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

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 of anthropogenic problems, including over-fishing, nutrient pollution, and increased turbidity (Lenihan et al., 1999). The Holocene record of bay mollusks may provide a useful baseline for ecological restoration, but the quality of this record and the effects of taphonomic bias need to be explored.

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?

CHESAPEAKE BAY

The Chesapeake Bay is a drowned river valley that flooded approximately 8000 years ago in response to sea-level rise (Johnson and Peebles, 1985; Colman and Mixon, 1988; Hobbs, 2004). The bay receives sediment and discharge from several major rivers, including the Potomac, York, and James rivers, and bay deposits consist of fossiliferous marine sands and silt, organic-rich clays, and fluvial sediments (Johnson and Peebles, 1985; Cronin et al., 2000). Today, the bay drains approximately 166,000 km^2 of watershed in Maryland, Virginia, Delaware, West Virginia, Pennsylvania, The District of Columbia (Washington, D.C.), and New York (Cronin et al., 1999). Ecologically, bay ecosystems are thought to be nearing collapse, due to a combination of climatic and anthropogenic 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 upper bay (Fig. 1). These sites were selected to span the length of the upper bay, to sample a variety of environments (differing according to sediment type and salinity regime), and to maximize the amount of live census data available for comparison (Table 1). The benthic monitoring

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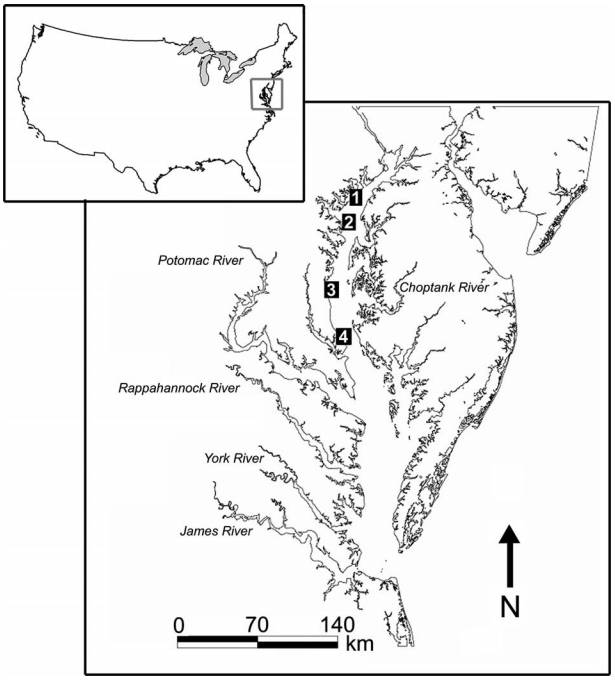

FIGURE 1—Location map for the Chesapeake Bay (Atlantic coast, North America). Detailed map illustrates sample sites used in this study.

division of the Chesapeake Bay Program (CBP) has sampled benthic communities in the Chesapeake Bay for 20 years and generously provided access to their live census data and death-assemblage material (Diaz et al., 2003). This collaboration made it possible to standardize site location and sampling techniques for the live and dead collections.

Samples were collected by the CBP and site location was established using GPS (accurate to within 10 m). Two samples were collected at each site (one in May and one in September of 2002) using a Wildco box corer (which samples an area of 225 cm^2 to a depth of 23 cm) for sites 1 and 2 and a hand-operated box corer (which samples an area of 250 cm^2 to a depth of 25 cm) for sites 3 and 4 (VERSAR, 2002). Sample volume and penetration depth were measured for all samples, and water-column profiles of temperature, conductivity, salinity, dissolved-oxygen concentration, and pH were measured using a Hydrolab H_2O during each sampling event. Two surface-sediment subsamples of ~120 ml each were collected for grain-size, carbon, and nitrogen analysis from an additional grab sample at each site. Samples were sieved in the field through a 0.5-mm mesh using an elutriative process, and detritus retained on the screen was preserved in a 10% buffered formaldehyde solution stained with rose bengal (VERSAR, 2002).

