

EVALUATING HUMAN MODIFICATION OF SHALLOW MARINE ECOSYSTEMS: MISMATCH IN COMPOSITION OF MOLLUSCAN LIVING AND TIME-AVERAGED DEATH ASSEMBLAGES

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ABSTRACT.—Time-averaged death assemblages of molluscan shells sieved from seafloors during conventional biological surveys represent an important under-exploited resource for retrospective evaluation of the magnitude and nature of recent community change. Benthic biologists usually discard these death assemblages (DAs) because of concerns for postmortem bias and time averaging of multiple generations. However, quantitative synthesis of ~100 “live-dead” comparisons establish that the time-averaged nature of DAs can be used to advantage in conservation biology. The strongest correlate of poor live-dead (LD) agreement is the magnitude of anthropogenic eutrophication of the water body (AE), because the DA retains a memory of the former abundance of species that are now rare or absent in the living assemblage. In areas with a known history of AE, seagrass-dwelling species tend to be significantly more abundant dead than alive, and species that prefer organic-rich sediments or tolerate low-oxygen episodes tend to be more abundant alive than dead. Bottom-trawling (BT) of seafloors for fin- and shell-fish is also associated with LD mismatch but only in gravelly habitats where species are generally not naturally adapted to frequent physical disturbance. The overall degree of LD mismatch and the identities of the species most responsible for that mismatch can thus be used to recognize AE and BT in areas where human activities are unknown or unregulated. Further, LD agreement is remarkably high in areas unaffected by human activities, so LD analysis can also be used to identify regions that can serve as restoration baselines. The high LD agreement found in pristine settings is also the current best estimate of how confidently we can reconstruct, in presented degraded areas, what the local living community was originally like, using DAs extracted from historic layers of sediment cores. LD comparison fails to detect ecological change in almost half of all habitats where human stresses definitely exist, and thus this is a conservative tool that will tend to under-estimate human impacts. However, given the scarcity of information on present-day communities and especially on their recent past, historical ecological information is at a premium and LD comparisons will be valuable.

INTRODUCTION

ECOLOGICAL ASSESSMENT and restoration at the habitat to regional scales where conservation efforts are focused face many basic scientific challenges. These include such rudimentary questions as:

1. *What is it like now?* Unfortunately, both on land and under the sea, even “today” is usually under-sampled, with knowledge rarely reflecting more than a single season of collection and taking the form of a regional checklist.

2. *Is it stable?* Past trajectories that have brought the local system up to today and thus might carry it into the future are usually unknown.

3. *What was natural?* The composition and structure of unaltered systems—both those still existing and those past—are usually unknown. Ideally, baselines for restoration efforts should be based on genuinely

natural conditions and not simply the state of the system at the time it was first surveyed, which in most settings is well after the onset of human modification.

An historical perspective on the system is important for answering all three questions. How long (deep) that that time perspective needs to be depends upon the system and the question at hand. The more inherently variable the environment, the deeper the suspected roots of human impact(s), and/or the longer lived the individuals of species, then the longer the window of observation needed to evaluate the status of the biota for questions 2 and 3 (Fig. 1). Because some species are short-lived or seasonal in occurrence, even a picture of “now” (question 1) should be based on more than a single season of sampling and arguably on return visits over several years given inter-annual variability in seasons. Many regions including tropical ones also undergo decadal scale variability in response to natural

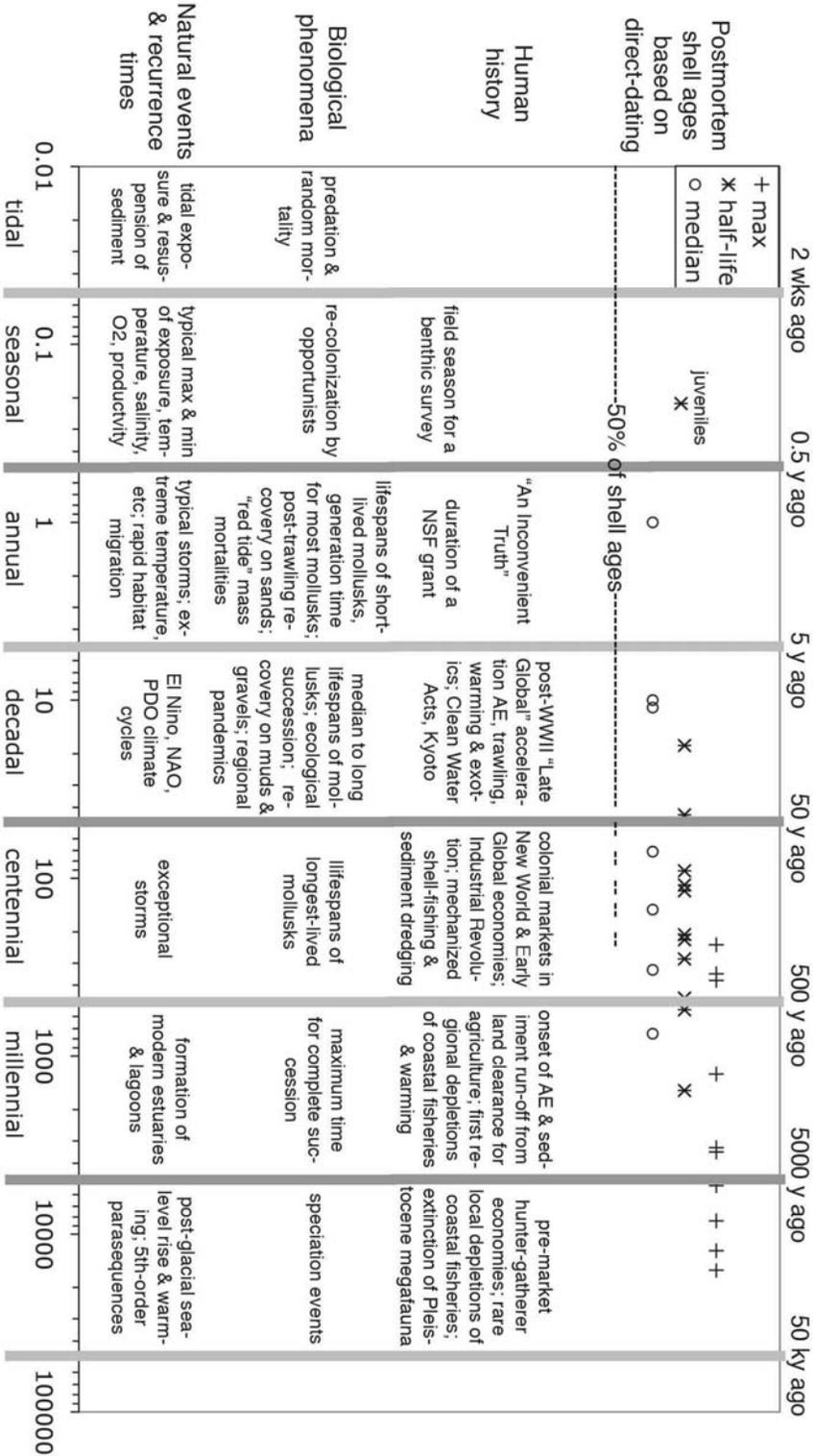


FIGURE 1.—Time frames of time-averaging, biological and other natural phenomena and chronology of human history relevant to shallow marine systems. Following a convention of sequence stratigraphy, time frames on a log scale (bottom) are *characterized* by their integer order of magnitude (e.g., decadal = 10¹ years) but are operationally *defined* (bounded) by mid-point values (e.g., 10^{0.5} and 10^{1.5} years). Chronology (top scale) is pinned at today or, for direct-dated shells, the date of publication. Economic phases of Lötze et al. (2006); Lifespans from compilation of Kidwell and Rothfus (in prep.); recovery times from bottom-trawling are generally 1-5x the generation time of the species in the community (e.g., Collie et al., 2000; NRC, 2002); maximum, half-life and median shell ages compiled from Meldahl et al., 1997; Kowalewski et al., 1998; Kidwell et al., 2005; Kosnik et al., 2007; Kidwell, 2005; Kowalewski, 2009; Kosnik et al., in press; Krause et al., in press; juvenile half-lives from Cummins et al., 1986b.

