

The living, the dead, and the expected dead: variation in life span yields little bias of proportional abundances in bivalve death assemblages

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Abstract.—All else being equal, species with short life spans are expected to be overrepresented in time-averaged death assemblages relative to their standing abundance in the living community, but the magnitude of the distortion of proportional abundance and assemblage evenness has received little attention. Here, information from 30 data sets on the living and dead abundances of marine bivalves in local habitats is combined with a global compilation of bivalve life spans to determine whether bias from mortality rate can explain observed differences in species proportional abundances. Although bivalve maximum life spans range from one to 75 years in these data sets, indicating annual mortality rates of 0.97 to 0.09, the “life span bias” (LB) of a species—the difference between its proportional abundance expected dead and that observed alive—is consistently small in magnitude (average change <2%, maximum about 20%) and random in sign relative to observed discordance (OD = difference between that species’ proportional abundance observed dead and that observed alive). The aggregate result for 413 living species occurrences is a significantly positive but weak correlation of OD to LB, with only 10% of variation in OD explained. The model performs better among longer-lived species than among shorter-lived species, probably because longer-lived species conform better to the model assumption that species maintain a constant proportional abundance in the living assemblage over time. Among individual data sets, only seven exhibit significant positive correlations between OD and LB. The model also under-predicts the cases where a death assemblage is dominated by a species that is shorter lived than the dominant species in the living assemblage, indicating that some factor(s) other than or in addition to mortality rate is responsible for OD. We can find no evidence of preservational bias linked to life span, for example through body size. This negative outcome reflects a weak biological relationship between life span and living abundance among bivalves in local habitats, contrary to the terrestrial paradigm, and points toward a simpler model of time-averaged death assemblage formation where higher abundances reflect (under-sampled) past populations. Contrary to long-held expectations, variation in population turnover among species is not a major source of taphonomic bias in time-averaged death assemblages among bivalves and perhaps among other marine groups: bias must arise largely from other factors.

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Introduction

Many factors might modify the composition of a death assemblage relative to the local living community. These factors include preservational taphonomic biases (postmortem distortion of species’ relative abundances arising from differential preservation of species and age classes or out-of-habitat transportation), the time-averaging of naturally variable populations (which lengthens the window of observation on local community composition), and “supply-side” taphonomic biases such as differential turnover of populations among species, affecting their contribution of dead individuals. Of these potential

factors, *life span bias*—the expected overrepresentation in time-averaged death assemblages of species whose individuals have short life spans—has long been suspected to significantly distort species’ relative abundances but has received little analytic attention (Van Valen 1964; Levinton and Bambach 1969; Levinton 1970; Behrensmeier and Chapman 1993; Callender and Powell 1997; Powell et al. 2001; Vermeij and Herbert 2004; Tomašových 2004).

Life span bias (our term) was first identified as an issue by Van Valen (1964). Assuming no other sources of bias in fossil land-mammal assemblages (or at least none that covary with

life span), Van Valen (1964) corrected for life span bias by multiplying the frequency of occurrence of each species in the fossil assemblage by an estimate of the typical life span of its individuals in years, thus generating a profile of the standing relative abundances of species in the original living community. Van Valen did not report how different his modeled living assemblages were from the observed fossil assemblages, but reported that the shape of the rank-abundance distribution of the modeled living assemblage qualitatively resembled MacArthur's broken stick model of nonoverlapping species niches. The taphonomic implication is that variation in life span among species (variation in population turnover rates) was the dominant bias in the formation of these fossil assemblages.

The only other analysis of the effects of differential longevities was of modern mammal death assemblages in Amboseli National Park by Behrensmeyer and colleagues (Behrensmeyer et al. 1979; Behrensmeyer and Dechant Boaz 1980). They combined data on (stable) population sizes from a long-term program of wildlife censusing and data on species' birth rates to generate "expected death assemblages" from the implicit differences in mortality rates (if a species' population size is constant, then a high birth rate must be counterbalanced by a high mortality rate). They found that differences between living assemblages and naturally occurring bone assemblages were largely contrary to those predicted from variation in mortality rates and were instead consistent with differential preservation (and probably discovery) of species as a positive function of body size. Small-bodied species were mostly underrepresented in death assemblages despite their short life spans and large-bodied species were mostly overrepresented. Variation in population turnover rates among species was not the dominant biasing factor in the relative abundances of species in death assemblages.

Here, we adopt the basic approach of Behrensmeyer et al. (1979)—using mortality rate to model expected death assemblages from observed living abundances—to conduct a broader test of life span as a biasing

factor in proportional abundance. We use 30 marine bivalve data sets from subtidal soft-sedimentary seafloors as a source of abundance data, and a global database of knowledge on bivalve maximum life spans to estimate mortality rates. Compared to observed live-dead differences in species' proportional abundances, we find that modeled life span bias is small in magnitude and random in sign, and has no consistent effect on assemblage evenness (such as increased dominance by a few short-lived species). Thus, although observed differences are significantly correlated with life span bias in a few of the 30 data sets examined and a weak correlation exists among species occurrences in aggregate, the distortion of proportional abundances created by mortality rate in these marine death assemblages is best described as low-level noise.

Methods

The expected numerical abundance of a species in a death assemblage can be modeled as the product of its standing abundance in a local living assemblage multiplied by the (annualized) mortality rate of that species (explained below), which is low for species having long-lived adults but ranges up to about 1 (100% mortality) for species whose individuals have maximum life spans of only one year. If the relative abundances of species are constant over time within the local living assemblage—a critical assumption of our model—then the changes in their dead *proportional* abundances expected from one year of differential mortality will also apply to death assemblages time-averaged over longer periods. Life span bias (LB) is the difference between the *expected* proportional abundance of a species in a death assemblage and its *observed* proportional abundance in the living assemblage; each species occurring in a living assemblage will have an expected abundance in the local death assemblage, and thus some positive or negative value of LB. The explanatory power of LB is evaluated by comparing modeled LB against observed live-dead discordance (OD) for the same species. OD is the difference between the *observed* proportional abundance of a species in a death assemblage

and its *observed* proportional abundance in the local living assemblage. Our analysis focuses on marine bivalves because information is available both on living and dead abundances of species in local habitats and on their maximum life spans. With this sketch of methods, many readers may wish to skip directly to "Results."

Database of Living and Dead Abundances and Observed Discordances.—Raw data on the numerical abundance of bivalve species in living and death assemblages come from 30 "live-dead" data sets collected originally by other authors from subtidal soft-sediment habitats in tropical to temperate study areas (Johnson 1965; Jackson 1968; Ekdale 1972, 1977; Peterson 1972, 1976; Bosence 1979; White et al. 1983, 1985; Smith 1985; Carthew and Bosence 1986; Reguero and Garcia-Cubas 1989, 1991, 1993; Garcia-Cubas et al. 1992; Zenetos and Van Aartsen 1994; Staff and Powell 1999; Kowalewski et al. 2003; for details, see Suppl. Table 1 in the online supplemental information at <http://dx.doi.org/10.1666/09004.s1>). Each data set is based on sieving living and dead individuals from a set of seafloor samples collected during a single season. To compensate for differences in sedimentary volume among studies and to reduce error from small samples, only data sets that contain at least 100 living bivalve individuals (the "living assemblage," LA) and 100 dead bivalve individuals (the "death assemblage," DA) are used here. These LAs have a median richness of 13 species and range in abundance structure from very even to very uneven (Hurlbert's PIE ranges from 0.91 to 0.06, denoting dominance by a single species of 0.24 to 0.97 of all individuals in a LA). Seven data sets are from open shelves or straits and 23 are from coastal embayments, and human impacts at the time of sampling range from negligible (no anthropogenic eutrophication, no bottom trawling) to severe.

Aggregating all data sets into a single database, there are 413 *living* species occurrences (= a species encountered alive in a habitat-level data set) where that species constitutes at least 0.001 of all individuals in its LA. These 413 living occurrences reflect

205 unique species and are the focus of analysis. Each of these species also occurs in the local DA. The difference between a species' proportional abundance as sampled in the DA and its proportional abundance as sampled in the LA is its *observed discordance* in proportional abundance in that data set ($OD = \text{proportional abundance dead} - \text{proportional abundance alive}$). The ODs of these 413 living species occurrences range from +0.625 to -0.749 (Table 1), and each is the net effect of all taphonomic, biological, and sampling factors affecting a species' local abundance in the DA and LA.

In calculating the proportional abundance of a species in a local DA we take into consideration all other co-occurring species in the DA, including species that occur only in the DA. Such "dead-only" species may have several origins. Some are probably indigenous species that by chance were not encountered alive (limited sampling or random dip in living population size at the time of sampling), some may be relicts of locally extinct species (no amount of sampling today would encounter them alive), and others may be allochthonous specimens from other habitats. In aggregate, the 30 data sets contain 348 dead-only species occurrences. Dead-only species occurrences are excluded from our evaluation of life span bias because of concern that they would overwhelm the analysis with zeros: species occurring dead-only can only have zero life span bias because a standing abundance of zero multiplied by any mortality rate yields zero expected dead individuals. The analysis of LB is focused instead on the 413 living species occurrences whose LB can be non-zero. This focus should maximize our estimate of the average size of LB and increase our chance of finding a significant overall effect of LB on OD.

Database of Maximum Life Spans.—Data on the maximum life spans of individuals of marine and estuarine bivalve species were gathered from secondary compilations (Comfort 1957; Robertson 1979; Powell and Cummins 1985; Powell and Stanton 1985; Heller 1990; Callender and Powell 1997; websites "MarLIN BIOTIC" and "MSAP") and about 100 primary references, yielding data for 283

TABLE 1. Summary of results from aggregate analyses of all 413 living species occurrences and of occurrences partitioned according to abundance (species constituting ≥ 0.05 of a LA); life span (long-lived >9 years, short-lived <8 years); human modification of the study area (considering both eutrophication and bottom-trawling; see Suppl. Table 1); and whether the life span is known based on study of that species rather than congeners. n = number of species occurrences; OD = observed discordance in the proportional abundance of a species between DA and LA; LB = life span bias, which is the difference between expected dead and observed living proportional abundances of a given species; proportional contribution = LB/OD within the limits [0,1], where LB and OD of opposite sign are scored as zero.

Set of species occurrences	n	Proportion with known life span	OD		OD		LB	
			Min	Max	Med	Mean	Min	Max
All	413	0.32	-0.749	0.625	0.014	0.06 \pm 0.01	-0.234	0.183
Most abundant	107	0.36	-0.749	0.590	0.090	0.16 \pm 0.03	-0.234	0.183
Long-lived	137	0.20	-0.604	0.590	0.013	0.06 \pm 0.02	-0.234	0.050
Short-lived	216	0.40	-0.749	0.625	0.015	0.07 \pm 0.017	-0.209	0.183
Pristine areas	193	0.29	-0.513	0.474	0.013	0.04 \pm 0.012	-0.234	0.161
Modified areas	220	0.30	-0.749	0.625	0.017	0.08 \pm 0.019	-0.166	0.183
Known life span (pristine areas)	131 (64)	1	-0.604	0.625	0.029	0.08 \pm 0.02	-0.234	0.183

Min = minimum, Max = maximum, Med = median.