Live organisms were sorted from detritus under dissecting microscopes, identified to the lowest practical taxonomic level, and counted by the CBP. Silt-clay composition and carbon/nitrogen content were determined from the sediment subsamples collected at each site. For silt-clay determination, sand and silt-clay particles were separated by wet sieving through a 63-μm, stainless-steel sieve, and the residue was weighed. Carbon and nitrogen content of dried sediments were determined using an Exeter Analytical Inc. Model CE440 analyzer. Twenty years worth of additional live census (sampled 3 to 30 times per year), sedimentological, and physical data were provided for each site by the CBP (VERSAR, 2002).

The death-assemblage material remaining after removal of live specimens was gently re-sieved into four fractions (>4 mm, 4–2 mm, 2–1 mm, and 1.0–0.5 mm), washed in fresh water, and air-dried in the lab. Past work has demonstrated that the choice of mesh size can affect taphonomic results significantly (e.g., Staff and Powell, 1990; Kidwell, 2001b; Kidwell et al., 2001; Callaway et al., 2002; Kowalewski and Hoffmeister, 2003). Using mesh sizes greater than 2 mm avoids two potential problems: (1) inflated dominance of newly settled juvenile shells and (2) effects of chemical dissolution and transport on shell material less than 1 mm in size (Cummins et al., 1986; Kidwell, 2001b; Kidwell, 2003). Although the minimum mesh size used in this study is considerably smaller than recommended, it was selected to match the size used in the live census. Additional mesh sizes were selected in accordance with and to permit comparison to previous work (see compilation in Kidwell, 2001b; Kowalewski et al., 2003). Whole specimens and fragments of molluscan material were sorted under a dissecting microscope and identified to species level using a variety of shell guides (Gosner, 1971; Wass, 1972; Abbott, 1974; Gosner, 1978; Meinkoth, 1981; Rehder, 1981; Abbott and Morris, 1995; Abbott, 1996).

Composition, richness (i.e., number of species), and abundance of species were compiled for each sample. Fidelity of species composition was assessed by calculating the percentage of: (1) species in the live community found in the death assemblage (live-dead fidelity), (2) species in the death assemblage found in the live community (dead-live fidelity), and (3) individuals in the death assemblage that are represented as species in the live community (following Kidwell and Bosence, 1991). Resampling and rarefaction of fidelity metrics were performed using Ecosim 7.72 (Gotelli and Entminger, 2005). Rarefaction of richness estimates was performed using Analytic Rarefaction 1.3 (Holland, 2003). Abundance data were compiled by counting the maximum number of right or left hinges for each bivalve species, and apices or apertures for gastropod species (following Gilinsky and Bennington 1994; Aller, 1995). Rank abundance was determined by ranking species in each dataset on the basis of raw abundance (i.e., number of individuals), and assigning a rank of one to the most abundant taxon.

Supplementary data on life habit (infaunal versus epifaunal following Best and Kidwell, 2000) and shell composition were compiled from the literature (Taylor et al., 1969; 1973; Kidwell and Brenchley, 1996). Shell composition incorporated information on mineralogy (calcitic versus non-calcitic) and microstructure (nacre, prismatic aragonite and calcite, cross-lamellar, complex cross-lamellar, homogenous aragonite, and foliated calcite) from Taylor et al. (1969; 1973). Shell mineralogy and microstructure were established from data on specimens within the same genus or

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)
1	2	May 02	696	2.7	39°16.28′N	94.5	WildCo	4.4
		Sept 02	680	11.3	76°17.42′W	94.4	Box	4.5
2	2	May 02	51	9.9	39°07.32′N	95.2	WildCo	7.5
		Sept 02	195	15.2	76°21.34′W	92.5	Box	7.5
3	2	May 02	229	16.0	38°42.90′N	1.1	Modified	2.7
		Sept 02	526	14.5	76°30.84′W	1.9	Box	2.8
4	2	May 02	439	16.5	38°25.19′N	1.0	Modified	2.6
		Sept 02	1095	14.9	76°25.02′W	0.2	Box	3

families as those represented in the dataset (when data were consistent within the genus/species). Taxa possessing cross-lamellar, complex cross-lamellar, and homogenous aragonite, and foliated calcite microstructures were categorized as low organic content; taxa with nacreous, prismatic aragonite and prismatic calcite microstructure were categorized as high organic content (following Glover and Kidwell, 1993).