TABLE 1.— Abbreviations and measures of LD agreement.

Abbreviations
AE = Anthropogenic eutrophication
BT = Bottom trawling
DA = Death assemblage (mollusks collected as empty shells)
LA = Living assemblage (mollusks collected alive)
LD = Live-dead
Measures of LD agreement
JC = Jaccard-Chao index of taxonomic similarity
Rho = Correlation coefficient of a Spearman rank-order test
Delta-richness = Ratio of the DA richness to LA richness, after sample-size standardization
PIE = Hurlbert's evenness metric, Probability of Interspecies Encounter
Delta-PIE = Difference between DA PIE and LA PIE

climate cycles such as El Niño/La Niña and the NAO (North Atlantic Oscillation). Habitats where few species are sampled alive at any given instant in time (i.e., have few abundant year-round occupants) may thus constitute genuine diversity hotspots when species occupation over time is considered (e.g., White et al., 2006).

Information on the composition and structure of a target community should thus minimally reflect knowledge of the system on a decadal scale even in fully natural systems, and preferably on a centennial to millennial scale given the early onset of human pressures on ecosystems and their intensification over time. For example, even in the marine realm, humans have been capable of depleting targeted food species locally for more than 5000 years based on archeological evidence and depletions of favored food and luxury species became regional in scope well before the mid-19th century Industrial Revolution (e.g., Jackson et al., 2001; Lötze et al., 2006; Rick and Erlandson, 2009; Fig. 1). Marine environmental deterioration—from excess nutrients, solid sediment runoff, and habitat destruction—as well as species depletions, pandemics, and introductions of alien species have all intensified significantly and become truly global in the last ~50 years, leaving no oceans untouched (Halpern et al., 2008; Baum and Worm, 2009).

The rhythms of biological phenomena such as in-

dividual lifespans and recolonization rates need to be compared to natural environmental rhythms and the monotonic increase in pressure on exploited species and habitats (Fig. 1). The recovery time of a community to physical disturbance, for example, is typically 1 to 5x the generation time of constituent species (e.g., Collie et al., 2000; NRC, 2002). Populations of species that grow rapidly and reproduce early will thus recover within a few months or years after a disturbance (e.g., wipe-out by an exceptional hurricane, bottom-dredging, or dynamiting). On the other hand, a minimum of years to decades are required for the community to reacquire fully functioning populations of species that do not reproduce until individuals are several years old (e.g., most mollusks, with a median lifespan of ~8 years) or that will not recolonize an area until the seafloor has reached some condition that depends on elapsed time (e.g., degree of sediment shelliness, firmness, or oxygenation; presence of grassbeds or other bio-constructed habitat). Coral reefs, which are the stereotypic image of a seafloor community, entail centuries to millennia to construct *de novo* and require at minimum decades or centuries to recover fully, assuming no further abuse.

Unfortunately, few areas have a history of scientific surveys much less the high-frequency biomonitoring that is needed to characterize natural temporal variability within systems and, with the exception of

some targeted food species, quantitative data rarely extend back more than a few decades even in the most intensely studied areas. Alternative sources of quantitative historical information are thus needed to acquire basic information on the status of present-day systems, on their genuinely natural baselines, and on the biological consequences of human pressures on wild populations (NRC, 2005).

Naturally occurring death assemblages (DAs) of skeleton-bearing animals—the shells of dead invertebrates and the bones and teeth of vertebrates present in the uppermost part of the sedimentary record of a modern-day habitat—are a promising “subfossil” source of such historic information (Table 1). For example, on average, a ~10-liter sample of seafloor mud or sand will contain ~ten-times more dead molluscan individuals than living molluscan individuals (Fig. 2), representing a tantalizingly large sample size of the local fauna. The shells in molluscan DAs are clearly time-averaged over multiple generations, in contrast to the temporally acute “snapshot” of standing populations provided by a conventional biological survey. Dead individuals outnumber living individuals even on seafloors where the introduction of shells by post-mortem transportation from other habitats is extremely unlikely, range in physical condition from excellent to poor suggesting a spectrum of postmortem ages, and can include species that are almost certainly relicts from past decades when different environmental conditions existed (e.g., see early “live-dead” studies such as Johnson, 1965, early quantitative assessments of benthic stocks such as Davis, 1923, and early actualistic biofacies studies such as Ladd et al., 1957).

Radiocarbon and amino-acid racemization dating of DAs sampled from the surface of modern seafloors indicate that mollusk shells can range in age up to 10–20 ky old on open continental shelves that have experienced slow net rates of sedimentation during Holocene sealevel rise (e.g., Fischer, 1961; Flessa and Kowalewski, 1994; Flessa, 1998) and can range up to several thousand years even in estuaries and lagoons that are natural sinks of sediment accumulation and have only existed for a few thousand years (see sources for Fig. 1, and see Kowalewski, 2009; Kosnik et al., in press; Krause et al., in press). Notwithstanding these maximum shell ages, surface-sampled DAs in subtidal settings tend to be *dominated* by shells from the youngest part of the age-spectrum and typically come from the

most recent decades to centuries (see median ages and half-lives in Fig. 1). Although such temporal resolution seems coarse at first glance, centennial and particularly decadal resolution of community composition would provide insight into a wide range of issues important to conservation (Fig. 1). Moreover, in the absence of other historical data, even a blurry view of the past is valuable.

Here, I summarize some key findings on using molluscan death assemblages—and particularly mismatches in the species compositions of death and living assemblages—as a source of otherwise unattainable historical information on modern benthic communities. The analytic results reflect a global meta-analysis (quantitative synthesis) of the raw data from ~100 habitat-level “live-dead” studies (summarized from Kidwell, 2001, 2002a, 2002b, 2007, 2008, plus new work first reported here; Olszewski and Kidwell, 2007; see Kidwell, 2007, for complete list of raw data sources). The focus is on soft-sedimentary seafloors—various admixtures of mud, sand, and gravel, with and without seagrass—that constitute the majority of shallow marine and estuarine seafloors. The surface and upper few cm to tens of cm (exceptionally the upper meter or so) of these substrata are occupied by diverse and abundant macroscopic bottom-dwelling invertebrate life (“macrobenthos” >1 mm; Fig. 3). Polychaetes almost always constitute the majority of live-collected individuals and species in quantitative bottom samples, with mollusks ranking second or third (after arthropods). However, mollusks typically constitute the majority of living macrobenthic *biomass* owing to their relatively large body size (e.g., see summary info in Gray and Elliott, 2009) and constitute the majority of species if the DA is included (regional checklists of species almost always include species known only from empty shells).

Mollusks also play many ecological roles both during life (e.g., as suspension feeders, deposit feeders, predators, grazers, reef-builders, bioturbators, bioeroders, and prey items) and after death (e.g., dead shells as islands of hard substrata and as creators of coarser and physically more complex habitat; Kidwell and Jablonski, 1983; Palacios et al., 2000; Hewitt et al., 2005). Being able to reconstruct historical changes in the composition and structure of molluscan communities would thus give insights into a major component of shallow marine ecosystems, as well as a possible surrogate for the entire system.