Mean \pm 95% confidence interval on the standard error. Significance $p^* < 0.05$, $** < 0.01$, $*** < 0.001$.

unique bivalve species from 186 genera in 50 families based on 543 reports (Suppl. Table 2). We find that the maximum life spans (hereafter denoted simply as life spans) of bivalve species range globally from 1 yr to several hundred years with a median value of 9 years (mean life span = 18 years). The most frequent life span (mode) in this bivalve compilation is 2 years, which is very similar to the modal 3 years reported by Powell and Cummins (1985) for all mollusks.

Of living species occurrences in our abundance database, 32% could be assigned a life span on the basis of data for that same species in the life span database (131 of 413 living occurrences; we used the maximum of all reported life spans for a species as its maximum life span; for possible bias, see notes in Suppl. Table 2 and Discussion). For the remaining species occurrences, life span is estimated as the median of the maximum life spans of congeneric species (method applied to 26% of living species occurrences), and when no life span data for congeners were available life span was estimated as the median of maximum life spans of other genera in the family (method applied to 37% of living species occurrences; substituting the mean life span had no substantive effect on results). For species for which life span data could not be located for any species or genus within the family, life span was estimated as

the median life span of all species in the global life span database (9 years; 5% of occurrences; dropping these species from the analysis did not affect our results).

The life spans of the 205 unique species that occur in our *abundance* database range from 1 to 75 years with a median of 8 years. Within individual data sets, the average spread in life span is 2 to 18 years, i.e., a ninefold difference (Suppl. Table 1).

Life span is used as a continuous variable in most analyses. However, for some analyses and purposes of discussion we use the median bivalve life span (9 years based on the life span database, 8 years among unique species in the abundance database) to partition living species occurrences into the categories of long-lived species (life spans >9 years, 137 species occurrences), intermediate-lived species (life spans 8–9 years, 60 occurrences), short-lived species (life spans <8 years, 216 occurrences), and shortest-lived species (life spans ≤ 3 years, 104 occurrences; this is a subset of the short-lived category; 3 years is the first modal life span in the abundance database [see Suppl. Fig. 1]).

Expected Death Assemblages.—Calculating an expected death assemblage is straightforward if the finite mortality rate of each species is known, that is, the proportion of individuals from a standing population that die during a finite interval, usually one year. Operational-

TABLE 1. Extended.

LB		Linear regression OD & LB		Spearman rank correla- tion OD & LB		Proportion where OD & LB have same sign	Proportional contribu- tion of LB to OD	
Med	Mean	<i>r</i>	adj. <i>r</i> ²	<i>rho</i>	<i>rho</i> ²		Med	Mean
0.003	0.017 ± 0.003	0.153***	0.095	0.252***	0.064	0.54	0.05	0.25 ± 0.03
0.033	0.052 ± 0.010	0.202***	0.101	0.367***	0.134	0.55	0.09	0.26 ± 0.06
0.004	0.020 ± 0.007	0.226***	0.240	0.557***	0.310	0.67	0.33	0.38 ± 0.06
0.003	0.016 ± 0.004	0.064*	0.021	0.040	0.002	0.44	0	0.16 ± 0.04
0.003	0.016 ± 0.005	0.229***	0.143	0.275***	0.076	0.54	0.04	0.26 ± 0.05
0.004	0.017 ± 0.004	0.120***	0.070	0.229***	0.052	0.54	0.06	0.23 ± 0.04
0.004	0.02 ± 0.008	0.257***	0.280	0.387***	0.150	0.55	0.03	0.21 ± 0.05
		(0.24***)	(0.198)	(0.362**)	(0.131)			

ly, finite mortality is one minus the (more easily measured) survival rate, which is the proportion of individuals from an initial standing crop that are still alive after a given period of elapsed time. Empirical survival and mortality rates are not known for bivalves in any of the study areas where abundance information is available, and so we use knowledge of the global maximum life spans of species to estimate the likely finite (annual) mortality rates of our local species occurrences, applying an empirical relationship between maximum life span and *instantaneous* mortality rate for mollusks discovered by Hoenig (1983):

$$\ln(Z) = 1.23 + (-0.832 * \ln(t_{\max}))$$

where *Z* is the instantaneous mortality rate (or coefficient; this is the slope of a plot of the number of individuals surviving over time; this per capita rate is assumed to be constant during adulthood, following very high mortality of individuals early in life), t_{\max} is the maximum observed life span for a species in years, and 1.23 and -0.832 are constants found from linear regression of age-class data from 28 largely unexploited mollusk populations (Hoenig 1983). Instantaneous mortality rate is the total rate from all processes of mortality (e.g., predation, senescence, disease, harvesting). The *finite* mortality rate used in our model is derived from the instantaneous mortality rate *Z* by the relationship $1 - e^{-Z}$.

Finite mortality rates and life spans are used here as species-level attributes. For the species in our abundance database, the finite (annual) mortality rates calculated using the Hoenig equation range from 0.967 (species having a maximum life span of 1 year) to 0.090 (maximum life span of 75 years).

The finite mortality rate of a species multiplied by the standing crop of that species (the number of individuals sampled alive during a survey) yields the number of individuals expected to die in a finite interval (the annual "expected dead"). For each of our 30 abundance data sets, we calculated the number of expected-dead individuals for each species present in the LA, with the sum of expected dead individuals from all species producing an "expected death assemblage" from one year's worth of mortality. A species' expected proportional abundance in the DA is that species' proportional abundance in the expected DA.

Our model of the expected proportions of species arising from one year of mortality is the same as the expectation for a fully time-averaged DA if we assume that the proportional abundances of species in the local living assemblage do not change over time, despite repeated recruitment and mortality events. Constant proportional abundances in the LA is the simplest assumption regarding community dynamics in the absence of other

knowledge—from long-term wildlife surveys Behrensmeier et al. (1979) knew this to be true on a multi-decadal scale for their system (see Western and Behrensmeier 2009 for changes in that system since the 1970s). Constant proportional abundances signify that any increase (or decrease) in the mortality of a species in the local habitat has been counterbalanced by an increase (or decrease) in its local birth or immigration rate, and that any change in environmental conditions over the duration of time-averaging—whether a change that results in a net increase or decrease in the carrying capacity of the system—has affected all species proportionately. A species that has a very high per capita birth rate and thus great potential for absolute population growth—because individuals reach sexual maturity at an early age, reproduce several times per year or per life span, have large clutch sizes or high survivorship to reproductive age, or have a long reproductive life—must have a counterbalancing high mortality rate if its population is not to grow disproportionately to co-occurring species.

This assumption of constant living proportional abundances of species is not necessarily realistic given the decades and centuries of time-averaging that characterize many molluscan death assemblages (some shells can be thousands of years old [Flessa et al. 1993; Meldahl et al. 1997; Kowalewski et al. 1998; Kidwell et al. 2005; Kosnik et al. 2009; Krause et al. 2009]). However, the assumption allows us to model expected DAs without having to estimate the many other life-history parameters of species and their interactions, which are largely unknown, and isolates the effects of life span from these other factors. Violations are considered in the Discussion.

Life Span Bias (LB).—The difference between the expected proportional abundance of a species in a DA and its observed proportional abundance in the LA is the *life span bias* (LB) for that species in that data set. Thus LB is the distortion of a species' proportional abundance predicted (modeled) to arise from a species having a relatively large (or small) mortality rate compared to other species in the LA. The LB of a species

occurrence can be positive (the expected proportional abundance dead is larger than the observed proportional abundance alive) or negative. $LB < |0.001|$ is considered to be zero. Focusing on change in a species' *proportional* abundance (1) allows us to compare LB among occurrences of the same or related species among data sets, (2) reduces the effects of variation in sample size among data sets, and (3) evaluates bias for a measure of abundance that is widely used in ecology and paleoecology.

LB modeled in this way can vary considerably among species depending on how strongly species differ in living abundance (the evenness of the LA) and how life span varies as a function of abundance. For example, assuming a LA of five species that range in life span from 2 to 20 years (average range observed in our 30 data sets; Suppl. Table 1) and assuming a perfectly even distribution of individuals (each species constitutes 0.20 of the LA), the model predicts that the shortest-lived species will increase in proportional abundance and the longest-lived species will decrease (LBs of +0.13 and -0.10 respectively), producing a less even DA assuming that the LA remains constant over time and that species have equal preservation rates. Given more realistic LA abundance structures (Fig. 1B–D) the largest values of $|LB|$ are generated among the most abundant species in the LA regardless of life span because LB is a positive function of standing abundance. For any given LA—say, the fairly even LA of Figure 1B—a monotonic increase in life span with declining living abundance (the most abundant species in the LA is the shortest-lived species) generates an expected DA that exaggerates the dominance of the top-ranked species in the LA and decreases evenness (dashed black line), whereas a monotonic decrease in life span with rank-abundance tends to flatten the abundance structure (dotted black line; the most abundant species in the LA is the longest-lived species, the rarest species is the shortest lived; see caption for description of other scenarios). Regardless of how life span varies with abundance, the effects of LB are damped as the evenness of the LA decreases (e.g.,

