PALAIOS
Emphasizing the impact of life on Earth's history

PALAIOS, 2006, v. 21, p. 376–383
Research Report
DOI: 10.2110/palo.2005.P05-74e

1926 SEPM Society for Sedimentary Geology

QUANTIFYING TAPHONOMIC BIAS OF COMPOSITIONAL FIDELITY, SPECIES RICHNESS, AND RANK ABUNDANCE IN MOLLUSCAN DEATH ASSEMBLAGES FROM THE UPPER CHESAPEAKE BAY

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ABSTRACT

Years of over-fishing combined with increased nutrient pollution have had a catastrophic effect on the ecology of the Chesapeake Bay. The Holocene record of bay mollusks may provide a baseline for ecological restoration, but the effects of taphonomic bias on these assemblages first must be assessed. In this study, a live-dead comparison was carried out on four sites distributed in the main channel of the upper bay. Molluscan death-assemblage data were obtained from replicate box-core samples from which whole specimens and fragments were sorted, identified, and counted. Data on live communities at the same sites, sampled over the past twenty years, were provided by the Chesapeake Bay Program, making it possible to examine the degree to which death assemblages reflect long-term changes in the live community. Traditional live-dead metrics document a strong agreement between live-community and death-assemblage estimates of species composition, richness, and abundance—77% of the species in the live community are found in the death assemblage, and 99% of the individuals of species found in the death assemblage are found in the live community. Correlations between live and dead estimates of species richness are not statistically significant, although they do improve with longer-term sampling of the live community. Rank abundance of taxa in the death assemblage is correlated strongly and significantly with live rank abundance regardless of the duration of live sampling. These results suggest that Holocene molluscan assemblages may provide useful estimates of richness and abundance for Chesapeake Bay restoration.

INTRODUCTION

The Chesapeake Bay, which is one of the largest and most productive estuaries in the world, faces a myriad r(of)-325.3(t457.8(mnthropogenic(of)1325e)]blemsface[illegible]5(of)]dance5(wr)42tiv-fish5(o,f)]danc

The degree to which these Holocene bay assemblages reflect their source communities (i.e., their fidelity) is an important metric of taphonomic bias (Johnson, 1965; Behrensmeyer et al., 2000). Compositional fidelity, which focuses on the reliability of species composition, richness, and abundance measures, can be assessed using live-dead comparisons, in which live communities are sampled and compared with death assemblages (Kidwell and Bosence 1991; Kidwell and Flessa, 1995). This technique has been applied successfully to a variety of marine benthic environments, with particular attention paid to molluscan assemblages (Johnson, 1965; Cadee, 1968; Warme, 1971; Peterson, 1976; Staff et al., 1985; Staff et al., 1986; Feige and Fürsich, 1991; Kidwell and Bosence, 1991; Kidwell and Flessa, 1995; Greenstein and Pandolfi, 1997; Kidwell, 2001b; Kidwell, 2002). Several findings have emerged from this work, including the recognition that most taxa with preservable hard parts are represented in the death assemblage (commonly in correct rank order), and that out-of-habitat transportation affects relatively few individuals (Rich, 1989; Kidwell and Bosence, 1991; Kidwell and Flessa, 1995; Kidwell, 2001a; Kidwell, 2003).

One common limitation of these studies is a dearth of long-term census data for the live communities (Kidwell, 2001b). Species composition and abundance can fluctuate dramatically from year to year, and weak correlations between live communities and death assemblages often arise from an inadequately sampled live community (Kidwell and Flessa, 1995). Recent meta-analyses of live-dead comparisons have demonstrated the importance of multi-year, replicate sampling of live communities (Kidwell and Bosence, 1991; Kidwell and Flessa, 1995; Kidwell, 2001a, b). The Chesapeake Bay is one of the few coastal regions for which substantial multi-year live census data are available, making it an ideal site for such a study. Although fidelity has been assessed in a handful of estuarine environments, it has yet to be examined in detail in the Chesapeake Bay (MacDonald, 1969; Zenetos, 1990, 1991; but see Jackson, 1968).

