area. However, some of the live–dead discrepancy in fine-mesh datasets almost certainly results from the high surface-area-to-mass ratios of small shells, lowering their durability and increasing their vulnerability to transport. Other taphonomically important corollaries to body size and ontogenetic age in mollusks might be the degree of mineralization, microstructure type, and porosity (density) of skeletal elements, as well as absolute shell mass itself.

Taphonomic persistence linked to body size and/or ontogenetic stage should be general to many taxonomic groups, and thus, a post-juvenile focus might also prove key to isolating high-fidelity data in other metazoan records. Adult body size, for example, has already been identified as strongly influencing the preservation potentials of land mammals (e.g., taxa with body weights > 5 kg have proportionally higher representation in death assemblages than those < 5 kg; Behrensmeyer and Dechant Boaz, 1980). At the very least, the pervasiveness of the mesh-size effect (all three live–dead metrics tested, all habitats) and the magnitude of the effect (more important than dataset size and sediment grain size) that has been discovered through this meta-analysis of molluscan studies suggest that factors linked to mesh size need greater attention in future taphonomic studies and greater consideration in the collection and analysis of (paleo) ecological data.

Acknowledgements

Appendix A

Characteristics and original authors of live–dead molluscan studies used in this analysis, arranged onshore to offshore ("2001 database"). Each study provides data from one or more distinct study areas and one or more physically distinct facies-level habitats. Each habitat-level dataset consists of numerical abundance data for complete lists of live and dead species, including rare species, and is based on the pooling of at least two samples from a single visit (single census). This appendix, plus a list of 26 additional studies excluded from this meta-analysis, is also published in Science Online to accompany Kidwell (2001a) ("2001 database") (Table).

Table

Study area	Latitude (° N)	Environments	Facies level datasets	Mesh size (mm)	Author
Pacific North America (11 estuaries) [a, b]	28–47	Marsh	9	0.5	MacDonald (1969)
State to Baja California [a, b]		Tidal creek	10	1	
Eden estuary, Scotland	56	Intertidal flat	4	2	Zenetos (1980, 1990, 1991)
Seto Sea, Japan [a, b]	34	Intertidal flat	2	5	Tanabe et al. (1986) + au
Mugu Lagoon, CA [a, b]	34	Intertidal flat, subtidal sand, and grassbeds	3	3	Warme (1971)
Mugu Lagoon, CA	34	Subtidal sand	1 + m	2	Peterson (1972, 1976)
Tijuana Slough, CA	32.5	Subtidal sand	1 + m	2	Peterson (1972, 1976)
Mannin Bay, Ireland [a, b]	53	Algal gravels, sands, mud	5	0.5	Bosence (1979a, b)
Mljet Island, Croatia	43	Gravelly sand to mud	4	5	Peharda (2000)
Tomales Bay, CA	38	Muds, muddy sand, sand/gravel	4	1.5	Johnson (1965) + au
Chesapeake Bay, VA	37.5	Sand, mud, grassbed	3	1	Jackson (1968)
Copano Bay, TX [a, b]	28	Marginal sandy mud	1 + m	0.5	Staff et al. (1985, 1986)
Copano Bay, TX	28	Sands, muds, oyster reef, shell gravels	6	1	Calnan (1980)
Lagunas Carmen and Machona, Tabasco, Mexico	18.5	Muds to sands	5	1.5	Reguero and Garcia-Cubas (1994); Antoli and Garcia Cubas (1985)
Laguna Mecoacan, Tabasco, Mexico	18.5	Muddy sand	1	1.5	Reguero and Garcia-Cubas (1994); Galaviz-Solis et al. (1987)
Laguna La Mancha, Veracruz, Mexico	19.5	Oligohaline to mesohaline muds, sandy mud	4	1.5	Reguero and Garcia-Cubas (1994); Flores-Andolais et al. (1988)
Cancun, Yucatan, Mexico [a, b]	21	Backreef, channel, and open shelf	4	3	Ekdale (1972, 1977)
Smuggler's Bay, US Virgin Islands	18	Grassbeds to non-vegetated sand	3 + m	4	Miller (1981, 1988)
Helgoland Bight, Germany [b]	54	Shoreface sand to open shelf mud	3	0.63	Reineck et al. (1967, 1971)
Gulf of Gaeta, Italy [b]	41	Shoreface sand to open shelf mud	3	0.8	Hertweck (1971); Dörjes (1971)
Plymouth Sound and shelf, English Channel [a, b, c]	50	Shell gravels	3 + m	2	Carthew and Bosence (1986b)
Sapelo Island, GA [a, b]	31	Estuarine sand, shoreface channel, and inner shelf	3	1.5	Henderson and Frey (1986)
Amazon shelf, Brazil	0–4	Muds, muddy sand, relict shelly sand	3 + m	0.3	Aller (1995); Aller and Stupakoff (1996) + au
30 different study areas (two areas have been the subject of two different studies)	Range 0–56° N latitude	Eighty-five single-census datasets (total 1386 samples) and 12 multi-season datasets (additional 137 samples)		Range 0.3–5 mm sieves	Nineteen independently conducted studies

Notation: + m = multi-season census data also available (12 habitats); + au = dataset augmented with unpublished data provided by the original author.

[a] Dataset included in analysis of Kidwell and Bosence (1991) ("1991 database").

[b] Datasets included in analysis of Kidwell (2001b) ("1998 database").

[c] Using authors' field samples only; live data gathered in the study area by earlier workers were collected using other (finer) sieve sizes.

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