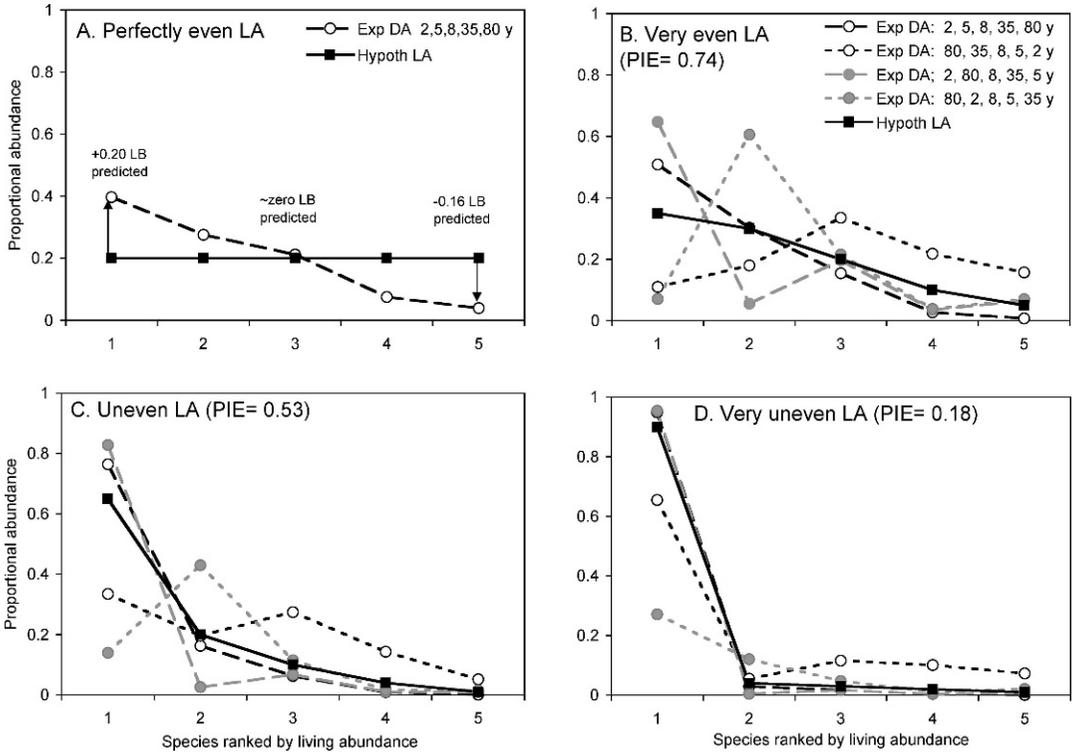


FIGURE 1. Examples of how variation in mortality rates affect the expected proportional abundances of species in death assemblages (Exp DA; various discontinuous lines) given a hypothetical living assemblage of five species (hypoth LA; black squares and continuous lines) whose life spans are drawn from the set 2, 4, 8, 12, and 20 years (reflects the average minimum, median, and maximum life spans observed in our 30 data sets). A, Where all species are equally abundant in the LA, the shortest-lived species (in this scenario, species ranked 1) increases in proportional abundance from 0.20 in the LA to 0.33 in the expected DA—a life span bias (LB) of +0.13—whereas an intermediate-lived species (species ranked 3) experiences approximately zero LB and the longest-lived species (species ranked 5) has a negative LB of -0.10 (see arrows). The expected DA is less even than the source LA. Given more realistic abundance structures (graphs B–D, evenness measured using Hurlbert's PIE), the magnitude of LB and its effect on assemblage evenness depends upon how life span varies with abundance. If the most abundant species is also the shortest lived, then the dominance of that top-ranked species becomes exaggerated in the DA and evenness decreases (dashed black lines in B–D produced by a monotonic increase in life span with declining living abundance; life span values given in key). In contrast, if the most abundant species in the LA is the longest lived, then the abundance structure of the DA flattens and in some cases the top-ranked living species drops in proportional abundance sufficiently to fall to a lower rank in the DA (dotted black lines, monotonic decrease in life span). Large values of LB can be generated if the two most highly ranked species in the LA have strongly contrasting life spans (dashed and dotted gray lines; here LB up to about $|0.25|$ from a 10-fold difference in life span that represents a 3.5-fold difference in annual mortality rate). The small number of dead individuals produced by the abundant longest-lived species not only creates a strong negative LB for that species occurrence but, by contributing so little to the total expected DA, magnifies the *proportional* abundance and positive LB of the large number of dead individuals produced by the also abundant shortest-lived species. For all scenarios of variation in life span with abundance, the effects of LB on the proportional abundance of a given species and on assemblage evenness are damped as LA evenness decreases (compare across plots B–D). In general, the largest $|LB|$ arises among the most abundant species in an assemblage because LB is a positive function of living abundance. Rare species show little change in proportional abundance regardless of LA evenness and of how life span varies with living abundance because a small number of living individuals will produce a small number of expected dead individuals regardless of mortality rate. This conservatism makes it difficult for rare species to shift into the ranks of the most abundant species of the DA by LB alone, allowing the expected DA to preserve the gross rank-ordering of species in the LA despite some shifting in ranks among the most abundant species.

compare any discontinuous line among B–D in Fig. 1). Given a very uneven LA (e.g., a single species constitutes 90% of living individuals), the top-ranked species will dominate the expected DA even if it is ten times

longer lived than any other species in the assemblage (as in Fig. 1D).

Note also that species that are relatively rare in the LA (e.g., species ranked third, fourth, and fifth in the hypothetical LAs of

Fig. 1B–D) show little change in proportional abundance between the LA and the expected DA regardless of LA evenness and of how life span varies with living abundance. This resistance to change in proportional abundance among rare species helps preserve the gross rank-ordering of species between the observed LA and expected DA in these hypothetical examples, notwithstanding some shifting in ranks among the most abundant species. The LAs of our bivalve data sets have a median 13 species (Suppl. Table 1) and thus have longer tails of relatively rare species, further reducing the likely impact of rank-switching among the most abundant species.

Larger spreads in life span among species increase $|LB|$ but within limits and have no qualitative effect on the trends evident in Figure 1 (Suppl. Figs. 2 and 3). For example, whereas the 10-fold contrast in life span modeled in Fig. 1 generates a maximum LB of about $|0.25|$ (life spans range from 2 to 20 years, average spread in bivalve data sets), a 20-fold contrast generates LB up to about $|0.40|$ and a 40-fold contrast generates LB up to about $|0.45|$ (latter approximates the largest range in life spans observed within any of our 30 data sets, from 2 to 75 years, and represents a 10-fold contrast in mortality rate from 0.85 to 0.085). An 80-fold contrast in life span generates LB up to $|0.47|$ (approximates entire range of life spans in the abundance database, from 1 to 75 years, and represents an 11-fold contrast in mortality rate).

Ability of Life Span Bias (LB) to Predict Observed Discordance (OD).—The power of modeled LB is assessed by using (1) the proportion of species occurrences where LB and OD have the same sign, (2) the average proportional contribution of LB to OD among species occurrences (a measure of relative magnitudes), and (3) the r^2 of correlations of LB and OD (see “Analyses” section that follows). In all approaches it is helpful to conceive of LB and OD as vectors that can have opposite signs and any length from 0 to 1. Where the LB of a species occurrence has the same sign as OD it can explain some proportion of that OD up to 100% (LB/OD ; proportional contribution is capped at 1, even

where LB exceeds the magnitude of OD). Where LB has the opposite sign to OD it clearly does not contribute constructively: counteracting bias(es) or conditions must be inferred to generate OD in the face of LB. Rather than characterize the contribution of LB as negative in such cases, zero is set as the lowest possible contribution of LB to the OD of a species occurrence. The estimated proportional contribution of LB to OD for a species occurrence, one measure of model performance, is maximized using these $[0,1]$ limits. In analyses of individual data sets, the *total* proportional contribution of LB to OD is the sum of absolute values of LB for all species occurrences where LB and OD share sign, divided by the sum of absolute values of OD for the entire data set.

The OD that is not explained by LB—more precisely, the vector $|OD-LB|$ —represents (1) all taphonomic bias from sources other than interspecies variation in life span (e.g., loss from out-of-habitat transportation, dissolution, fragmentation, bioerosion, and other modification that either destroys shells or makes them taxonomically unidentifiable; plus any introduction of allochthonous shells) and (2) the effects of any violation of the assumptions of our approach, including inaccuracy in life span estimates, variability in community composition during the period of time-averaging, and random sampling effects. These potential factors are considered in the Discussion, but a complete explanation of OD in proportional abundance is not our analytic focus.

Analyses.—The strength of association between OD, LB, and life span was evaluated by Spearman rank-order tests of raw data and by least-squares linear regression of normalized data (log-transformation of life span, angular-transformation of LB and OD with signs restored). Transformation does not fully normalize values of LB and OD in all partitions of the aggregate database and in all individual data sets, and thus rank-correlation tests are probably most reliable. All tests were conducted using the R statistical framework (R Development Core Team 2005).

Tests were first conducted using the aggregate database of 413 living species occurrence-

es and were then repeated for the “most abundant” species (107 living species occurrences whose proportional abundance in the LA is ≥ 0.05), for occurrences of longer-versus shorter-lived species (partitions defined above), for occurrences in pristine versus human-modified study areas (193 and 220 occurrences respectively), and for each of the 30 data sets in order to test for sources of variation. DAs from pristine settings (no excess nutrient input or bottom-trawling) reflect accumulation under natural levels of temporal variability in benthic communities (within-habitat time-averaging that includes succession and decadal fluctuations). DAs from modified settings reflect communities under greater stress and are likely to be environmentally condensed records of multiple communities or community states. LB should have less explanatory power for these DAs because the composition of the LA is less likely to have been stable over the duration of time-averaging.

Because LB can substantially alter the proportional abundances of species in DAs (hypothetical examples in Fig. 1), we tested the effect of LB on the evenness of death assemblages for each of the 30 data sets, using the relatively unbiased estimator PIE (Hurlbert 1971). PIE stresses the proportional abundance of the most abundant species (it is basically 1 minus the sum of squared proportional abundances divided by the number of species), and so ranges from ~ 1 when evenness is high (no single species dominates) to ~ 0 (vast majority of individuals are of a single species). “Delta-PIE” (Δ PIE) is the difference between the PIE of a DA and that of the local LA and in principle can range from $+1$ to -1 (Olszewski and Kidwell 2007). We test (1) whether *observed* Δ PIE (PIE of the observed DA minus PIE of the LA) has the same sign as *expected* Δ PIE (PIE of expected DA minus PIE of the LA) and (2) in data sets where these two Δ PIE values match in sign, whether PIE of the expected DA differs significantly from either the LA or observed DA. This latter analysis is simplified to a test of differences in the proportional abundance of the most abundant taxon using a G-test of raw frequencies because this takes into

account the sizes of the two assemblages being compared.

Previous meta-analyses have already observed good live-dead agreement in species rank abundances in these and other molluscan data sets: species that are dominant in the DA tend to be dominant in the counterpart LA, and species that are rare in the DA tend to be rare or absent in the LA, particularly in settings unaffected by human activities (Kidwell 2001, 2007). Good live-dead agreement in species' *rank* abundances, however, does not require agreement in species' *proportional* abundances. For example, a species that is top-ranked in both LA and DA may constitute 90% of individuals in one and only 30% in the other. Consequently, good live-dead agreement in rank abundance does not rule out strong LB of species occurrences or of assemblage evenness. The robustness of rank-abundance to life span bias is evaluated by comparing observed and predicted changes in the identity of the top-ranked species.

Results

Patterns of OD and LB in Aggregate Data.— Among the 413 living species occurrences, life span bias (LB) ranges from $+0.18$ to -0.23 but on average shifts the proportional abundance of a species upward or downward by less than two percentage points (median and mean $|LB|$ of 0.003 and 0.017 in Table 1; Fig. 2; for histogram and cumulative frequency plot, see Supplemental Fig. 4). The observed discordances (ODs) of these same species occurrences range more broadly from $+0.62$ to -0.75 but the average shift in proportional abundance is still small (median and mean $|OD|$ of 0.014 and 0.06; Table 1, Fig. 2). Even among the most abundant species in a LA, the average magnitude of LB is small both in absolute terms and relative to OD (median $|LB|$ of 0.03, median $|OD|$ of 0.09; Table 1).