Methods involving live-dead assemblage comparisons recently have been reviewed and critically evaluated by Kidwell (2001b) and Kidwell et al. (2001), resulting in a proposed standardization of procedures across a range of marine communities. The use of multiple sieve sizes, standardization of taxonomic identifications, and the metrics of compositional fidelity were influenced heavily by these procedural recommendations.

RESULTS

Species Composition

A total of 23,466 live and 3911 dead specimens (representing 33 molluscan species) were obtained from the samples. The effect of short- versus long-term sampling of the live community was assessed by compiling live data for intervals of one year (2003), five years (1999–2003), ten years (1994–2003), and twenty years (1984–2003). Due to discrepancies in sampling procedures, the number of CBP live-census events varied from three to 30 events per year. To standardize the timing and number of live sampling events, live samples were limited to two per year, collected at approximately the same time as the dead samples. This culling of the live data yielded 6197 specimens representing 22 species.

Compositional fidelity was assessed both within and across all sites (Fig. 2). When compositional fidelity is quantified across all sites, and live data are compiled for twenty years, 77% of species in the live community are found in the death assemblage, 71% of species in the death assemblage are found in the live community, and 99% of individuals in the death assemblage are represented as species in the live community. Fidelity is high for the first metric (live-dead fidelity; Fig. 2A), although it decreases with longer-term sampling of the live communities because as rare taxa accumulate gradually over time in the live census, they are not necessarily recorded in the death assemblage. Although species recorded in both the live community and death assemblage are more abundant in the live community, more likely to exhibit calcitic shell mineralogy, and more likely to exhibit low shell organic content than those that are missing from the death assemblage, none of these differences is statistically significant (abundance $Z_{5,17}=-0.95$, $p=0.34$; mineralogy $Z_{4,17}=-0.7$, $p=0.48$; organic content $Z_{1,9}=-0.82$, $p=0.41$). Taxa that occur in both the live and dead samples also are more likely to be epifaunal, but this difference is not statistically significant either ($Z_{4,17}=-1.7$, $p=0.09$).

The second metric, the percentage of species in the death assemblage that also are found in the live community, is quite low given one to ten years of live data (dead-live fidelity; Fig. 2B), and does not reach the 70th percentile until at least twenty years of live data are compiled. Species recorded in both the live community and death assemblage are statistically significantly more abundant in the death assemblage ($Z_{17,7}=-1.96$, $p=0.05$) than those that are missing from the live community.

Longer-term sampling of the live community also improves the fidelity of the third metric (Fig. 2C), which effectively is an abundance-standardized version of the second metric (Kidwell and Bosence, 1991). This metric suggests that, although the death assemblage is recording a handful of anomalous species not censused in the live community, these species are not dominant numerically. These metrics show no discernible geographic pattern with respect to north-south distribution, salinity, or sediment type.

Species Richness

At two out of the four sites (Sites 1 and 3), species richness (i.e., number of species) in the live community equals or exceeds death-assemblage levels when 20 years of live data are compiled. At Sites 2 and 4, dead richness is higher than live richness, regardless of the duration of live sampling. When live and dead samples are rarefied down to the same number of individuals, three out of the four sites show greater richness in the death assemblage compared to the live community. Live richness at Site 1 exceeds dead richness only after 20 years of live data have been compiled.

When species richness is compiled for both the live community and death assemblage and rarefied down to the same sample sizes, Pearson Product Moment correlations document a positive but statistically non-significant ($p>0.05$) relationship between the two (Fig. 3; 1 yr: $r_4=0.11$, $p=0.89$; 5 yrs: $r_4=0.91$, $p=0.10$; 10 yrs: $r_4=0.90$, $p=0.10$; 20 yrs: $r_4=0.94$, $p=0.06$). With multi-year sampling of the live community, the correlation between live and dead richness is quite tight (i.e., the r-values are always positive and high) and the lack of statistical significance is due to low sample size rather than live-dead agreement. It is particularly interesting to note that the r-values increase and approach statistical sig-