WHAT IS A DEATH ASSEMBLAGE?

Death assemblages (DAs) constitute the whole and broken invertebrate shells and other organic debris (e.g., seagrass fragments, worm casings, fish otoliths) that exist in the uppermost few cm of seafloor that are sampled for living benthos. The *molluscan* death assemblage is the portion of this “grunge” or “sieve residue” that is molluscan in origin and identifiable to the species level. Benthic biologists regularly handle—and dispose of—this material when picking samples for living specimens. Dead molluscan individuals are operationally defined as whole shells or large fragments that signify a unique individual (e.g., fragments that include >50% of the bivalve hingeline, or that include the apex of a gastropod shell). Individual dead specimens can range in physical condition within a single DA from “like new” (the shell interior lacks flesh but retains its original luster) to slightly modified (dull surface, loss or flaking of periostracum, discoloration) or strongly modified (notable postmortem polishing, bioerosion, corrosion, bioencrustation). Empty shells that retain some adhering flesh are usually categorized as living individuals, both by biologists and taphonomists.

Because benthic sediment samples contain on average ~10x more dead mollusk individuals than living individuals (Fig. 2.1), molluscan DAs typically contain more species than the associated living assemblage (LA)—on average, about 3x more species (Fig. 2.2; raw values in Table 3). However, this “surplus richness” of DAs does not owe entirely to their greater sample size. When a DA is subsampled down to match the number of individuals that are present in the LA, the DA usually still contains a larger number of species (sample-size standardized values in Table 3). On average, DAs are ~1.2x richer if resampled with replacement (binomial distribution, Kidwell 2002a) and ~1.5x richer if resampled without replacement (hypergeometric distribution, Olszewski and Kidwell, 2007; Tomasovych and Kidwell, in prep.). DAs are thus clearly not simply one-to-one substitutes for conventional biological surveys of living molluscan communities.

Death assemblages sampled from the uppermost mixed layer of the sedimentary record—the 5 to 20 cm-deep “bite” of a Van Veen grab, small box-core, naturalist’s dredge, or hand or air-suction excavation (Fig. 3)—are subject to a wide array of postmortem processes that are fundamentally destructive. These include

physical and biological reworking (vertical advection that mixes generations and promotes disarticulation, fragmentation, and lateral transportation of shells), *bioerosion and bioencrustation* (especially during intervals when shells are exposed at the sediment-water interface, promoting obliteration of morphology critical to species-level identification), *microbial maceration* of microstructure (promoting shell disintegration, even when buried), and *modification by overlying and pore waters*, which may be under-saturated with respect to carbonate minerals (promoting shell dissolution) or oversaturated (promoting precipitation of minerals that tend to preserve morphology). These processes vary in strength among environments (“taphofacies”) and species differ in their inherent susceptibility to these processes (variation in “intrinsic durability”; the majority of the taphonomic literature concerns these issues, see Behrensmeyer et al., 2000, for a general review). This large number of factors makes it difficult to predict, *a priori*, the degree to which a given DA might differ in composition from the local LA.

On the positive side, DAs within this uppermost mixed layer of the sedimentary record are still receiving new, freshly dead individuals from the local LA, which should continuously refresh the composition of the DA to make it to more closely match that of the local LA (Fig. 3). Infaunal (burrowing) mollusks live within this same uppermost increment of the substrata and epifaunal mollusks such as scallops, oysters, and grazing snails live on the sediment-water interface itself. The steady input of newly dead shells from the living community should promote agreement between DAs and co-sampled LAs, counteracting the biasing effects of destructive postmortem processes.

With progressive burial below the sediment-water interface, the DA encounters new pore water regimes that may be more or less favorable to shell preservation than the regime(s) within the uppermost mixed layer, but the intensity of all other postmortem processes decreases. DAs become progressively less subject to vertical mixing, and thus rates of shell loss should decrease along with rates of new-shell supply (for a probabilistic treatment, see Sadler, 1993; Fig. 3).

WHAT IS A “LIVE-DEAD” STUDY?

Live-dead (LD) studies compare the numbers of individuals occurring alive and dead for species in

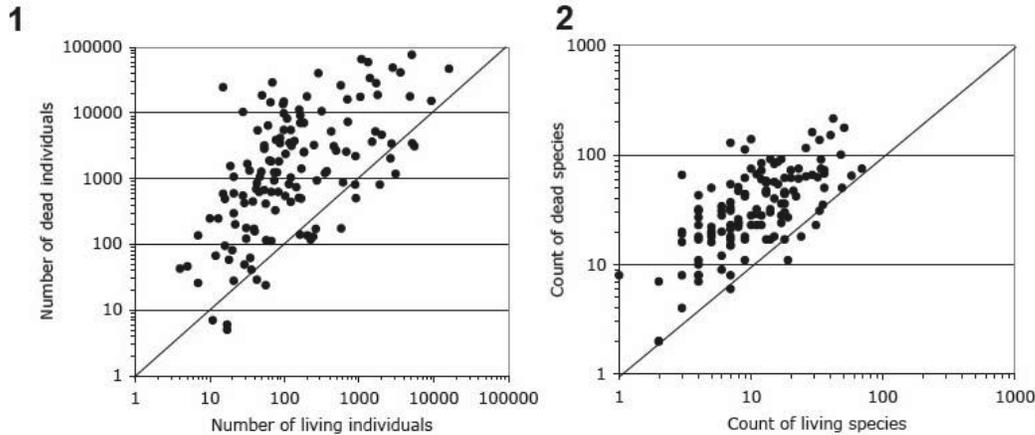


FIGURE 2.—1, Numbers of living and dead individuals and 2, counts of species occurring alive and dead in subtidal soft-sedimentary seafloors, based on 115 molluscan “live-dead” datasets compiled from the global literature. Each point indicates the raw results for living and dead mollusks from the uppermost part of the seafloor, based on pooling specimens from samples at two or more stations within a single habitat. Dead individuals are on average $\sim 10\times$ more abundant than living individuals and represent on average $\sim 3\times$ more species than are sampled alive in the same sedimentary volume. Although abundant and rich, dead skeletal remains are usually ignored—in fact, discarded—in whole-fauna benthic surveys and in biomonitoring efforts. If we can be confident of their fidelity to the living assemblage, then we gain a large increase in sample size and temporal perspective on the molluscan community. Analyses here focus on the 109 datasets having >20 living and >20 dead individuals.

modern environments and are the most common means of evaluating the ability of time-averaged death assemblages (DAs) to capture the composition and structure of local living assemblages (LAs; see Kidwell and Flessa, 1995, for review). Molluscan LD datasets are generated in soft-bottoms settings by taking sediment samples of standardized volume, sieving them to remove sediment (volume and mesh size varies among studies), picking living and dead specimens from the sieve residue, and generating a list of all species encountered and the numbers of living and dead individuals for each species.

Using these raw data, LD agreement can be assessed for any number of ecological attributes. Virtually any metric developed to describe a living community can be applied to a death assemblage, and thus that attribute of the DA can be compared to that attribute of the co-sampled LA. Examples covered here include LD agreement in *species richness* (is the count of species occurring dead the same as, greater than, or less than the count of species occurring alive?), *taxonomic similarity* (do the living and dead species lists share many or few species in common?), and *species relative abundance* (e.g., in a rank-order test, are the spe-

cies that are most abundant in the LA also numerically dominant in the DA, or are they instead randomly distributed through an abundance-ranked list or perhaps exclusively rare?). We can also assess LD agreement in how species composition varies along an environmental gradient, LD agreement in the magnitudes of alpha versus beta diversity, and the comparability of spatial or temporal variability (dispersion) among replicate samples of the LA or DA (e.g., Tomasovych and Kidwell, 2009a, b, c, in prep.). LD agreement can also be assessed for single species, for example the degree of similarity in the size- or age-frequency distributions of a particular species in the DA and that in the LA (e.g., Hallam, 1967; Cummins et al., 1986a; Tomasovych, 2004).