OD is significantly positively correlated with LB but only weakly ($r^2 \leq 0.10$, $p < 0.001$, Table 1, Fig. 3A,B). This low predictive power is expected given the low variance in LB compared to OD (Fig. 2) but also reflects that OD has the same sign as LB in only about half of all species occurrences (54%, not

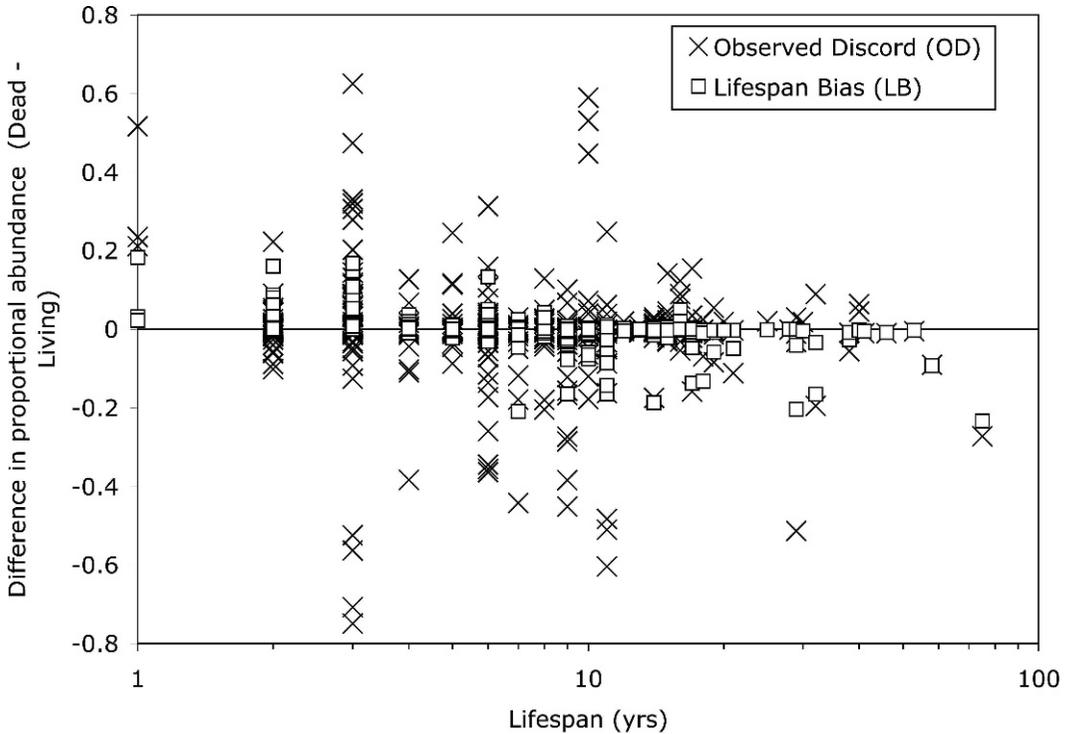


FIGURE 2. Scatter plot of variation in observed live-dead discordance (OD) and life span bias (LB) as a function of life span (log scale) for 413 living bivalve species occurrences. OD exhibits a much broader range of positive and negative values than does LB, but the majority of values of both variables are very small (median live-dead difference $\leq |0.02|$; Table 1). A significant negative correlation exists between OD and life span but the explanatory power of life span is essentially nil (e.g., coefficient of linear regression is -0.44 at $p < 0.001$, but the adjusted $r^2 = 0.02$). OD, observed proportional abundance in the death assemblage minus observed proportional abundance in the living assemblage; LB, expected proportional abundance in the death assemblage minus observed proportional abundance in the living assemblage.

significantly different from chance; G -test of raw frequencies, $p = 0.05$; same result among the most abundant species; Table 1). LB has no predictive value for the sign of OD, indicating that an array of other taphonomic biases and effects from time-averaging and sampling are more important (Fig. 4).

As a proportion of OD, LB contributes little on average (median 0.05 of OD; Table 1). It makes the largest contribution (up to 1) where OD is small, that is among species occurrences where there is little live-dead difference in proportional abundance that needs explanation (Fig. 5). LB makes a larger average contribution to OD among the most abundant species in the database, but this value is still small (median contribution of 0.09; Table 1).

Doubling the size of both the abundance and life span databases since our initial analysis (Rothfus and Kidwell 2006) has

increased our confidence in these patterns (e.g., the p -values of various correlations) but has not altered the outcome substantively (average values of LB and their explanatory power remain small).

Variation in Explanatory Power with Life Span.—LB—or other bias that covaries with life span—explains more variation in OD among long-lived species than among short-lived species but still explains less than a majority of variation. For example, the correlation of OD to LB yields an r^2 of 0.24 to 0.31 among the 137 long-lived species occurrences depending on the test, contrasted with an r^2 of basically 0 among the 216 short-lived species occurrences, and the median proportional contribution of LB to OD is 0.33 contrasted with 0 (Table 1, Figs. 3A, 5). A slight majority of long-lived species (67%) fall in either the lower-left or upper-right quadrants of

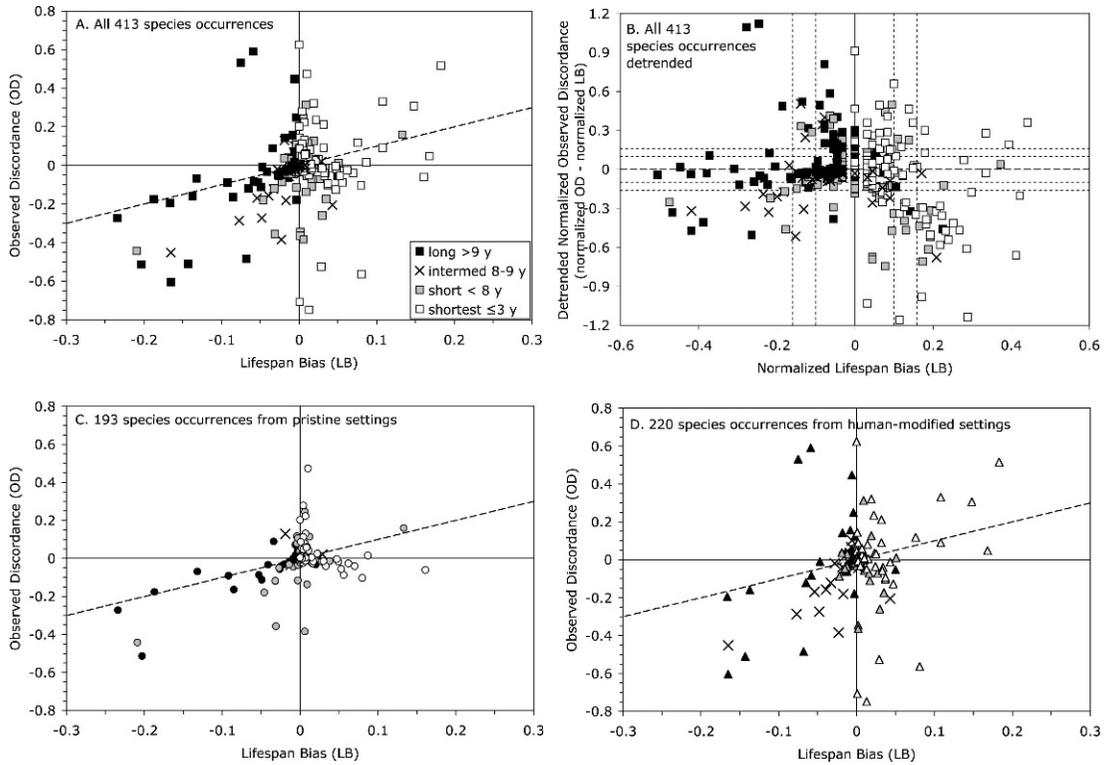


FIGURE 3. Species show a large scatter in observed discordance (OD) as a function of life span bias (LB) both using raw data (plots A, C, D) and normalized data (plot B), with the latter detrended for clarity. In all graphs, x- and y-axes have different scales, dashed line is unity; in B, dotted lines denote ± 0.01 and ± 0.025 envelopes in raw rather than normalized units. A, Species occurrences cluster densely around the origin, where OD and LB are about zero. The explanatory power of LB for OD is significantly positive but weak. OD is more consistent with LB among long-lived species than among short-lived species (including the shortest-lived species). B, Opening up the middle part of the distribution by arcsine-transformation of the data and rotating it to display OD that cannot be explained by LB clarifies that LB does a good job of explaining OD for some occurrences of long-lived species (tail of points to left of origin that fall within the envelope of ± 0.01 or ± 0.025). Overall, however, most species occurrences have very little OD needing explanation (i.e., fall close to the midline; and see Fig. 5). Gap in data points on either side of vertical midline is created by our collapsing all values of $|LB| \leq 0.001$ to zero; OD was treated similarly, but no gap appears because of difference in plotting scale. OD shows less variance in pristine settings (C) and LB has greater explanatory value among species occurrences there than in areas subject to anthropogenic eutrophication and/or bottom trawling (D), but the difference is slight and not robust to test method (Table 1). In pristine settings (C), occurrences of long- and intermediate-lived species show the strongest negative ODs (less abundant dead than alive) and short-lived and especially the shortest-lived species do show the strongest positive ODs. However, many occurrences having positive OD are not predicted to be so biased by the model (series of shortest-lived species along vertical midline), and many occurrences exhibit essentially no positive OD despite predictions that they will be more abundant dead than alive (species falling around x-axis to right of origin). Thus the effect of mortality rate on species proportional abundances in time-averaged death assemblages is only indirect, even in pristine settings. In modified areas (D), the strongest negative ODs are encountered and occur among species in all life span categories (points in lower half of graph), suggesting that these species were formerly less abundant in the system or have been preferentially lost through postmortem processes. Some occurrences of long-lived species have large positive ODs, which are not predicted by LB but are consistent with these species being ecological relicts of pre-impact community states. Many occurrences of the shortest-lived species have positive ODs as predicted but they are mostly more abundant dead than the LB model predicts. Again, the effect of life span on observed discordances in species abundances is weak and indirect.

Figure 3A,B where LB correctly predicts the sign of OD, whereas LB has predictive power in less than half (44%) of short-lived species occurrences (both frequencies are significantly different from chance at $p = 0.001$ using a G-test; Table 1). Intermediate-lived species

tend to plot among long-lived species (Figs. 3A, 5).

Variation with Human Impact.—The predictive power of LB for OD was expected to be higher in pristine settings than in modified settings, but differences are small and mostly

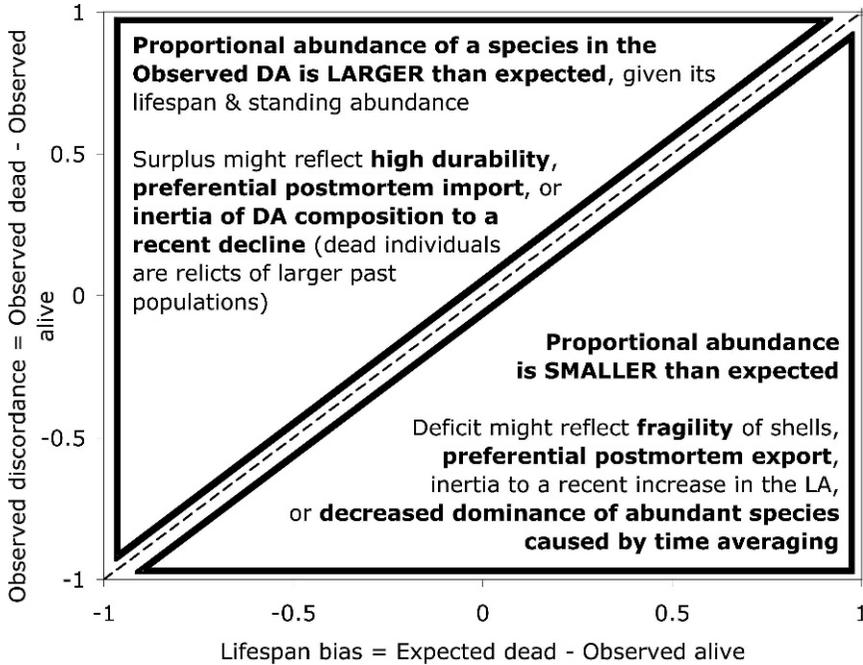


FIGURE 4. Conceptual counterpart to the scatter plot of Figure 3A, listing some of the biological, taphonomic, and sampling conditions that might explain why a species in a data set (species occurrence) might be more abundant in the DA than modeled on the basis of its mortality rate (upper triangle) or less abundant than modeled (lower triangle). DA, death assemblage; LA, living assemblage.