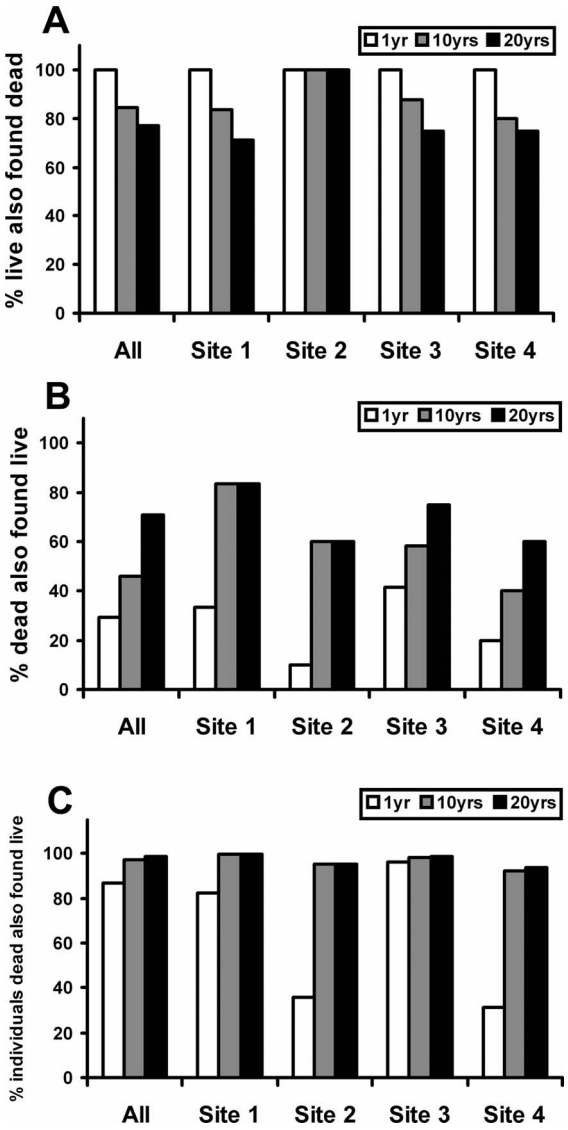

FIGURE 2—Bar graphs illustrating the results for compositional fidelity; shading represents the number of years of live data compiled. (A) Percentage of species in the live community that are found in the death assemblage across all sites and at each site (live-dead fidelity). (B) Percentage of species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

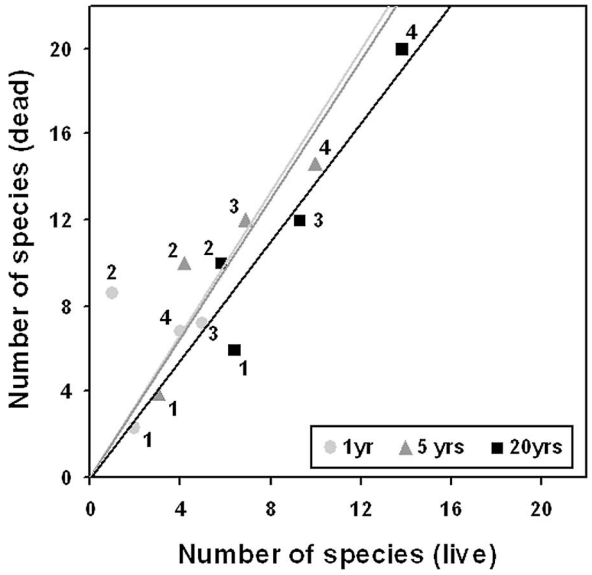

FIGURE 3—Bivariate scatterplot of species richness in the live community versus species richness in the death assemblage across all sites; samples are rarefied down to the same sample sizes. Each point in the plot represents a site and is labeled with the site number; trend lines represent least-squares 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 live abundance in these Chesapeake Bay molluscan communities. In contrast to the patterns obtained for species richness, R-values for these correlations actually decrease with longer-term sampling of the live community (from 0.68 to 0.47).

Although the differences are not statistically significant, species that show a statistically significant decrease in abundance from the live community to the death assemblage (i.e., outside the 95% confidence intervals) are more likely to possess non-calcitic shell mineralogy ($Z_{16,5}=-1.02$, $p=0.31$) and high organic shell content ($Z_{9,1}=-0.66$, $p=0.51$) than species that show no significant change in abundance. These underrepresented species are statistically significantly more likely to be infaunal ($Z_{16,5}=-2.17$, $p=0.03$). Turning to species that show a statistically significant increase in abundance from the live community to the death assemblage, these overrepresented species are more likely to possess calcitic shell mineralogy ($Z_{16,7}=-0.51$, $p=0.61$) and low shell organic content ($Z_{9,4}=-1.34$, $p=0.18$) than species that show no significant change in abundance, although these differences are not statistically significant. Although the data on shell mineralogy, shell organic content, and life habit are somewhat limited, they suggest that these factors are not exerting a strong effect on the patterns of rank abundance examined here.