Finally, LD agreement can be assessed at any spatial scale (spatial resolution). For example, what is LD agreement within a *single sample* (e.g., Staff et al., 1986), within a single *habitat* (living and dead individuals are tallied after multiple samples from a single seafloor type in a region have been pooled; e.g., Peterson, 1976; meta-analytic focus here and in my earlier papers), and within a *multi-habitat region* (similarity of all pooled DA samples to all pooled LA samples,

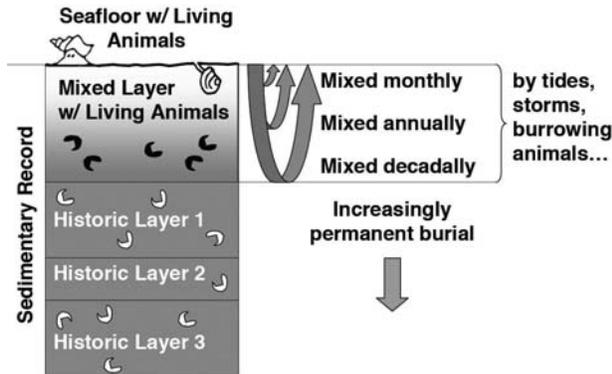


FIGURE 3.—Schematic cross-section of a seafloor. The surface and upper few cm to tens of cm (exceptionally the upper meter or so) of soft-sedimentary seafloors are occupied by diverse and abundant macroscopic bottom-dwelling invertebrate life (“macrobenthos” >1 mm), whose skeletal remains constitute the local macrobenthic death assemblage. The uppermost part of the sedimentary column is mixed with highest frequency because so many kinds of animals and physical processes intersect with it, and the deepest parts of the column are mixed least frequently (e.g., only by the burrows of deeply-penetrating infauna, during once-a-century storms, or during sealevel lowstands). Conventional biological surveys sample the upper 5 to 10 cm of the seafloor, which is generally well within the mixed layer.

e.g., Johnson, 1965; Bouchet et al., 2002, or similarity of a single DA sample to the known regional species pool, e.g., Warwick and Light, 2002; Smith, 2008)? A large number of molluscan LD studies including such classics as Warne (1971), Ekdale (1977), and Miller (1988) test the ability of DAs to reflect a facies mosaic or gradient evident in LAs within a small region (resolution of *spatial grain*).

Conservation and restoration efforts focus almost exclusively at the scale of habitats and small multi-habitat regions, and thus the ability of death assemblages to capture biological information at these scales will be stressed here.

The findings summarized here reflect analysis of the raw data from 109 habitat-level LD datasets generated by diverse authors from subtidal seafloors in ~50 different regions globally (for a complete list of sources and description of areas, see Kidwell, 2007). Each dataset reflects pooling of at least two samples of the given habitat, with a total of at least 21 living and 21 dead molluscan individuals. Habitats are defined as areas that are relatively homogeneous in sediment grain size, subaquatic vegetation, and water depth—for example,

clean sand from the margin of a bay versus broad areas (“facies”) of muddy sand, sandy mud, or mud from the same bay. A single study area—e.g., Tomales Bay—thus typically yields several habitat-level datasets and one regional-level dataset. Most datasets come from siliciclastic settings. Datasets are otherwise diverse: mesh sizes used to collect living and dead individuals range from 0.3 to 5 mm, seafloors range from pure muds to gravels and grassbeds, and study areas range in latitude from 2° to 55°, i.e., from tropical to cold temperate conditions.

CONCEPT OF LIVE-DEAD MISMATCH AS A SIGNAL OF RECENT ECOLOGICAL CHANGE

Mismatch (disagreement, discordance) between the richness or species composition of a DA and the local LA is typically attributed to natural post-mortem processes and particularly to preservational bias. However, biologists and actualists alike have long been tantalized by the evidence that death assemblages with unexpected compositions might provide about recent changes in population sizes (e.g., Davis, 1923) and environmental conditions (e.g., Ladd et al., 1957), including changes wrought by human activities. For example, Bourcier (1980) noted the abundance of exclusively dead specimens of grass-dwelling mollusks in Mediterranean bays and argued that these probably signified recent and otherwise unappreciated environmental deterioration from untreated wastewater and a weakening of winter storms that might have cleansed the system. Several taphonomists have also suggested that LD mismatch within their study area indicated a recent shift in community composition driven by human activities—for example, the possible impact of shrimp-trawling on Texas shelf faunas (Staff and Powell, 1999), of point-source nutrients on Florida Bay mollusks (Ferguson, 2008), and of unknown pressures on Caribbean coral reefs (Greenstein et al., 1998).

As a tool for conservation biology, LD mismatch would take advantage of the intrinsic durability of molluscan shells, and thus the potential for the composition of a time-averaged death assemblage to lag behind any strong directional change in the composition of the living assemblage. The stronger the shift in LA composition, the lower the rate of production of dead shells from the new LA relative to the original LA, the greater

the relative durability of dead shells from the original LA, or the slower the rate of permanent burial that moves the DA beyond the influence of the LA (with the last two factors determining the window for time-averaging), then the more likely that the composition of the DA will lag behind a compositional shift of the LA. Such *taphonomic inertia* of the DA to changing ecological conditions is particularly likely when the community has been modified by human activities because they tend to be more rapid, monotonic, intense, and/or multi-factorial than natural forces (e.g., Jackson, 1997; Jackson et al., 2001; Pandolfi et al., 2003; Lötze et al., 2006; Orth et al., 2006; Airoidi and Beck, 2007).

However, even in fully natural settings and in the absence of any postmortem bias, we would still expect some degree of LD mismatch to exist in seafloor samples. LAs could differ from local DAs in composition, richness, etc owing to (1) random events of mortality and colonization, which can temporarily push the LA to an unusual composition, albeit still within normal range, (2) incomplete sampling of the LA (LA samples are often quite small; Fig. 2), and (3) non-random variation in LA composition linked to seasonal and decadal cycles or other natural environmental changes (Fig. 1), all occurring within the window of molluscan time averaging. The practical question is thus whether, in

general, DAs in areas of known strong human activities show higher levels of mismatch with the local living community than do DAs in areas where human activities are mild or non-existent. If so, then the effects of human activities on LD agreement (and on molluscan LAs) are stronger than the effects of natural ecological and taphonomic factors on LD agreement (and on molluscan LAs).

TURNING LD MISMATCH INTO A CONSERVATION TOOL

Although we may suspect that LD mismatch in a given area may be due to human activities rather than due to natural causes, a global meta-analysis of all available LD datasets permits the strength of the link to be assessed quantitatively, and thus indicates the confidence with which LD mismatch can be used as a practical means of recognizing strong shifts in ecological baseline in areas where historical biological data and/or knowledge of human stresses are lacking (Kidwell, 2007, 2008).

To test this correlation, I scored the intensity of human activities relevant to benthos stress for all LD study regions in the global database, using independent scientific reports and the expert knowledge of original

TABLE 2.— Semi-quantitative scale used to score anthropogenic stress in a region at the time of LD sampling. This approach permits diverse kinds of information to be incorporated in the score, e.g. government reports on trends in water quality or quantities of fish caught, academic research reports on pollution, date when local or state governments imposed regulations on pollution or fishing, economic and cultural history of the region, historical insights from sedimentary cores, and the expert but unpublished knowledge of scientists who have worked in the area. Different kinds of data were available in different regions.