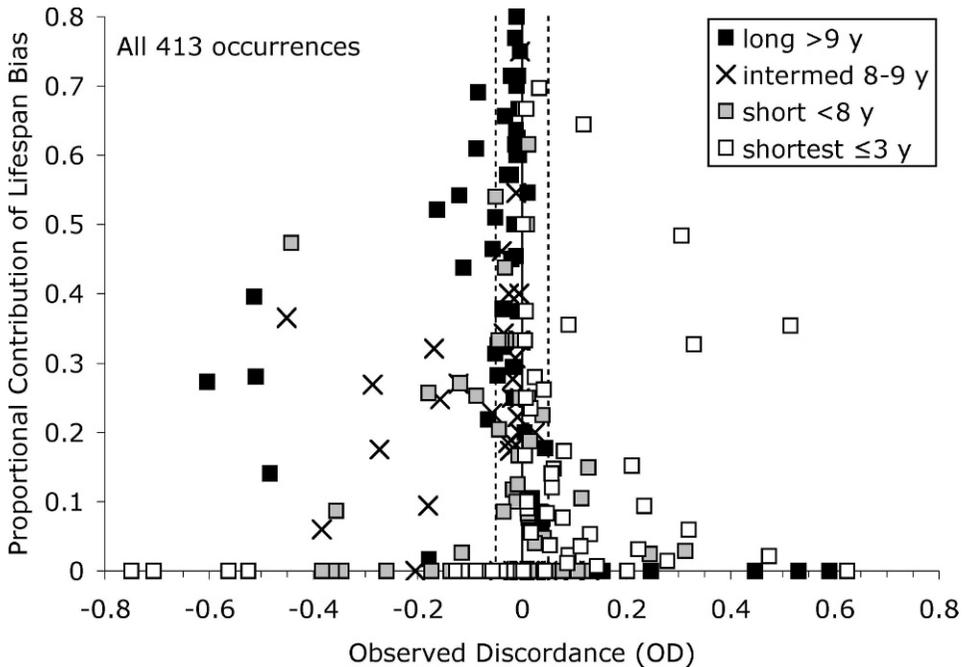


FIGURE 5. Life span bias contributes approximately zero (dense data points on or near the x-axis) toward observed discordance except where OD is itself quite small (strong peak of points at midline; dotted lines are arbitrary ± 0.05 OD, i.e., observed living and dead abundances differ by 5% or less).

insignificant (Table 1, Fig. 3B,C). Variance of OD is significantly larger in modified settings (F_{\max} -test at $p = 0.01$), creating a larger challenge for LB to explain. For example, in modified settings a few occurrences of long-lived species are notably *more* abundant dead than alive (contrary to LB and consistent with their being ecological relicts of pre-impact LAs; midline and upper left quadrant of Fig. 3C), and a few occurrences of the shortest-lived species are unexpectedly much *less* abundant dead than alive, which can have several explanations (strongly negative OD, midline and lower right quadrant of Fig. 3C; Fig. 4). On the other hand, modified settings contain most of the shortest-lived species occurrences where LB at least predicts the positive sign of OD, presumably because these species are present as large living populations more consistently than they are in pristine settings (category includes the annual *Nutricola tantilla* and the opportunist *Mulinia lateralis*; upper right quadrant of Fig. 3C; Suppl. Fig. 5).

Model performance is weak in pristine settings largely because of poor performance among occurrences of the shortest-lived species (Fig. 3C). Considerable positive OD exists that is not explained by life span bias (dense array of data points along the midline above the origin) and life span predicts considerable positive bias that does not exist (dense array of data points along x-axis to the right of the origin).

Variation among Individual Data Sets.—Repeating these analyses in each of the 30 abundance data sets reveals considerable variation in (1) the spread of LB values (range from 0.01 to 0.40; spread of LB values in aggregate database is 0.41); (2) the strength of association of OD and LB (Spearman rho ranges from -0.52 to 0.97); (3) the proportion of species occurrences where OD and LB agree in sign (ranges from 0 to 0.91); and (4) the total proportional contribution of LB to OD (ranges from 0 to 0.57; Table 2; additional description Suppl. Table 1).

Although the explanatory power of LB for OD is good within some data sets, it is unpredictable (Table 2). For example, only seven of the 26 large data sets where a

correlation test is warranted show a significant positive correlation of OD and LB (after a sequential Bonferroni correction for multiple tests, only three correlations are still significant at $p < 0.05$; Table 2; note that four data sets show negative correlations, albeit none are significant). Data sets showing the strongest *positive* relationship of OD and LB (regardless of how we define strong) are all from coastal embayments rather than open continental shelves, but they do not encompass all available data sets from embayments. They also come from diverse seafloor types (muds to shell gravels), tropical to temperate latitudes, and both pristine and anthropogenically modified study areas, and reflect both fine-mesh (≤ 1 mm) and coarse-mesh processing of original samples (coarse-mesh data sets should represent the best match to our model's use of adult mortality rates per Hoenig 1983). If we focus on the seven data sets that were processed using coarse mesh (> 1 mm adult individuals only) and conducted in pristine areas, where the DA is most likely to be in equilibrium with time-averaged input from the local LA, only one shows a significant positive correlation of OD with LB (does not survive Bonferroni correction; Table 2). The model does not perform any worse—or better—among fine-mesh data sets that include juveniles and the adults of small-bodied, perhaps opportunistic species.

Data sets that exhibit significant agreement of OD to LB—that is, habitats where DAs are arguably more sensitive to mortality rates than they are to other taphonomic and biological variables—thus cannot be predicted using the basic kinds of sampling, environmental, and biological information that are consistently available for systems. It is clear that (1) had we tested only a single data set we might have found reasonably good agreement between modeled LB and OD but would have been as likely to encounter poor agreement, and (2) patterns in the aggregate database would have emerged quickly as multiple habitats within a study area or from a few regions were examined.

The set of relatively “well behaved” long-lived species that create the lower-left tail in the aggregate scatter plot (Fig. 3A) are drawn

TABLE 2. Summary of results from individual data sets, arranged by degree of human modification in the study area and mesh size used by original author to process samples (see Suppl. Table 1 for details). Pristine study areas = neither anthropogenic eutrophication nor bottom-trawling suspected; Modified study areas = anthropogenic eutrophication and/or bottom-trawling either suspected or well-documented. S = number of bivalve species occurrences used in analysis (each species constitutes at least 0.001 of individuals in the LA). PIE = Hurlbert's metric of assemblage evenness; Δ PIE = difference between PIE of observed DA and observed LA (observed Δ PIE) or between PIE of expected DA and observed LA (expected Δ PIE). Other abbreviations as in Table 1. A G-test of the proportional abundance of the top-ranked species is used to determine whether the evenness of the expected and observed DAs are significantly different when they have the same sign.

Study area & habitat	Lead author	LA S	LA PIE	OD min, max	LB min, max	Spearman rho of OD & LB
Pristine areas, collected using coarse-mesh >1 mm						
Laguna Madre shelly sand	Smith	16	0.47	-0.035, 0.114	-0.016, 0.030	0.541*
Lower Laguna Madre well-sorted sand	Smith	19	0.89	-0.115, 0.245	-0.053, 0.053	0.162
Mugu Lagoon sand (LA census 5)	Peterson	13	0.56	-0.112, 0.089	-0.049, 0.038	-0.068
San Juan Strait shell gravel	Kowalewski	23	0.82	-0.272, 0.159	-0.234, 0.161	0.167
Yucatan backreef muddy shell gravel	Ekdale	21	0.79	-0.175, 0.078	-0.187, 0.056	0.013
Yucatan mangrove lagoon sandy mud	Ekdale	23	0.86	-0.136, 0.107	-0.132, 0.062	-0.394
Yucatan strait shell gravel	Ekdale	12	0.16	-0.383, 0.223	-0.009, 0.007	0.177
Pristine areas, collected using fine-mesh \leq 1 mm						
Mannin Bay algal bank	Bosence	14	0.76	-0.356, 0.279	-0.032, 0.070	0.634*
Mannin Bay clean algal gravel	Bosence	17	0.21	-0.513, 0.131	-0.165, 0.087	0.212
Mannin Bay fine sand	Bosence	13	0.57	-0.442, 0.202	-0.027, 0.017	0.632*
Mannin Bay muddy algal gravel	Bosence	22	0.84	-0.179, 0.474	-0.046, 0.080	0.737***
Human-modified areas, all mesh sizes						
Tijuana Slough sand (LA census 5)	Peterson	13	0.58	-0.195, 0.058	-0.166, 0.051	0.072
Laguna Chica mud	Garcia-Cubas	8	0.25	-0.483, 0.313	-0.068, 0.032	0.738
Tomales Bay mud	Johnson	11	0.57	-0.451, 0.516	-0.165, 0.183	0.242
Tomales Bay muddy sand	Johnson	11	0.77	-0.384, 0.211	-0.050, 0.056	0.141
Tomales Bay sand	Johnson	10	0.69	-0.204, 0.235	-0.137, 0.043	-0.015
Chesapeake Bay eelgrass	Jackson	10	0.73	-0.345, 0.142	-0.018, 0.037	-0.517
West Bay muddy sand	White	16	0.73	-0.168, 0.118	-0.054, 0.076	0.511*
West Bay sand	White	10	0.64	-0.286, 0.306	-0.077, 0.148	0.966***
West Bay sandy mud	White	14	0.81	-0.157, 0.127	-0.039, 0.108	0.913***
Corpus Christi shelf sand	White	11	0.10	-0.707, 0.625	-0.002, 0.003	0.171
Corpus Christi shelf sandy mud (LA census 4)	Staff	20	0.17	-0.749, 0.144	-0.006, 0.013	0.116
Laguna Pueblo Viejo mud	Reguero	7	0.63	-0.51, 0.330	-0.143, 0.108	0.357
Galveston shelf shelly muddy sand	White	14	0.85	-0.273, 0.320	-0.048, 0.043	0.334
Plymouth Sound shell gravel (LA census 1)	Carthew	10	0.06	-0.178, 0.024	-0.003, 0.003	0.202
Rhodes shelf silty sand (LA census summer)	Zenetos	37	0.91	-0.126, 0.156	-0.065, 0.098	0.314
Small data sets ($S < 7$), all areas and mesh sizes						
Laguna Camaronera shell gravel	Reguero	4	0.12	-0.525, 0.447	-0.018, 0.029	NA
Laguna Pueblo Viejo muddy sand	Reguero	4	0.48	-0.604, 0.496	-0.165, 0.168	NA
Laguna Alvarado sand	Reguero	4	0.57	-0.563, 0.531	-0.075, 0.081	NA
Laguna Alvarado shell gravel	Reguero	6	0.72	-0.364, 0.590	-0.059, 0.037	NA
Total (median)	30 data sets	413 (13)	(0.64)	(-0.32, 0.22)	(-0.05, 0.05)	

from many different data sets—no single data set or kind of data set is responsible. The well-behaved long-lived species in the aggregate pattern are drawn from multiple bivalve clades and functional groups (e.g., infaunal subsurface-deposit-feeding Nuculidae; epi- to endo-byssate suspension-feeding Mytilidae, Arcidae, and Carditidae; infaunal suspension-

or surface-deposit-feeding Astartidae, Tellinidae, Psammobiidae, and Veneridae).