DISCUSSION

Does The Composition Of The Death Assemblage Reflect The Original Live Community?

A number of researchers have examined the compositional agreement between molluscan live communities and death assemblages across a variety of marine environments (see reviews in Kidwell and Bosence, 1991; Kidwell and Flessa, 1995; Kidwell, 2001b), making it possible to compare the results obtained for the Chesapeake Bay to the results obtained in similar environments.

Estimates for live-dead fidelity obtained here are quite high when one (100%) to ten (85%) years of live data are compiled. These results favorably compare with estimates obtained by previous workers, which range from 82 to 100% (mean=95%) for well-mineralized species in coastal subtidal habitats (Kidwell and Bosence, 1991). It should be noted that the majority of past studies rely on single-census or single-year sampling of the live community. Long-term sampling of the live communities in the Chesapeake Bay produces an apparent decrease in live-dead fidelity (20 years: 77%). Although recent studies have examined the effects of increased sampling of the live community on other fidelity metrics (Kidwell, 2001b), this particular metric has received little attention. The metric is calculated as follows:

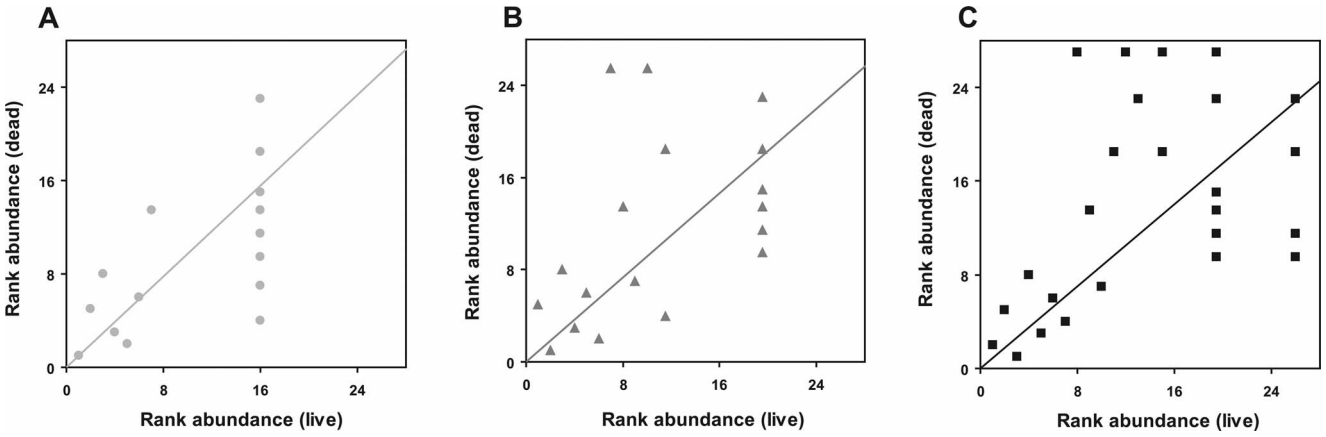

FIGURE 4—Bivariate scatter plot of rank abundance in the live community versus rank abundance in the death assemblage for each species across all sites. Each point in the plot represents a species; trend lines represent least-squares regression lines constrained to pass through the origin (0,0). (A) 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, to 42% with five years, to 46% with 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=10–58%; mean=33%; Kidwell and Bosence, 1991). Fidelity is even lower for studies, such as the present one, that employ fine mesh sizes (Kidwell, 2001b). Low values for dead-live fidelity traditionally have been interpreted as an artifact of inadequate sampling of live communities, as opposed to transport, local extinction, or selective destruction (Kidwell and Bosence, 1991; Kidwell and Flessa, 1995). This interpretation has been supported empirically by Peterson (1976) and Knight (1988) for lagoonal and open-shelf habitats, and is supported by the results of this study. It is worth noting that several more years of live sampling are required in the bay to reach the fidelity levels documented in Peterson's (1976) three-year study of temperate lagoons.