Score	General meaning	Anthropogenic eutrophication	Bottom trawling
0	Stress absent or negligible	AE0 = no human settlements in area nor active land clearance	BT0 = no exploitation or only artisanal harvesting with minimal habitat destruction
0.5	Stress possibly present	AE0.5	BT0.5
1	Stress definitely present	AE1 = coastal development and/or major development in the watershed	BT1 = commercial harvesting, gear can dislodge benthos other than target species
1.5	Stress definite & possibly intense	AE1.5	BT1.5
2	Stress definitely present and intense	AE2 = near to large point source, usually in addition to diffuse sources	BT2 = especially intense commercial trawling, e.g. more than once a year

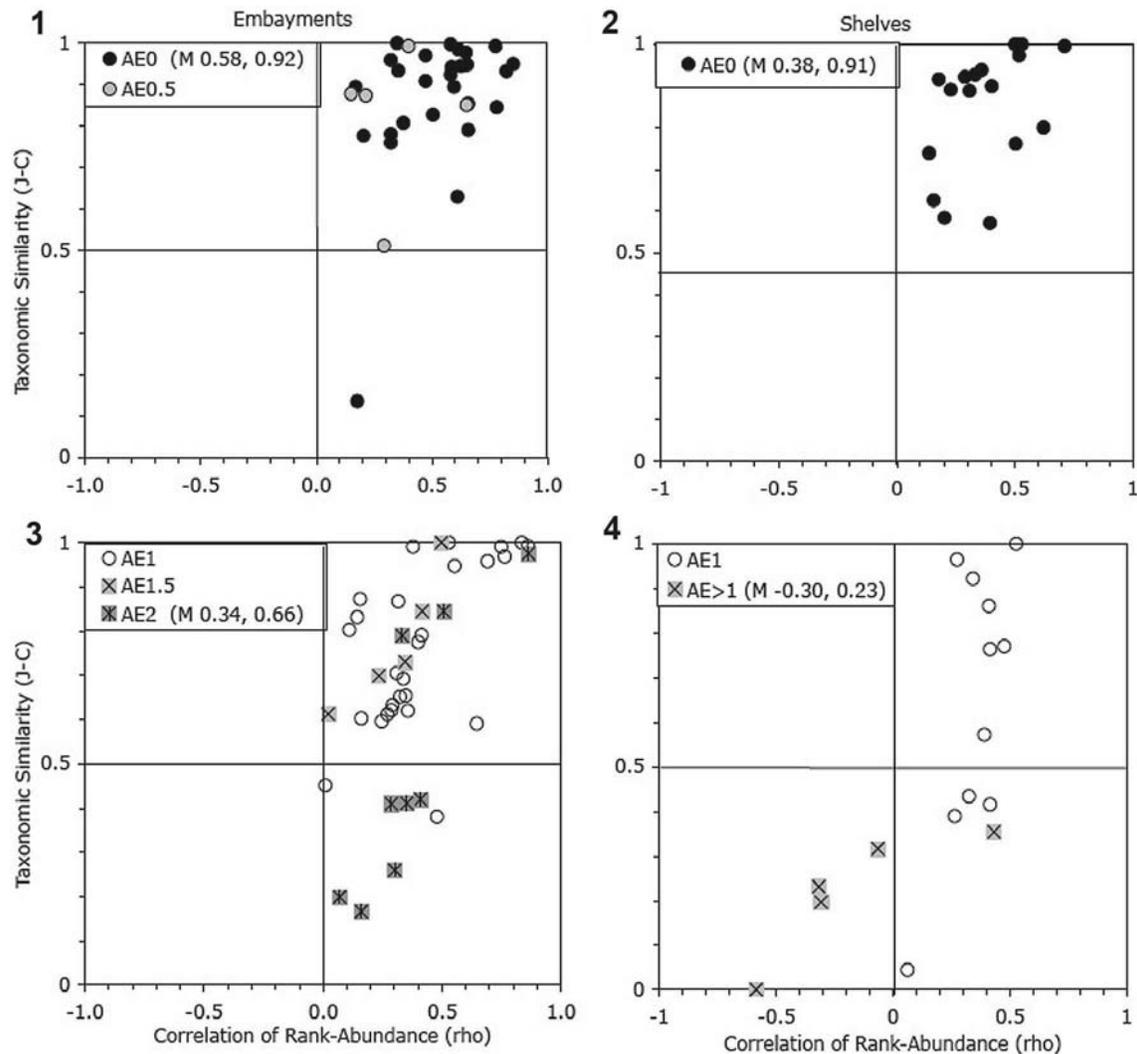


FIGURE 4.—Scatterplots of live-dead (LD) agreement in the taxonomic composition (y-axes; Jaccard-Chao index of similarity) and rank-abundance of species (x-axes; Spearman rho) of 73 datasets from coastal embayments (1, 3) and 34 datasets from open continental shelves (2, 4) under natural (AE0 or AE0.5; 1, 2) and definitely altered nutrient conditions (AE1 to AE2; 3, 4). In fully natural settings, LD agreement is very good (datasets fall well within the upper right quadrant of cross-plots; M = median value for AE0). LD agreement in AE \geq 1 datasets can be as good but ranges to significantly lower values where fewer than 50% of species are shared between LA and DA species lists (low JC similarity; bottom right quadrant) and formerly dominant species have become rare or vice versa (negative rho; bottom left quadrants of plots; M = Median value for AE $>$ 1). (Adapted from Kidwell, 2007.)

authors about human activities in the watershed at the time of their LD sampling effort (see Kidwell, 2007, for dataset-level characterizations and sources of information). Seven categories of human stresses were considered: *anthropogenic eutrophication* (AE; input of extra nutrients from cities, agriculture, coastal industries including fish-farms), *bottom-trawling* (BT) to

harvest fin- and shellfish, *solid sediment runoff* from land clearance, *dredging and spoil-dumping*, *salinity modification* related to channelization or impoundment, *chemical pollution*, and *thermal pollution*.

In order to combine diverse kinds of information and compare areas, I developed a single semi-quantitative scale to apply to all stressors (Table 2). My

assessments of local stresses based on the literature either matched or under-estimated those recognized by original LD authors in the instances when those authors could be interviewed. Anthropogenic eutrophication (AE) and bottom-trawling (BT) were most pervasive and other human impacts tend to increase with them, and so analyses focus on these two factors. I consider change in response to stress using two measures of molluscan *community composition* (the identity and relative abundances of species) and using two measures of *community structure* (richness and evenness):

1. Change in the identity of species that are present

Environmental degradation may lead to the local extinction of some species (these become “dead only”) and also to the immigration of new species that tolerate or perhaps prefer the new conditions (the first generation will exist “alive only”). *LD agreement in species presence/absence* is measured here using the Jaccard-Chao (JC) index of taxonomic similarity, which adjusts for LD differences in sample sizes (Chao et al., 2005). When $JC = 0$ the LA and DA share no species in common, and when $JC = 1$ all species occur both alive and dead in the habitat. A $JC = 0.5$ indicates that ~half of all species in the habitat occur both alive and dead and the others occur either alive-only or dead-only (1 and 0 are the upper and lower bounds).