LB of Assemblage Evenness.—LB does not predict a consistent change in assemblage evenness nor is it able to predict either the sign or the magnitude of observed Δ PIE (Table 2) (Olszewski and Kidwell [2007] found a similar spread of observed Δ PIE but

TABLE 2. Extended.

rho ²	Proportion where OD & LB have same sign	Total proportional contribution of LB to OD	Observed ΔPIE, Expected ΔPIE	ΔPIE's have same sign?	PIE of expected & observed DAs different at $p < 0.05$?	Spearman rho of living abundance & life span
0.29	0.75	0.27	-0.17, -0.02	Yes	Yes	-0.363
0.03	0.58	0.15	-0.07, -0.05	Yes	Yes	-0.172
0	0.46	0.24	0.11, 0.06	Yes	Yes	0.347
0.03	0.30	0.52	0.04, 0.01	Yes	No	-0.000
0	0.33	0.42	0.10, 0.08	Yes	No	0.269
0.17	0.30	0.24	0.03, 0.02	Yes	No	0.245
0.03	0.43	0.03	0.49, -0.01	No	NA	0.039
0.40	0.71	0.11	0.10, 0	No	NA	-0.260
0.04	0.70	0.35	0.60, 0.24	Yes	Yes	0.130
0.40	0.54	0.10	0.30, 0.06	Yes	Yes	-0.585 *
0.54	0.77	0.21	-0.14, -0.02	Yes	Yes	-0.229
0.01	0.77	0.57	0.20, 0.14	Yes	No	0.612 *
0.54	0.75	0.14	0.46, 0.11	Yes	Yes	0.168
0.06	0.91	0.35	-0.52, -0.06	Yes	Yes	-0.416
0.02	0.55	0.12	0.10, 0.02	Yes	No	-0.147
0	0.50	0.26	0.14, 0.07	Yes	No	0
0.27	0.30	0.03	0.12, -0.02	No	Yes	-0.258
0.26	0.63	0.28	-0.04, -0.06	Yes	Yes	-0.128
0.93	0.60	0.40	-0.32, -0.12	Yes	Yes	-0.746 *
0.83	0.71	0.39	-0.06, -0.06	Yes	Yes	-0.504
0.03	0.40	0.004	0.44, 0	No	NA	-0.039
0.01	0.29	0.01	0.74, -0.02	No	NA	-0.287
0.13	0.57	0.26	-0.02, 0.08	No	NA	-0.248
0.11	0.50	0.09	-0.07, 0.03	No	NA	-0.341
0.04	0.55	0.04	0.31, 0.01	Yes	Yes	0.192
0.10	0.51	0.20	0.01, 0	No	NA	0.178
NA	0.50	0.02	0.50, -0.05	No	NA	NA
NA	0.75	0.50	0.11, 0.04	Yes	No	NA
NA	0.00	0	-0.11, -0.08	Yes	No	NA
NA	0.17	0.01	-0.40, 0	No	NA	NA
	(0.54)	(0.21)				

used the *complete* molluscan assemblages from these and 11 other regional live-dead data sets, rather than bivalves only.) Overall, expected ΔPIE is positive in 15 data sets and negative in 15, which is not significantly different from a random draw. Observed ΔPIE has the same sign as expected ΔPIE in 20 of the 30 data sets: compared to the LA, the observed DA has either a flatter (13 data sets)

or steeper (8 data sets) abundance distribution that is consistent with the changes in species abundances predicted by life span bias. This frequency (20/30) of matched signs is not significantly different from a random draw at this small sample size (G -test, $p = 0.05$). Even among the 20 data sets where signs match, expected ΔPIE is smaller than observed ΔPIE—i.e., is less strongly positive

TABLE 3. Observed and expected changes in the identity of the top-ranked species in 26 large data sets. The top-ranked species in the observed DA is shorter lived than that of the LA in 11 data sets, but this elevation in rank is correctly predicted by the model in only four cases, indicating that mortality rate alone has little power to generate this change. The identity of the top-ranked species does not change between the LA and DA in 12 other data sets, and the model correctly predicts no change in all of these data sets. This live-dead stability in the identity of the top-ranked species is a meaningful absence of life span bias given the availability of shorter-lived species in the LA that could have been elevated to the top rank postmortem. These results suggest that the model design is basically sound and that bias from mortality rates is neither widespread nor particularly strong. On average, the top-ranked species in the observed DA has moved up only one rank from its position in the LA (median shift among 26 data sets; in two data sets, the most abundant species in the DA occurs only as dead individuals, and thus is tied with other dead-only species as the lowest ranked species in the LA).

Study area and seafloor type	Min, max life span (years) in LA	Top-ranked species in LA and its life span (y)	Top-ranked species in expected DA and its life span (years)	Top-ranked species in observed DA and its life span (years)	Rank in LA of top-ranked species in observed DA / total number of species in the LA
Pristine areas, coarse-mesh					
Laguna Madre shelly sand	3, 19	<i>Anomalocardia cuneimeris</i> 5	Same	Same	1/16
Lower Laguna Madre sand	2, 19	<i>Chione cancellata</i> 6	Same	Same	1/19
Mugu Lagoon sand	4, 53	<i>Cryptomya californica</i> 21	Same	Same	1/13
San Juan Strait shell gravel	2, 75	<i>Modiolus modiolus</i> 75	<i>Monia cepio</i> 6	<i>Monia cepio</i> 6	2/23
Yucatan backreef gravelly	2, 38	<i>Transennella cubaniama</i> 14	Same	Same	1/21
Yucatan lagoon sandy mud	2, 18	<i>Cardianera floridana</i> 18	<i>Lucinisa nassula</i> 2	<i>Lucinisa nassula</i> 2	4/23
Yucatan Strait shell gravel	2, 18	<i>Ervilia nitens</i> 4	Same	Same	1/12
Pristine areas, fine-mesh					
Mannin Bay algal bank	2, 14	<i>Musculus discors</i> 6	Same	<i>Parvicardium exiguum</i> 3	9/14
Mannin Bay clean algal gravel	2, 29	<i>Goodallia triangularis</i> 29	Same	Same	1/17
Mannin Bay fine sand	2, 19	<i>Thyasira flexuosa</i> 7	Same	<i>Parvicardium exiguum</i> 3	8/13
Mannin Bay muddy algal gravel	2, 19	<i>Kurtiella bidentata</i> 7	<i>Lucinoma borealis</i> 2	<i>Parvicardium exiguum</i> 3	6/22
Human-modified areas, all meshes					
Tijuana Slough sand	3, 32	<i>Nuttallia nuttallii</i> 32	Same	Same	1/13
Laguna Chica mud	2, 17	<i>Cyrenoida floridana</i> 11	Same	Same	1/8
Tomales Bay mud	1, 21	<i>Lyonsia californica</i> 9	<i>Nutricula tantilla</i> 1	<i>Nutricula tantilla</i> 1	2/11
Tomales Bay muddy sand	1, 17	<i>Lyonsia californica</i> 9	Same	<i>Nutricula tantilla</i> 1	7/11
Tomales Bay sand	1, 17	<i>Cadella nuctuloides</i> 17	<i>Angulus modesta</i> 8	<i>Cadella nuctuloides</i> 17	1/10
Chesapeake Bay eelgrass	3, 46	<i>Amysgdalum papyrium</i> 6	Same	<i>Gemma gemma</i> 4	2/10
West Bay muddy sand	2, 19	<i>Mulinia lateralis</i> 3	Same	Same	1/16
West Bay sand	3, 19	<i>Mulinia lateralis</i> 3	Same	Same	1/10
West Bay sandy mud	3, 15	<i>Mulinia lateralis</i> 3	Same	Same	1/14
Corpus Christi shelf sand	2, 14	<i>Abra aequalis</i> 3	Same	<i>Mulinia lateralis</i> 3	6/11
Corpus Christi shelf sandy mud	2, 40	<i>Abra aequalis</i> 3	Same	<i>Mulinia lateralis</i> 3	2/20
Laguna Pueblo Viejo mud	3, 17	<i>Cyrenoida floridana</i> 11	Same	<i>Mytilopsis leuophaeta</i> 6	Dead-only, 7
Galveston shelf shelly muddy sand	2, 17	<i>Saccella concentrica</i> 9	Same	<i>Mulinia lateralis</i> 3	8/14
Plymouth Sound shell gravel	2, 15	<i>Spisula elliptica</i> 10	Same	Same	1/10
Rhodes shelf silty sand	2, 29	<i>Nuculana fragilis</i> 10	Same	<i>Limaria loscombei</i> 9	Dead-only, 37

or less strongly negative—in 19 cases and falls significantly short in most (Table 2).

LB of Species Ranked Abundance.—Some DAs are dominated by a shorter-lived species than the one that dominates (i.e., is top-ranked in) the LA, consistent with bias from mortality rate (11 of 26 data sets in Table 3). However, the model consistently underestimates the frequency at which this change occurs, predicting this outcome in only four data sets and correctly identifying the new top-ranked species in three (Table 3). Differential mortality is thus not sufficient to explain observed shifts to dominance by a shorter-lived species in most of the data sets where such a shift occurs: change in the identity of the top-ranked species must instead reflect other factors, such as formerly larger population sizes or the preferential preservation of short-lived species. Moreover, 12 of the remaining data sets show no change in the identity of the top-ranked species and the model (correctly) does not predict any change, further underscoring the general weakness of mortality rate as a biasing factor. On average, the top-ranked species in the observed DA has moved up only one position from its rank in the LA (most have shifted zero positions; last column in Table 3), and this top-ranked species is usually not the shortest-lived species in the available living assemblage (second column in Table 3).

Discussion

The lack of consistent bias arising from interspecies differences in life span might have several explanations. The modeled sign and magnitude of life span bias for these molluscan data sets might be poor approximations of observed discordances because (1) our life span data are incomplete or biased and/or (2) species' proportional abundances in the local living assemblage were not stable over the duration of time-averaging (i.e., the LA sampled by a single survey does not capture the true average composition), a crucial assumption in extrapolating an annual mortality model to time-averaged death assemblages. It is also possible that our modeled LB values are reasonably good approximations but that in actual DAs the effects

tend to be neutralized or swamped by a counteracting preservational bias that is linked to life span (e.g., as found in the Amboseli mammals studied by Behrens-meyer et al. [1979]).

Assumption of Correct Information on Life Span.—Error in our model predictions might arise from incomplete knowledge of life span. The reliability of our extrapolations from congeneric and confamilial species is difficult to assess because the scattered data on life span provide little guidance on interspecies variation within clades (Suppl. Table 2, but see Note 4 there on phylogenetic structure in life span that would support extrapolations).

Error might also arise from incorrect (biased) life span estimates even for species whose maximum life span has been documented. The accuracy of a life span estimate is subject to fairly well known environmental and sampling factors. For example, the maximum life spans of ectothermic species are inversely related to growth rate and thus vary regionally with differences in water temperature and productivity as well as with pollution and exploitation (for general discussions, see Comfort 1957 and Zolotarev 1980; variation with latitude by Beukema and Meehan 1985, Harrington 1987, Dekker and Beukema 1993, Walker and Heffernan 1994, Fiori and Defeo 2006; variation between warm eutrophic and cool mesotrophic waters by Metaxatos 2004; between El Niño and La Niña regimes by Riascos et al. 2008; with depth by Weber et al. 2001; for analyses of the possible selective pressure of environmental cycles on life spans, see Powell and Cummins 1985 and references therein). Reported maximum life spans will thus generally tend to underestimate true maximum life spans owing to incomplete sampling and natural demographic variability (e.g., Beukema 1989), much as local stratigraphic ranges underestimate true ranges. Underestimates should not alter the outcome of our analysis unless they are nonrandomly distributed across our abundance database. They would instead simply increase all mortality rates, increasing the expected *numerical* abundances of species

in DAs but not altering *proportional* abundances.