In this study, a live-dead comparison was carried out on four sites located in the main channel of the upper Chesapeake Bay. The questions addressed include: (1) how well does the molluscan death assemblage record the species composition, richness, and abundance of the live community; and (2) to what extent are these measures of fidelity affected by the duration of live sampling?
genic factors, recently culminating in escalating episodes of hypoxia/anoxia (Officer et al., 1984; Newell, 1988; Rothschild et al., 1994; Nixon, 1995; Jonas, 1997; Caddy, 2000; Zimmerman and Canuel, 2000).

MATERIALS AND METHODS

For this study, four sites were sampled in the main channel of the

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FIGURE 1—Location map for the Chesapeake Bay (Atlantic coast, North America). Detailed map illustrates sample sites used in this study.

TABLE 1—Data on sites sampled in this study. Data include number of samples collected, sample dates, number of specimens in the death assemblage, salinity in parts per thousand (ppt), latitude (lat), longitude (long), the percentage of silt-clay, collecting gear, and water depth in meters for each sample (VERSAR, 2002).

Site	# Samples	Sample dates	# Specimens	Salinity (ppt)	Lat. Long.	Silt-clay %	Gear	Water depth (m)

FIGURE 2—Bar graphs illustrating the results for compositional fidelity; shading represents the number of years of live data compiled. (A) Percentage of species in the live community that are found in the death assemblage across all sites and at each site (live-dead fidelity). (B) Percentage of species found in the death assemblage that are found in the live community across all sites and at each site (dead-live

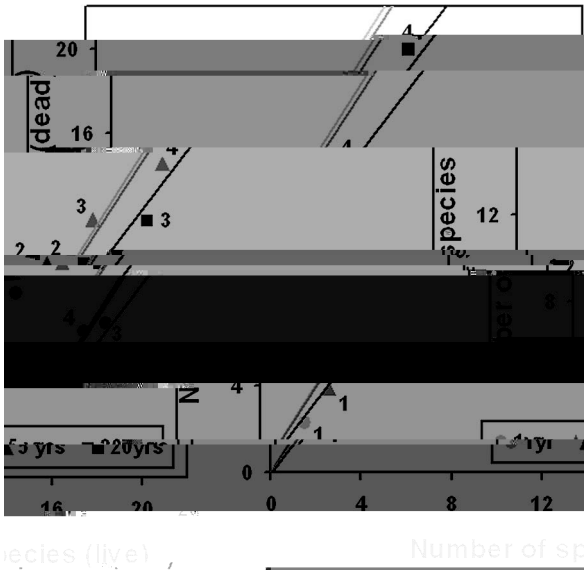

FIGURE 3—Bivariate scatterplot of species richness in the live community versus species richness in the death assemblage across all sites; samples are rarefied down to the same sample sizes. Each point in the plot represents a site and is labeled with the site number; trend lines represent least-squares regression lines constrained to pass through the origin (0,0).

nificance with longer-term sampling of the live community. Species richness appears to increase along a north-to-south transect in the upper bay—a pattern recorded in both the live and dead samples, with the exception of the single-year live census. This pattern may reflect the sandier substrates or the decreased seasonal variation in salinity regimes occurring in the middle of the bay.