2. Change in the relative abundances of species

The first signal of environmental degradation is usually a decline in the population sizes of some species, which may decline from being numerically dominant (highly ranked in abundance within the community) to being relatively rare (low ranked; represented by only a few individuals). At the same time, other species that were formerly rare (or absent) in the community may increase in population size and even become dominant (shift from low to high ranked abundance). *LD agreement in species relative abundances* is measured here using a Spearman rank-order test, which is especially sensitive to relatively large shifts in rank (e.g., from the top to the middle or bottom of the ranked list, rather than simply shifting ranks with a few similarly ranked species). Spearman correlation coefficients (ρ) are positive when each species in the DA has a similar rank to what it has in the LA (the species that dominate the DA also dominate the LA, and species that are rare in the DA are rare or absent in the LA). ρ is negative

when species’ ranks in the DA are flipped relative to their ranks in the LA (those that dominate the DA are rare in the LA) and ρ is ~zero when ranks in one assemblage are ~random relative ranks in the other (1 and -1 are the upper and lower bounds).

3. Change in the number of species that are present (richness)

When conditions change strongly, the new community (LA) may contain a completely different set of species than were found in the original community (represented by the DA), i.e., the taxonomic similarity is nil ($JC = 0$). However, if the new community contains the same number of species as the original, then there is no net change in species richness despite the complete turnover in species composition. *LD agreement in assemblage richness* is measured here as the ratio of dead richness to living richness after the larger sample (usually the DA, see Fig. 2) is sub-sampled to equal the size of the smaller sample (without replacement; expressed in logged units, this is “delta-S” of Olszewski and Kidwell, 2007, and the sample-size standardized “inflation” factor of Tomasovych and Kidwell, in prep.). Delta-S is 1 when the DA and LA have identical richness, is >1 when DA richness is $>$ than LA richness, and is <1 when DA is $<$ LA richness (no upper or lower bounds).

4. Change in the evenness (dominance) of species abundances

As environmental stress increases, fewer species find conditions tolerable. The community may thus change from containing a relatively large number of similarly abundant species (a fairly even abundance-structure) to being strongly dominated by a single species (low evenness in the distribution of individuals among species; = high dominance). *LD agreement in assemblage evenness* is measured here as “delta-PIE”, which is DA evenness minus LA evenness using Hurlbert’s evenness metric PIE, which stresses the proportional abundance of the most abundant species (as in Olszewski and Kidwell, 2007). Delta-PIE is positive when the DA is more even than the LA (individuals are distributed among species more evenly), negative when the DA is less even than the LA (individuals are more concentrated in a single or few species), and zero when no difference exists between the DA and LA (1 and -1 are the upper and lower bounds).

LD MISMATCH IN ASSEMBLAGE COMPOSITION INCREASES SIGNIFICANTLY WITH ANTHROPOGENIC EUTROPHICATION (AE)

In aquatic systems, nutrient enrichment—whether natural or anthropogenic—increases phytoplankton production beyond zooplankton grazing capacity, leading to increased water turbidity, decreased light levels, and morbidity and mortality of seagrass and other non-algal subaquatic vegetation, all leading to higher input of organic matter to the benthic boundary layer and seafloor. Because of the biological oxygen demand of the microbial decomposers of these organics, hypoxia and related die-offs of benthic animals become more likely. “Dead zones” characterized by low-oxygen bottom waters and high mortality have increased in many estuaries since World War II when the use of commercial (manufactured) fertilizers accelerated—what was once an occasional summer occurrence has become more frequent, more intense, and more extensive in coastal embayments worldwide (Rabalais and Turner, 2001). In the last several decades, “dead zones” began to appear even on open continental shelves and are now known from all world oceans (Diaz and Rosenberg, 2008). Climate change is implicated in the appearance or intensity of some of these dead zones (e.g., Chan et al., 2008; Brewer and Peltzer, 2009), but most are linked to nutrient run-off from agriculture, cities, and industries in the watershed.

The results of eutrophication in coastal waters are—from the molluscan perspective—the decline and eventual loss of species that require or prefer seagrass meadows as habitat or food (“grass-dwellers” including micro-grazers and macro-herbivores), a shift from largely suspension-feeders to mixed or largely deposit-feeders, loss of attached epifauna, and the general replacement of hypoxia-intolerant species by species that are either hypoxia-tolerant or are short-lived, with rapid generation times and high (re)colonization potential (Diaz and Rosenberg, 1995; Orth et al., 2006). One thus expects change in the relative abundances of species and, if conditions become sufficiently severe, change in species’ presence/absence as some species disappear entirely and new species arrive.

Analytic findings

Cross-plots of LD taxonomic similarity (JC index,

y-axis) against LD agreement in species rank-abundances (Spearman’s rho, x-axis) are a useful means of displaying how LD agreement varies as a function of AE (Fig. 4). Each data point signifies LD agreement in different habitat-level dataset. LD agreement is quite high in relatively pristine (AE0) settings, both in coastal embayments (lagoons, bays, estuaries) and on open continental shelves: all but one dataset falls well within the upper right quadrant of a JC/rho cross-plot (Fig. 4.1, 4.2). These AE0 settings include areas that are naturally nutrient-poor (e.g., carbonate shelf of Yucatan) and nutrient-rich (Patagonia and Amazon shelves, both with seasonal upwelling). The scatter in AE0 data points indicates the range in LD agreement that is created in completely natural circumstances by incomplete sampling, time averaging of natural biological variability, and postmortem bias (differential preservation, out-of-habitat transportation; Table 3).

LD agreement in areas of known human impact (AE scores ≥ 1) can be as high as that observed in pristine areas but ranges to significantly poorer levels (Fig. 4.3, 4.4). The decline in taxonomic similarity (JC) with increasing AE is significant in both coastal embayments and open shelves despite the overlap of values with AE0 settings. The decline in rank-abundance agreement (rho) is not significant in estuaries unless datasets are partitioned by mesh size, with coarse-mesh datasets registering significant declines in rank-abundance agreement with increasing AE. In shelf settings, rank-order correlations decline to *negative* rho values in AE2 areas (study areas adjacent to pulp mills and contaminated harbors; Fig. 4.4) and is significant without partitioning datasets by treatment (Kidwell, 2007, 2008).

Variation in LD agreement along a spectrum of AE globally implies temporal changes that are consistent with taphonomic inertia. The community first shifts in the proportional abundances of species already present, eroding rank-order agreement, followed by the total loss of some species (which may become “dead-only”) and, in some instances, the entry of new “alive-only” immigrants, progressively reducing taxonomic similarity. The composition of the DA equilibrates to stochastic variation within the new living community only as the remains of the previous community are destroyed and/or buried below the mixing zone, and are diluted by the input of dead shells from the new community. This same pattern is seen in biological analyses of