To explore the effects of increased live sampling on this metric, it is helpful to examine its equation:

$$\text{Dead-live fidelity} = (N_S \times 100)/(N_D + N_S)$$

where N_S=number of species found in both the live community and death assemblage and N_D=number of species found in the death assemblage only (Kidwell and Bosence, 1991). Increased sampling of the live community can produce an increase in N_S and/or a decrease in N_D, both of which act to increase dead-live fidelity. In fact, the structure of this metric precludes any decrease in fidelity with an increase in sampling simply because, by definition, N_S cannot decrease and N_D cannot increase in response to increased sampling if the death assemblage is only sampled once. Dead-live fidelity in the upper bay decreases with an increase in live sampling due to both an increase in N_S and a coincident decrease in N_D.

The third metric of fidelity is calculated as the percentage of individuals in the death assemblage that are represented as species in the live community. Once again, results for the Chesapeake Bay agree well with past work, and fidelity increases from one (87%) to five (97%), to ten (97%), to twenty (99%) years of sampling. These results strongly suggest that, even in bay sites where traditional metrics of dead-live fidelity are very low, the actual representation of abundant species is quite high. Kidwell and Bosence (1991) found that within coastal subtidal habitats, this metric ranged from 77–100% (mean=89%) when facies were assessed independently. The equation for the third fidelity metric is an extension of dead-live fidelity and will show a similar response to an increase in the duration of live sampling.

Traditional metrics of compositional fidelity clearly are affected by both compositional information and sample size. The link between sample size and fidelity suggests that samples should be rarefied to similar sample sizes before fidelity metrics are estimated, and that rarefaction should be applied to comparisons between live and dead samples, between sites, and between studies. Comparisons of metrics between studies

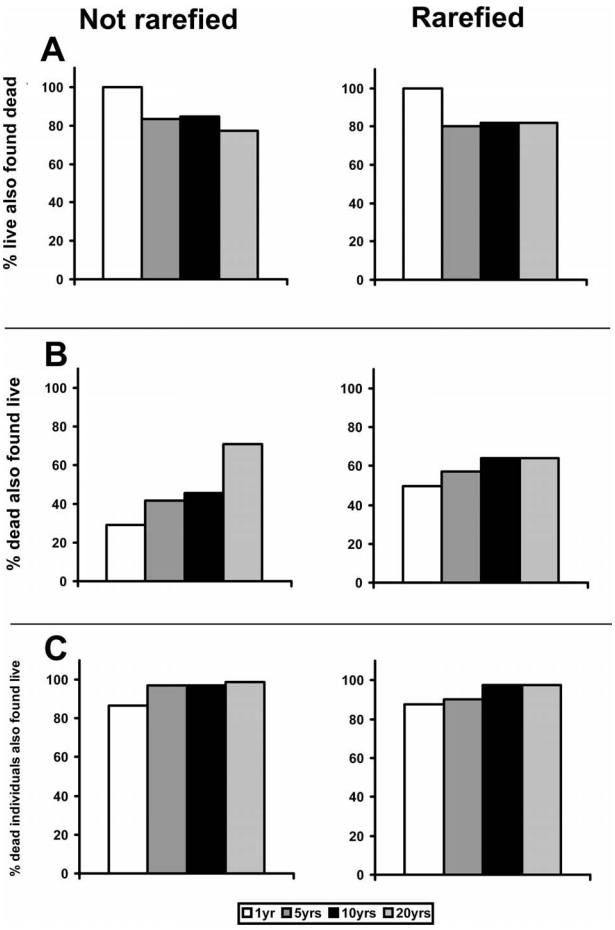

FIGURE 5—Bar graphs illustrating the effects of sample size standardization on metrics of compositional fidelity compiled across all sites. Graphs in the left and right columns display fidelity metrics before and after re-sampling and rarefaction, respectively; shading represents the number of years 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.

(including those outlined above) should be viewed with caution until some attempt has been made standardize for sample-size differences.