Rank Abundance

Raw abundance (i.e., number of individuals) in the live community does not exceed death-assemblage levels across all sites until 5–10 years of live data are compiled. When rank abundance of species in the live community is plotted versus rank abundance of the same species in the death assemblage, considerable scatter is evident (Fig. 4). Despite this, Spearman Rank correlations yield a statistically significant positive relationship between live and dead rank abundance (1 yr: $R_{24}=0.68$, $p=0.0001$; 5 yrs: $R_{26}=0.55$, $p=0.004$; 10 yrs: $R_{26}=0.57$, $p=0.002$; 20 yrs: $R_{29}=0.47$, $p=0.01$; Fig. 4). The significant correlation between live and dead abundance documented here provides preliminary but encouraging support for the use of death-assemblage abundance as a proxy for

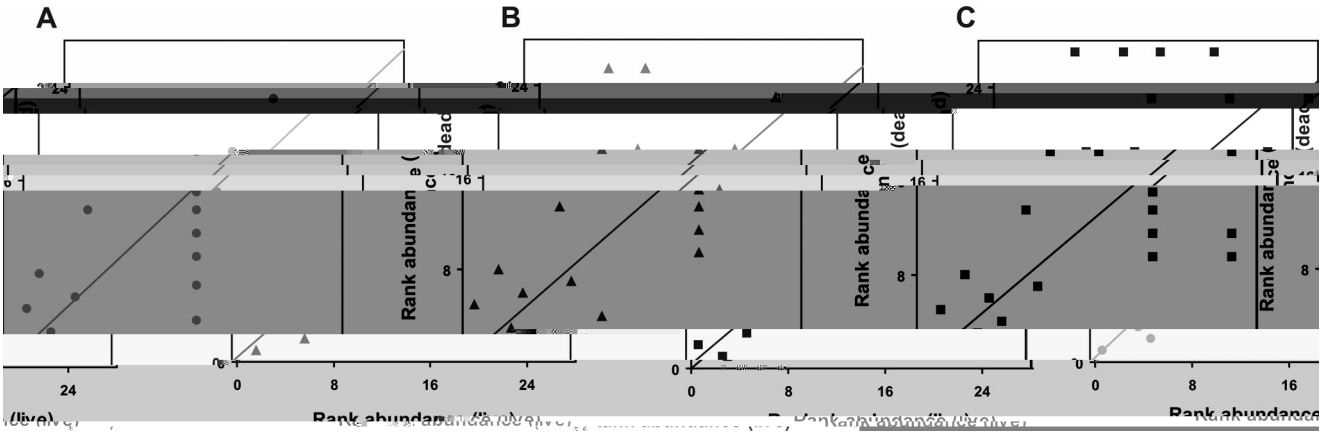

FIGURE 4—Bivariate scatter plot of rank abundance in the live community versus rank abundance in the death assemblage for each species across all sites. Each point in the plot represents a species; trend lines represent least-squares regression lines constrained to pass through the origin (0,0). (A) Data for one year of live sampling. (B) Data for five years of live sampling. (C) Data for twenty years of live sampling.

$$\text{Live-dead fidelity} = (N_S \times 100)/(N_L + N_S)$$

where N_S=number of species found in both the live community and death assemblage and N_L=number of species found in the live community only (Kidwell and Bosence, 1991). Increased sampling of the live community can produce an increase in N_S and/or N_L; however, live-dead fidelity will only increase if: (1) N_S increases faster than N_L; or (2) N_S and N_L increase at the same rate, but N_L is initially higher.

In the case of the upper bay, fidelity decreases with an increase in live sampling because, although N_S and N_L increase at approximately the same rate, N_S is initially higher than N_L. Given the high N_S to N_L ratios obtained for short-term sampling of the live community in most studies, N_S would have to increase substantially faster than N_L for this metric to increase with an increase in live sampling.