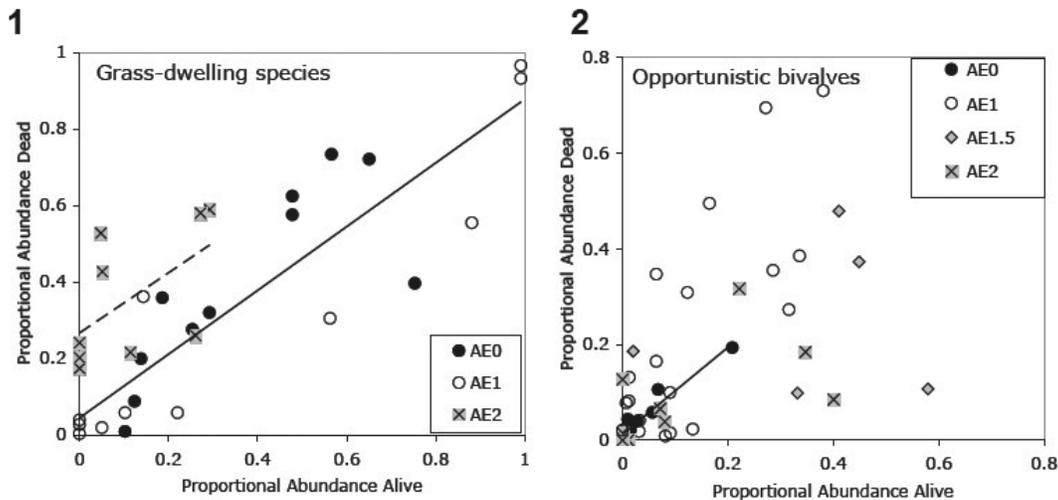


FIGURE 5.—Signals of anthropogenic eutrophication (AE) from LD mismatches in the proportional abundances of key species or sets of species. 1, In lagoons where AE is absent or only moderate, mollusks that prefer or are found almost exclusively in seagrass beds are about as abundant in the DA as in the LA, whereas they tend to be disproportionately abundant in DAs where AE is severe (AE2), signifying the former presence of seagrass habitat. Based on 31 datasets from tropical Gulf of Mexico; 2, The opportunistic bivalve *Mulinia lateralis* is relatively rare both alive and dead in natural lagoons (has proportional abundance <10% in all but one AE0 dataset), showing good LD agreement. In $AE \geq 1$ lagoons *Mulinia* ranges up to ~60% alive and 75% dead and is commonly among the most abundant or is the most abundant species in one assemblage or the other or both, consistent with greater stress such as from episodic hypoxia associated with AE. DAs in $AE \geq 1$ settings are not consistently enriched in *Mulinia* compared to LAs in part because of the abundance of grass-dwellers and other relictual species in many of these DAs. Based on 47 datasets from temperate and tropical Gulf of Mexico. (Both figures adapted from Kidwell, 2007.)

exclusively living assemblages. With progressive AE over time (or with increasing spatial proximity to the nutrient point source), the first changes are in species' relative abundances, followed by the complete loss of sensitive species and, in some instances, the appearance or rise to dominance of pollution-tolerant species (e.g., for review, see Gray and Elliott, 2009).

Implications for conservation biology

The strength of the association between LD agreement and AE is remarkable, given the array of natural processes, other human impacts, and methodological issues that can influence the match between a single census of the living community and the local DA. It thus implies that LD mismatch in the taxonomic composition and relative abundances of species, readily measured by taking advantage of dead shell residues in standard benthic samples, could be used to recognize significant modification of living communities by AE. This would be a significant boon for areas where historical survey data are sparse or lacking entirely, or

where human stresses are unknown or contentious.

LD comparison fails to detect AE in many instances. LD mismatch in taxonomic similarity and rank-abundance in some areas of known AE is not significantly greater than that in spatially analogous AE0 settings. About 40% of datasets from estuarine and shelf settings of certain AE fall within two standard deviations of the mean of AE0 datasets in these plots (Kidwell, 2007). That 40% can be taken as the failure rate of this method if one assumes that the LAs in these AE habitats did in fact undergo significant changes in response to AE and thus that significant LD mismatch should exist in all $64 AE \geq 1$ datasets. LD mismatch is thus a highly conservative test of AE, yielding false negatives (fails to detect AE when AE conditions exist) rather than false positives.

Biologically, the significantly higher average mismatch encountered in AE settings implies that the magnitude of impact of human activities on benthic communities exceeds the ecological consequences of any natural change in environmental conditions occur-

ring within the window of DA time averaging (Fig. 1). The strong impact of human activities on natural systems is well-known, but the LD results show how the magnitude of effect can be recognized in a temporal framework (the estimated duration of time-averaging of dead shells within the sampled mixed layer) without the use of sedimentary cores. The significantly higher average mismatch in AE settings implies considerable persistence of skeletal material within the mixed layer for DA composition (taphonomically interesting; corroborates independent direct-dating efforts, Fig. 1) and/or lower rates of molluscan shell production in the new community (biologically interesting).

Under AE, it clearly takes appreciable time for the “new” community to dilute the dead residua of the “old” pre-impact community—that is, to bring the time-averaged DA into equilibrium with the new LA composition. This lag contrasts with the relatively rapid temporal tracking by DAs of changes in LA composition that is implicit in the high LD agreement that characterizes fully natural conditions (i.e., the tight clustering of AE0 datasets in the upper right quadrants of Fig. 4.1, 4.2). Rapid tracking is documented explicitly in a time-lapse test of temporal stability in molluscan DA composition by Ferguson and Miller (2007), who found that the DAs of a tropical back-reef lagoon changed significantly over 20 years but in concert with comparable, apparently natural changes in LA composition over that same period. In their classic analysis of two Texas bays, Staff et al. (1986) also found rapid changes in species’ relative abundances among molluscan LAs sampled at successive 6-week intervals over 18 months, mostly followed by corresponding changes in those species in DAs that then faded quite rapidly, probably because most individuals were juveniles subject to rapid postmortem destruction.

The *lack* of LD mismatch in some datasets from areas of known AE (e.g., the AE1 datasets that fall within the range of AE0 datasets in the crossplots of Fig. 4; in estuaries, even some AE1.5 and AE2 datasets fall within the pristine range) might signify several things. For example, biologically, AE might have had relatively little actual effect on LA composition locally. Species that prefer organic-rich sediments or tolerate episodic dysoxia might already have been present or even dominant in the pre-impact community, so that AE caused no significant change in the LA and thus created no unusual degree of LD mismatch. Biologists

in fact commonly find no significant impact of anthropogenic nutrient loading on benthic communities in areas that are naturally eutrophic. An alternative or additional factor may be that, by the time of sampling, the DA might have already equilibrated to the new LA, resulting in little LD mismatch. Such equilibration is especially likely in areas of long-standing AE (long-standing relative to the scale of DA time-averaging) and/or high sedimentation rates, so that the DA record of the transition of the LA by AE is already buried below the mixed layer. Sediment coring into historic layers would be required to access the DAs that contain pre-impact species. Conditions of long-standing AE and/or high sedimentation rates are especially common in coastal embayments, which often have long multi-centennial histories as harbors and industrial centers and are natural sinks of sediment, promoting relatively rapid permanent burial of shells.

LD MISMATCHES IN SPECIES IDENTITIES ARE CONSISTENT WITH AE: SPECIFIC CAUSE CAN BE INFERRED

If the increase in LD mismatch associated with AE is truly caused by AE, then LD mismatches in species identities and relative abundances should be consistent with eutrophication or other human stressors, rather than, say, with postmortem transportation, differential preservation, or natural environmental change. AE should not simply change LA composition: it should bring to dominance and drive to local extinction *particular* species, namely those sensitive to the presence of seagrass, to sediment organic content, and to hypoxia (see background information on AE above). By examining the identities and autecology of species found dead only or anomalously abundant (or scarce) in the DA relative to the LA, we should get a sense of the kind of environmental change that the area has undergone, which narrows the search for cause.