To examine the effects of sample size on compositional fidelity across all sites, the death assemblage and multi-year live community data were resampled (n=100) and rarefied down to the sample size of a single-year live census (n=264; Fig. 5). Re-sampling and rarefaction produces little change in live-dead fidelity (Fig. 5A). This metric still decreases with longer-term sampling of the live community, although it does appear to stabilize after five years of live data are compiled. Dead-live fidelity is affected by re-sampling and rarefaction (Fig. 5B), although it continues to show an increase in fidelity with increased live sampling. With one year of live data compiled, this metric is higher with rarefaction (50%) than without (29%). The metric continues to increase until 10 years of live data are compiled, at which point the metric remains constant (10 yrs: 64%; 20 yrs: 64%). Rarefaction produces little or no change in the third fidelity metric (Fig. 5C).

The extent to which sample size differences actually affect fidelity metrics will vary from study to study, and may not be a significant problem for some studies. In the case of the upper Chesapeake Bay, sample size alone cannot account for changes in these metrics with increased sampling of the live community. Live-dead fidelity still decreases with an increase in the duration of live sampling, while dead-live fidelity

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 recorded in this study is generated using a single year of live data. Spearman R values actually decrease unpredictably (from 0.68 for 1 year to 0.55 for 5 years, to 0.57 for 10 years, to 0.47 for 20 years) with increased live sampling. This pattern primarily occurs because the first metric of fidelity—the number of species in the live community found in the death assemblage (Fig. 2A)—decreases unpredictably with increased sampling of the live community. As the number of live-only taxa increases, the correlation between live and dead rank abundance decreases in response. In fact, when the analysis was limited to species documented in both the live community and death assemblage, the correlation between live and dead rank abundance actually increases with an increase in the number of years of live data compiled (1 yr: $R_7=0.57$, $p=0.18$; 5 yrs: $R_7=0.42$, $p=0.23$; 10 yrs: $R_{11}=0.61$, $p=0.05$; 20 yrs: $R_{17}=0.76$, $p=0.0001$).

This represents one of the first explicit tests of the effects of long-term live sampling on rank-order correlations. In Kidwell's meta-analysis (2001b), live-dead correlation improved with increased sampling of the live data, but it should be noted that the maximum duration of live censusing incorporated into her analysis was 1.75 years. The results obtained in the present study suggest that the relationship between rank-order correlation and censusing of the live communities is not as straightforward as has been assumed previously, and that current estimates of rank-order correlation (e.g., Kidwell, 2001b), which often are based on single-year censuses, may represent best-case scenarios.

Application To Holocene Paleoecology In The Chesapeake Bay

Restoration of threatened ecosystems relies on accurate estimates of species composition, richness, and community structure over long timescales. Although historical data can inform restoration decisions, these data often are too short-term, poorly replicated, or anecdotal to yield accurate estimates of natural variability in these ecosystems. Holocene records of these ecosystems, when available, are a potential source for long-term data, but the preservational biases associated with these assemblages first must be examined.

This study represents one of the first taphonomic assessments of Chesapeake Bay assemblages and provides a foundation for future studies examining the effects of climate change versus human disturbance of benthic molluscan communities. The results of this study suggest that Holocene data can be used, albeit with caution, to reconstruct changes in species composition and community structure through time. For example, if 77% of live species are found in the death assemblage, then a compositional change involving at least 24% of the Holocene fauna through time is unlikely to be driven simply by preservational bias. Similarly, because rank abundance of the live community is statistically significantly correlated to rank abundance of the death assemblage, shifts in rank abundance through time that exceed the variability attributable to taphonomic bias would be considered true ecological signal.

The results of this study, when considered with past work on other estuaries (MacDonald, 1969; Zenetos, 1990,1991), suggests that death assemblages from estuarine environments faithfully record aspects of species composition, richness, and rank abundance. As ecologists strive to reconstruct long-term patterns in community structure in threatened ecosystems such as estuaries, information gleaned from naturally accumulated death assemblages will become increasingly important.

CONCLUSIONS

This study documents very strong agreement between the live community and death-assemblage estimates of species composition, richness, and abundance in Chesapeake Bay benthic mollusk communities. In the live community, 77–100% of species also are found in the death assemblage, and 87–99% of individuals of species found in the death assemblage also are found in the live community. Compositional fidelity shifts in response to an increase in live sampling, but whether this involves an increase or decrease in fidelity depends on the metric used. Although the strength of the correlation between species richness in the live community and death assemblage increases with longer-term sampling of the live community, it is not statistically significant. In contrast, live-dead mea-

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.

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ACCEPTED JANUARY 6, 2006