Turning to dead-live fidelity in the upper bay, this metric increases from 29% with one year of live data, towith ten years, to 71% with twenty years. Past work has suggested that when dead-live fidelity (i.e., the percentage of species found in the death assemblage that also are recorded from the live community) is quantified for coastal subtidal habitats, the resulting values are low (range

=33%; Kidwell and Bosence, 1991).Fidelityis evenlower

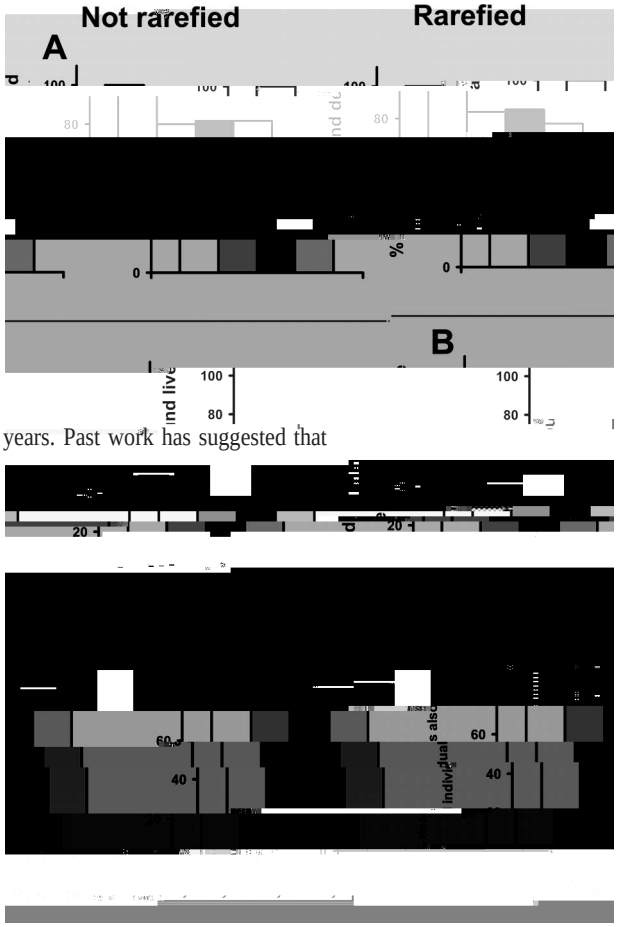

FIGURE 5—Bar graphs illustrating the effects of sample size standardization on metrics of compositional fidelity compiled across all sites. Graphs in the left and right columns display fidelity metrics before and after re-sampling and rarefaction, respectively; shading represents the number of years of live data compiled. (A) Percentage of species in the live community that are found in the death assemblage across all sites (live-dead fidelity). (B) Percentage of individuals of species found in the death assemblage that are found in the live community across all sites (dead-live fidelity). (C) Percentage of individuals in the death assemblage that are represented as species in the live community across all sites.

increases. Longer-term sampling of the live community (up to 5 to 10 years) clearly yields a different picture of species composition than single-year census data.

How Does Species Richness In The Death Assemblage Mirror Estimates From The Live Community?

Past authors have noted that the species richness of marine molluscan death assemblages is inflated relative to short-term sampling of the live community (e.g., Cadee, 1968; see reviews in Warme, 1971; Peterson, 1976; Russell, 1991; Kidwell, 2002). Transport and time-averaging cannot always account for this inflated richness, suggesting to some authors that it may be due to differential preservation of rare taxa (Kidwell, 2002). It also has been suggested that, even if rare taxa display a range of preservability similar to that of common taxa, rare taxa with high preservability will be overrepresented in the death assemblage and rare taxa with low preservability will be underrepresented in both assemblages, leading to inflated richness in the death assemblage (T. Olszewski, pers. comm., 2005).

Single-census data for the Chesapeake Bay demonstrate that median death-assemblage richness exceeds live richness by 2.33 to 1 (range=1.15–8.60 to 1) when richness is compiled at the site level and rarefied down to the same sample size. As duration of live sampling increases, this disparity decreases (see Peterson, 1976; Carthew and Bosence, 1986; Kidwell, 2001b). With five years of live sampling, the median dead richness is 1.98 times that of the live (range=1.30–2.38). With twenty years of live sampling, the median dead richness is 1.49 times that of the live (range=0.94–1.72), although live richness exceeds dead richness at one out of the four sites sampled. Increased sampling of the live community gradually decreases the disparity between live and dead species richness, even when sample size is controlled via rarefaction (Fig. 3). In a meta-analysis of 85 molluscan datasets, Kidwell (2001b) obtained very similar results, demonstrating that the median species richness of the death assemblage outweighed that obtained via one year of live sampling by 2.6 to 1 (range 0.6–22 to 1).