Concern with local undersampling and anthropogenic effects motivated our reliance on the globally longest reported life span of a species as its maximum life span. This protocol should reduce variance from other environmental factors on local mortality rate and favors data from populations (and species) from higher latitude because growth rates tend to be slower there. Mid- to high-latitude stocks have also received the most intense demographic study (see sources in Suppl. Table 2). The percentage of species occurrences in a live-dead data set whose life span is documented at the species level ("knowledge of life span") does increase significantly with latitude in our database (Spearman $\rho = 0.66$, $p < 0.0001$; data in Suppl. Table 1). Thus we do arguably have richer and more appropriate life span information for species occurring in higher-latitude data sets than for those in lower latitudes.

LB does have greater explanatory power for OD among the 131 living species occurrences in the database whose maximum life span is documented than it does among the rest of the abundance database where life spans are estimated from other species or genera (e.g., Spearman $\rho^2 = 0.15$ for known species versus 0.03 for all others; Table 1). Although the improvement in model performance is striking with this partition, LB on average nonetheless remains small relative to OD, makes the same small contribution to OD, and continues to have no ability to predict the sign of OD (nor does performance improve if only the 64 known species from pristine settings are considered; bottom row in Table 1).

Among data sets, model performance (as measured by the Spearman rank-correlation coefficient of OD and LB) does not increase significantly with knowledge of species' life span, although it does among data sets from pristine settings (Fig. 6A, drawing on data in Table 2; among pristine data sets, performance also increases with latitude, but partial correlations indicate that latitude has no effect when knowledge of life spans is controlled). If

we consider the four pristine data sets where life span is known for at least half of the species in the LA, model performance is quite good (all four are from a single study area, Mannin Bay). For example, three of four rank correlations of OD and LB are significant at $p < 0.05$ (although only one survives Bonferroni correction) and the median ability of LB to predict the sign of OD is 71% (Table 2). However, LB still tends to strongly underestimate the magnitude of OD (median total proportional contribution toward OD is only 0.16) and all four of these pristine data sets are from a single study area, reducing our confidence (adding the pristine San Juan Channel data set where about one-third of species have known life spans does not change the result notably). OD is consistently underestimated by the model regardless of degree of knowledge of life spans and setting (Fig. 6B).

Improving the quality of information on life spans thus simply improves our ability to predict the small effect of LB on OD—it does not reveal a large, otherwise hidden effect. This result clearly does not preclude finding good matches between LB and OD among key (e.g., very abundant) species in some data sets (e.g., occurrences falling near line of unity in Figure 3, and correlation coefficients of ~ 0.9 in some data sets [Table 2]). In a study in progress using *locally* determined annual mortality rates, Kosnik (2009, personal communication 2010) finds that, for all three of the abundant molluscan species tested, proportional abundances observed in the DA are better predicted by the expected DA than by standing abundances in the LA, with mortality-adjusted shifts in proportional abundance up to about 104%. Additional independent studies will be needed to determine if, as a general principle, model performance is improved significantly when local mortality rates are known. Our suspicion at this point is that, in terms of correctly modeling the effects on OD, the accuracy of information on life spans or mortality rates is less important than is the accuracy of information on the time-averaged abundance of species in the LA (see section below).

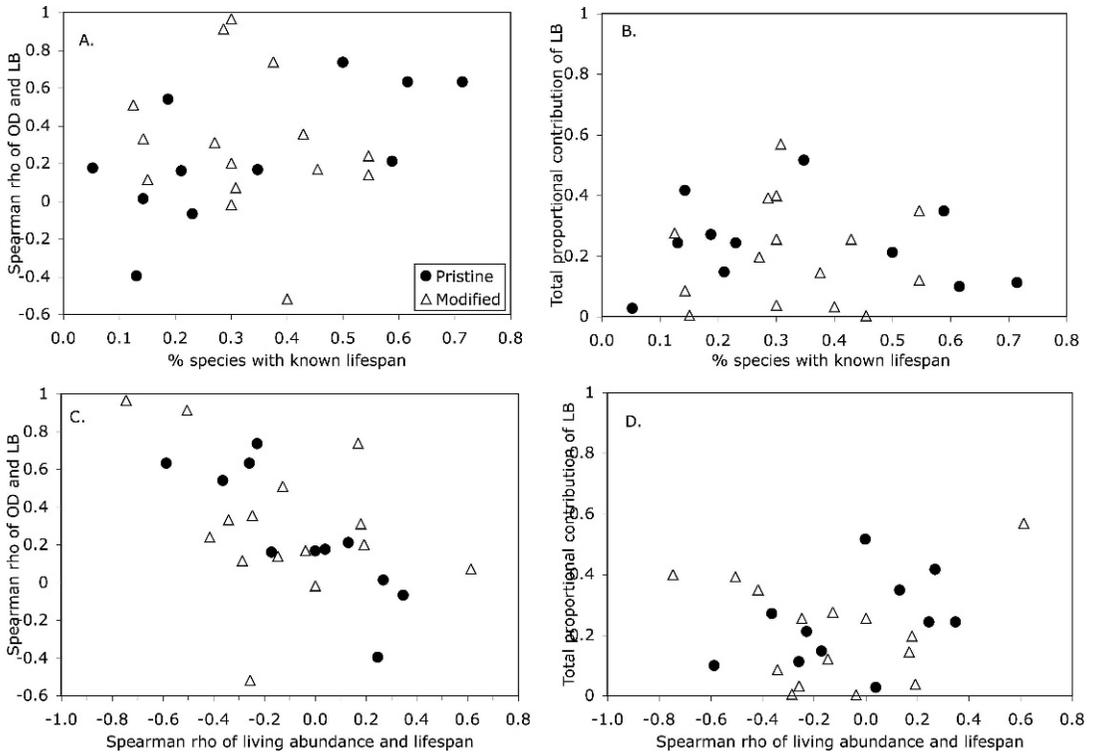


FIGURE 6. Sensitivity of model performance, as measured by the Spearman correlation coefficient of LB and OD in a data set, using the 26 large data sets in Table 2. A, Performance tends to improve with increased knowledge of life spans (measured here as the proportion of species in a data set whose maximum life span is known rather than estimated from other species or genera) but is only significant among data sets from pristine areas (Spearman rho = 0.72, $p < 0.05$). B, Even in data sets where life span is well known, LB consistently underestimates the total OD in the data set. Improving life span knowledge thus only increases the ability of the model to predict the small effect of life span bias on live-dead differences in species proportional abundances: improved knowledge does not reveal a large and otherwise hidden effect. C, Performance is significantly higher among data sets having the strongest negative rank correlations between living abundance and life span (rank-correlation coefficient = -0.55 among all 26 data sets and -0.80 among pristine data sets, both $p < 0.01$). D, However, even in data sets where living abundance and life span are negatively correlated, LB accounts for only a portion of OD.

Effects from Covariation in Preservation Rate.—Behrensmeier et al. (1979) found that, contrary to the prediction of bias from mortality rates, long-lived mammals were more abundant rather than less abundant in DAs, probably because mammal body size increases with life span, conveying higher rates of bone preservation and discovery to long-lived species. Rephrased in our terms, they found that OD was *negatively* correlated with LB, indicating that preservation rate was more important than mortality rate in driving postmortem changes in species proportional abundances.

Body size tends to increase with life span among bivalves and thus also might convey a higher preservational rate to longer-lived

species (Suppl. Fig. 6A). However, we find no evidence linking preservational bias to life span. For example, OD is not correlated significantly with body size among the 228 species occurrences where body size is currently available (Suppl. Fig. 6B). Partial Spearman correlations of those data also show no effect from body size when life span is controlled and only a slight increase in the power of life span when body size is controlled (from $r^2 = 0.18$, $p = 0.007$ to $r^2 = 0.20$, $p = 0.003$).

The impact of body size on the preservation of proportional abundances is thus apparently at the least nonlinear or perhaps is on a per capita basis (i.e., depends on the sizes of individuals in the assemblage, not the maxi-

imum size that adults of the species can attain). This result among modern death assemblages is consistent with the lack of effect of bivalve body size on presence-absence occurrences in fossil assemblages at a Phanerozoic scale (Behrensmeier et al. 2005). We previously postulated that molluscan DAs capture a relatively good picture of the *rank*-abundance of species in standing communities because the higher mortality rates of shorter-lived species might be largely counteracted by higher rates of postmortem loss (Kidwell 2002, using some of the same live-dead data sets as here, plus others). The analysis here finds that the effect of mortality rate on proportional (and thus rank) abundances in the expected DA is mostly quite small, which lessens the magnitude of counteracting effect needed from variation in intrinsic postmortem durability.

Assumption That Living Proportional Abundances Are Stable.—This assumption is likely violated to some degree by all of our data sets given well-documented random, seasonal, and interannual variability in macrobenthic systems worldwide (e.g., Gray and Elliott 2009) and the potential for natural and human-mediated shifts in environmental state over decadal to centennial time-scales, which are within the total frame of time-averaging. On the other hand, findings elsewhere that most individuals in molluscan death assemblages tend to be drawn from the most recent few centuries of skeletal production, and from the most recent few decades in estuaries and lagoons that are natural sinks for sediment, should moderate the impact of our limited knowledge of temporal variability in LAs (e.g., Flessa et al. 1993; Meldahl et al. 1997; Olszewski 1999; Kidwell et al. 2005; Kosnik et al. 2007, 2009; Krause et al. 2009). Most of our data sets are drawn from analogous coastal embayments. Variability over short terms will also tend to be less than over long terms (e.g., Lawton 1988). The temporal variability of LAs in our data sets cannot be quantified because original authors sampled LAs only once, with few exceptions (LAs in five habitats were sampled repeatedly for up to two years, allowing analytical time-

averaging of living abundances, but model performance is not improved).

Several lines of evidence indicate that the low explanatory power of our LB model arises at least in part from temporal variability in the living proportional abundances of species over the course of time-averaging.

First, LB is more effective in explaining the ODs of longer-lived species than it is at explaining the ODs of shorter-lived species (Table 1), which can be attributed to differences in the average temporal stability of populations. Once settled, a cohort of a long-lived species is by definition more persistent and thus LBs calculated on the basis of a single sampling of the LA are more likely to be correct. In addition, short-lived species as a category include species that are prone to strong local fluctuations in population size that would alter their *proportional* abundance in the LA. For example, fast-maturing iteroparous opportunists such as *Mulinia lateralis* undergo boom-and-bust changes in absolute population size (e.g., Levinton 1970) and other relatively short lived bivalves are known for dense patchy settlement of single cohorts. This temporal and spatial patchiness of living populations should yield a wide range of positive LB values for these species depending on the timing of sampling. The shortest-lived species in our data sets do exhibit greater variability in living proportional abundances *among* data sets than do any longer-lived species, a spatial analog of their suspected temporal variability. For example, *Mulinia lateralis* (three years maximum life span, occurs in 14 data sets) ranges from 0.3% to 94% in local LAs, *Hormomya exustus* (three years, 10 data sets) ranges from 0.5% to 60%, *Abra aequalis* (three years, 6 data sets) ranges from 0.3% to 95%, and *Nutricola tantilla* (one year, 3 data sets) ranges from 2 to 46%. These highly variable species yield many of the poorest matches of OD and LB in Figures 3 and 5.