How Does Rank Abundance In The Death Assemblage Mirror Estimates From The Live Community?

Species that are abundant in bay live communities tend to be abundant in the death assemblage. This study documents a statistically significant positive correlation between the rank abundance of species in the live community versus the death assemblage in the upper bay. The Spearman R values reported here (0.47–0.68) are slightly higher than expected, based on Kidwell's (2001b) meta-analyses of past work. In her reanalysis of 85 molluscan datasets, Kidwell (2001b) demonstrated that, when mesh size is taken into account, 92% of live-dead comparisons document a significant positive relationship between live and dead species rank abundance. The median R-value obtained in Kidwell's meta-analysis was 0.48; and the values for sand/gravel ($\sim$0.32) and coastal-mud ($\sim$0.45) environments sampled using fine mesh sieves were somewhat lower than the values documented for the upper bay.

Mesh size plays a crucial role in the strength of these live-dead rank-abundance correlations. Kidwell (2001b) found that 92% of studies using coarse mesh sizes (defined as $>$1mm) documented a statistically significant correlation between live and dead rank order, in contrast to only 60% of fine-mesh studies. The disparity that Kidwell (2001b) documented between coarse and fine mesh sizes makes the fine-mesh results obtained for the Chesapeake Bay even more impressive.

The duration of live sampling available for the Chesapeake Bay is significantly longer than most studies (Kidwell, 2001b), and suggests that longer-term sampling does not necessarily improve rank-order correlation (Fig. 4). The statistically highest correlation between live and dead rank abundance recorderant

sures of rank abundance are statistically significantly correlated with each other, but the correlation weakens with longer duration of live sampling. These results suggest that death-assemblage data can be used as an accurate proxy for species rank abundance in the live Chesapeake Bay molluscan community.

ACKNOWLEDGMENTS

This study would not have been possible without the live data and death-assemblage material generously provided by D. Dauer (CBP), B. Rodi (CBP), R. Llanso (CBP), and R. Seitz (VIMS). The authors also thank B. Rodi, S. Arcuri, and L. Scott for providing taxonomic support; J. Jackson and S. Kidwell for tracking down Jackson (1968); S. Kidwell for providing shell-mineralogy data; T. Rothfus and S. Kidwell for helping to design the study; J. Curry, M. Oreska, K. Leary, and C. Compton for lab assistance; T. Olszewski, K. Parsons-Hubbard, T. Rothfus, L. Work, E. Gercke, and J. Swaddle for comments on the manuscript; K. Farnsworth and S. Harris for designing Figure 1; and the Jeffress Memorial Trust and The College of William and Mary for financial support.

REFERENCES

ABBOTT, R.T., 1974, American Seashells: Van Nostrand Reinhold Company, New York, 663 p.

ABBOTT, R.T., 1996, Seashells of North America: Golden Field Guides: St. Martin's Press, New York, 280 p.

ABBOTT, R.T., and MORRIS, P.A., 1995, A Field Guide to Shells of the Atlantic and Gulf Coasts and the West Indies: Peterson Field Guides: Houghton Mifflin, Boston, 350 p.

ALLER, J.Y., 1995, Molluscan death assemblages on the Amazon Shelf: implications for physical and biological controls on benthic populations: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 118, p. 181–212.

BEH.3S70Tihe55.652.75nd(YT)TD((flin,)-307.1(Bo4dD0v)28bENCES)Tj7-3013o,.o4dD0v2e8.6(,)-R28r6(pl)(8)y8MfiED20vl,andPSTeAf:P.0d0(m,)-3y8, p. 181–212.