The more stable population sizes of longer-lived species do not mean that their *proportional* abundances are perfectly stable of course, because these are tied to the population sizes of all co-occurring species in the LA,

nor do stable populations ensure that OD will match LB given the array of other taphonomic and sampling factors that may be acting on the DA. Even among long-lived species the model predicts the sign of OD in only 67% of cases and explains on average only 0.33 of the magnitude of OD. However, the significantly higher success of the LB model among longer-lived species is consistent with biologically reasonable differences in the volatility of absolute population sizes along a spectrum of maximum life spans—among all aspects of a species' life history, the interaction of life span with OD is probably only indirect. The effect of fluctuating population sizes among the shortest-lived species upon the proportional abundances of stable species will be moderated if the shortest-lived species switch among themselves in dominance such that their *combined* proportional abundance in the LA is stable. Such switching is likely under an array of metacommunity models (e.g., Tomášovych and Kidwell 2009, and see qualitative treatment by Fürsich and Aberhan 1990). Temporal variability could thus account in part for the poorer than random model success for our shorter-lived species (some are sampled at moments of low population size, others at moments of high population size) and better than random success for our longer-lived species (absolute abundances are inherently more steady and proportional abundances are insulated by the switching in dominance among short-lived species).

Second, model success varies with the magnitude of human impacts on the study area but not significantly (Table 1). We suspected that the model would not perform as well in human-modified settings because those time-averaged DAs would encompass histories of stronger changes in LA composition than would comparably time-averaged DAs in pristine settings, violating a key model assumption. The persistence in the DA of shells from species that were formerly much more abundant (taphonomic inertia; Fig. 4) might create strong live-dead discordances in species proportional abundances, especially among the longer-lived species whose populations should be slowest to respond to changing environmental condi-

tions. However, model success ranged about as widely among species occurrences and data sets from pristine settings as it did among those from modified settings (Table 1, Fig. 3C,D). One inference from the scatter in Figure 3D is that, in human-modified settings, the shortest-lived species maintain relatively high population sizes (or reach high local standing abundances relatively frequently) compared to pristine settings, conveying an element of stability to the LA that compensates somewhat for the greater number of ecological relicts in the DA. Rephrased, temporal variability is perhaps higher in pristine settings, undermining the ability of the model to predict proportional abundances in DAs almost as much as the environmental condensation of secular shifts undermines model performance in human-modified settings.

Thus overall we suspect that much of the model error reflects inadequate data on the living abundances of species and particularly inadequate data on the shortest-lived species, which will tend to be most volatile and difficult to characterize via a single sampling.

Implicit Assumption That Living Abundance Varies with Life Span.—All else being equal, species with short life spans are expected to be overrepresented in time-averaged DAs relative to their standing crop in the LA, and species with long life spans should be underrepresented. In reality, however, “all else” is never equal because, at the very least, species differ in their living abundance (the hypothetical perfectly even LA of Fig. 1A is never seen). Life span bias is a product of both living abundance and mortality rate, and thus for life span to bias abundance data or abundance structure in the DA, living abundance must vary significantly with life span.

Contrary to patterns among terrestrial endotherms (Van Valen 1964; Behrensmeier et al. 1979; Blackburn et al. 1996), we find that local living abundance shows no correlation with maximum life span among marine bivalves in our aggregate abundance database (Fig. 7; $n = 413$ species occurrences, Spearman $\rho = -0.027$, $p = 0.587$; also true if one considers only the 131 occurrences where life span is known for that species). The entire

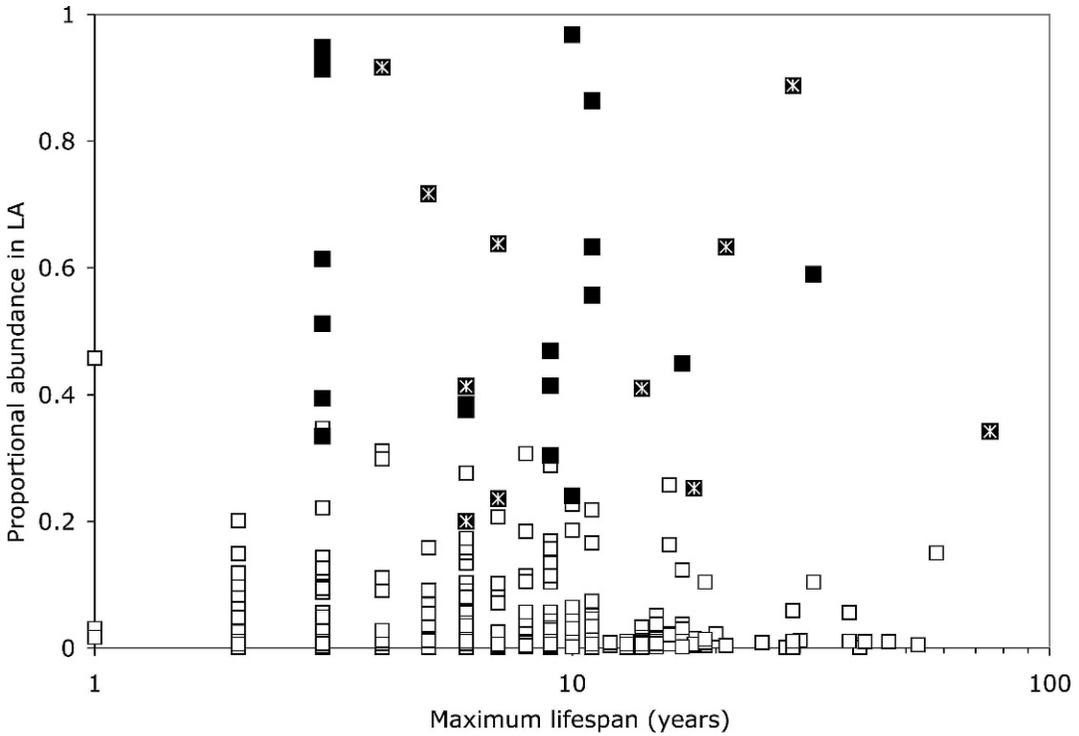


FIGURE 7. In local living assemblages, the (global maximum) life span of the most abundant species ranges widely from 3 to 75 years (black squares denote the life span and proportional abundance of the top-ranked species from each of the 30 data sets; black squares with superposed white asterisk are data sets from pristine settings; for identities of species, see Table 3). There is no tendency for living assemblages to be dominated by species having especially short maximum life spans, nor for living abundance to covary with life span among all species occurrences.

state-space is densely occupied: species of any life span can be rare and in a given LA the single most abundant species (black icons in Fig. 7) might have any life span, although no life span is less than three years (for log-log plot, see Supplemental Fig. 7). The 22 top-ranked species are in 15 families and six orders, an unexpected phylogenetic breadth (Suppl. Table 1).

Among data sets, the rank-correlation of living abundance and life span is random in sign and significant in only three (two correlations are negative, one is positive; Table 2). Thus the stereotype that short-lived species dominate LAs is untrue. Negative correlations (shorter-lived species are more abundant) are more common among LAs (and DAs) in modified settings, but even there LAs can be dominated by species of any life span (Table 3, x-axis in Fig. 6C,D, Fig. 7). Model performance (correlation of OD and LB) does increase significantly with the negative correlation of living abundance and

life span (Fig. 6C) but LB underestimates OD even in these data sets where a strong biological relationship between abundance and life span exists (Fig. 6D; LB explains ≤ 0.40 of OD and on average only about 0.2, Table 2).

Even focusing only on the top-ranked species in each data set, the model predicts only four of the 11 cases where the species that dominates the DA is shorter-lived than the dominant species in the LA, and 12 other data sets show no postmortem change in the identity of the top-ranked species (and the model predicts no changes; Table 3). Our model of postmortem bias based entirely on variation in mortality rate thus underestimates the postmortem dominance of short-lived species that does exist, consistent with our inference that fluctuations in living abundances (true past peaks in abundance) are a more likely explanation of high rank in a DA than mortality rate is. In the data sets showing no change, either the biological

relationship between life span and living abundance is too weak to shift a shorter-lived species into the top rank of the DA or the top-ranked species in the LA is so abundant that its top ranking in the DA is assured without the amplifying effect of high mortality (analogous to Fig. 1D). Both the postmortem persistence of species in the top ranking (about one-half of all data sets) and the postmortem shifting of short-lived species up into the top rank (the other half of all data sets) indicate the absence of any strong preservational bias against short-lived species.

The surprisingly weak links encountered here between the macroecological factors of life span, body size, and relative abundance in marine bivalves deserve further investigation in their own right, because in terrestrial groups longer-lived species do tend to be both larger-bodied and rarer, although the relationship becomes weaker as the study area becomes more localized (for a recent review, see White et al. 2007). Assumptions that LAs are dominated numerically by the shortest-lived species probably also reflect the disproportionate influence of studies from human-modified settings, where chronic environmental stress and exploitation favor populations of relatively short lived species. All of the data sets here that are dominated by species with life spans of less than three years are from modified settings.

Conclusions

The results of this analysis contrast with the long-held expectation that differential rates of population turnover among species are a major source of taphonomic bias in time-averaged death assemblages. Statistically, shorter-lived species do tend to be overrepresented in time-averaged death assemblages compared to their proportional abundance in the living assemblage, but the aggregate effect is small—just a few percent on average per species—and noisy. Some death assemblages are dominated by relatively long lived species (as are their living assemblages), some are dominated by opportunistic or other short-lived species (as are their living assemblages), and some are disproportionately dominated by shorter-lived species (but usually not by

the shortest-lived species in the living assemblage). Our model, which predicts changes in proportional abundance from mortality rate alone, generally underestimates the magnitude of live-dead discordance in all data sets, including ones where shorter-lived species are disproportionately abundant, indicating that factors other than or in addition to mortality rate are at work. We can find no evidence of preservational bias that is linked to life span, for example through body size. Moreover, contrary to terrestrial animals, we find no biological correlation between bivalve living abundance and life span at the habitat scale that would support a consistent bias of abundance information by mortality rate. Ecological factors and taphonomic factors other than mortality rate thus become the most important issues in the preservation of proportional abundance information.

This conclusion does *not* indicate that proportional abundance data are entirely robust to postmortem bias—quite the contrary, we have only rejected mortality rate and life span-linked preservation as important or pervasive factors in observed discordances, and only among bivalves. We have also only considered the effects of processes operating in the uppermost mixed layer of the seafloor, where death assemblages are vulnerable to modification by many forces but are open to continued input from living assemblages and are not yet subject to diagenesis associated with burial. Eliminating life span as a factor nonetheless reduces the dimensionality of the taphonomic problem in this key system, and points toward a simpler model where time-averaging of variable population sizes will necessarily be more important. The implication is that, in general, dominance of a time-averaged death assemblage probably owes largely to undersampled past large populations of species rather than to bias(es) associated with life span. Our findings do support the robustness of (paleo)ecological analysis of death assemblages using *rank* abundance, which is more forgiving of changes in proportional abundances among the few most abundant species in an assemblage, such as might be expected from

realistic fluctuations in living abundances and modest life span bias.

Finally, the range of life spans observed within local bivalve assemblages—approximately 10-fold on average and up to 40-fold, representing 3.5- to 10-fold differences in mortality rate among species within an assemblage—probably encompasses that of many other non-colonial marine groups. The small magnitude of life span bias found here should thus be broadly relevant, although it would be useful to determine whether other groups show a similarly weak relationship between living abundance and life span. Our analysis reveals contrasts in macroecological relationships between marine benthos and the terrestrial paradigm that are interesting in their own right and a basis of elucidating taphonomic differences between marine and nonmarine systems.

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