Analytic findings

A collection of 31 LD datasets from 11 tropical Mexican lagoons is a particularly powerful means of testing for this effect because all datasets reflect the same sampling procedure (1.5 mm mesh) and a single regional fauna but a range of AE conditions. In datasets from AE2 lagoons, many species that occur “dead only” or at very low abundance in the DA prefer grassy

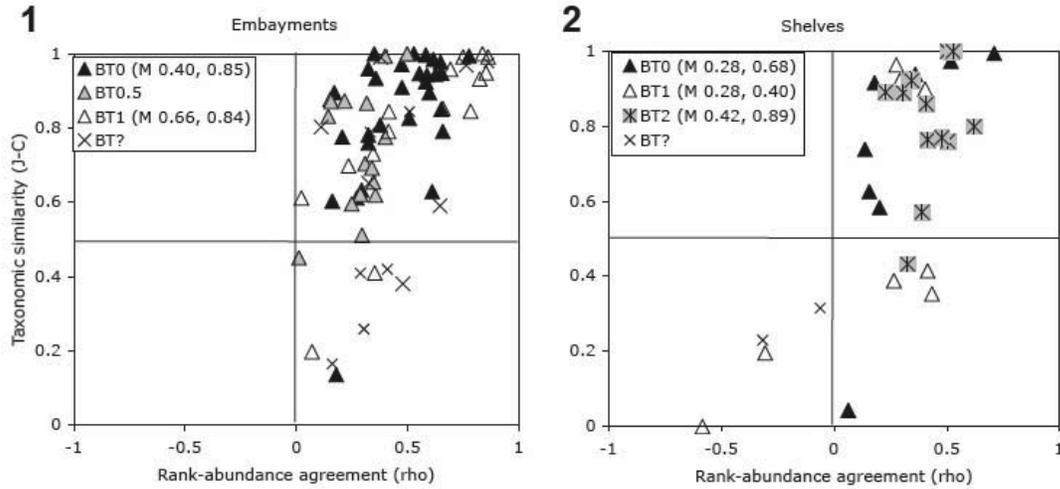


FIGURE 6.—Scatterplots of LD agreement in the taxonomic composition and rank-abundance of species as in Fig. 4 but with datasets now scored for the intensity of bottom trawling (BT). In general, areas subject to BT are also subject to AE so that these plots strongly resemble those in Fig. 3, but in itself BT has no significant effect on overall LD agreement as measured by JC and rho, either in embayments (1) or on open shelves (2). M = median rho and JC.

substrata (see Kidwell, 2007, for a complete listing of “grass-dwelling” bivalve and gastropod species). With two exceptions out of nine datasets, DAs in the five AE2 lagoons are enriched in grass-dwellers relative to living communities by 20% or more (dashed trendline in Fig. 5.1). In contrast, among datasets from pristine to mildly AE lagoons (AE0 to 1) the proportional abundance of grass-dwellers in the DA matches that in the local living community more closely. Loss of seagrass is a well-known consequence of AE (e.g., Twilley et al., 1985). The tendency for AE1 datasets to plot among pristine datasets makes sense in this regard, because fertilization initially stimulates grass growth.

The relative abundance of the opportunist bivalve *Mulinia lateralis* is also consistent with the episodic hypoxia, stunted animal growth, and pulsed mortality that can accompany eutrophication (e.g., Powers et al., 2005). Drawing on 47 datasets from both Mexican and Texas lagoons bordering the Gulf of Mexico, *Mulinia* is sparse both living and dead in the pristine AE0 lagoons (Fig. 5.2; with one exception, *Mulinia* constitutes <10% individuals). In contrast, it tends to be one of the most abundant species in AE1 and AE2 lagoons, where opportunistic colonization and strong mortality events would alternate with seasonal or other variation in water stratification. *Mulinia* is scarce both alive and dead

in some AE1 and AE2 datasets—a series of these datasets cluster among AE0 datasets in the plot of Figure 5.2. But with one exception, every dataset that contains abundant *Mulinia* either alive or dead or both alive and dead is from a lagoon where there is independent evidence of AE (wide scatter of points in Fig. 5.2).

Finally, LD mismatches in species identity in open shelf datasets also suggest eutrophication. LAs in AE1.5-2 areas (shelves immediately offshore of pulp mills or notoriously contaminated harbors) tend to have abundant deposit-feeding and chemosymbiotic bivalves that are rare in the DAs, where dead-only larger-bodied suspension feeding species are important (Kidwell, 2008). Although these mismatches might be magnified by (1) lower preservation potential among the relatively small-bodied species of the “new” community (solemyids, lucinids, tellinids, prosobranchs, thyasirids) and (2) more prolonged time averaging of death assemblages on shelves than in coastal embayments, the LD mismatches in species identities are incompatible with postmortem introduction of allochthonous shells and are not observed consistently in datasets from naturally nutrient-rich shelves. On the latter (e.g., Amazon and Patagonia shelves), the proportional abundances of organic-loving species in local LAs and DAs are more comparable than on shelves where nutrients are anthropogenic.

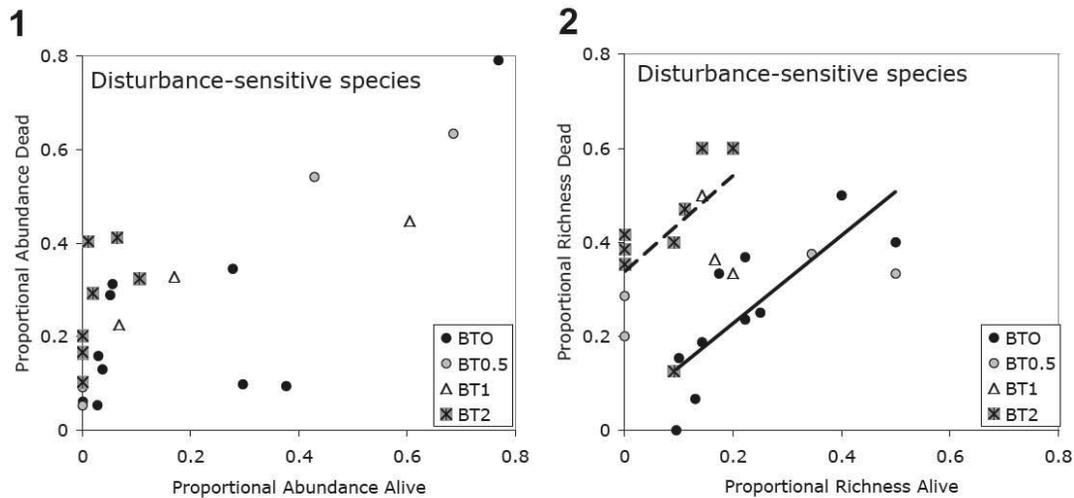


FIGURE 7.—Signals of bottom trawling (BT) from LD mismatches in (1) the proportional abundance and (2) proportional richness of bivalve species likely to be sensitive to physical disturbance, based on 25 datasets from gravels under all AE conditions. “Disturbance-sensitive species” includes all bivalves known to be facultatively or obligately byssate as adults (e.g., both semi-infaunal and epifaunal arcoids, pinnids, pteriids, isogononmonids, mytiloids, and infaunal corbulids) and all epifauna (including scallops that may swim as adults, spondylids that attach as adults, and continuously attached oysters, anomniids, plectaulids, chamids, and most limoids).

Implications for conservation biology

LD mismatches in species identities and relative abundances are consistent with eutrophication in areas where AE is judged likely, indicating that LD mismatches in key species and functional groups can be used to recognize the particular ways in which benthic communities have changed within the window of DA time averaging. Species that are dead-only or are far more abundant in the DA than in the LA probably are in fact relicts of past local populations, rather than biologically meaningless artifacts of taphonomic processes.

As a caveat, the evidence from meta-analysis is statistically strong but circumstantial (inferential). It assumes that variation in LD agreement among a *spatial* spectrum of study areas reflects the ability of DAs to capture *temporal* changes locally. Long-term biomonitoring data for living communities are not available for any of the LD study areas—such data would permit useful “hard” tests of the ability of DAs to pick up on and retain a signature of AE. Moreover, information on the cultural history of LD study areas was gathered from disparate sources, including regional rather than local assessments (Kidwell, 2007, 2008). Local tests with better-constrained environmental and/or biological data are thus needed to move beyond meta-analytic findings. As a powerful example, Ferguson (2008)

took advantage of known spatial variation in nutrient input within Florida Bay that had existed for only ~20 years—a series of posts that became roosting sites for seabirds—and found that molluscan DAs captured the signature of local eutrophication and retained its fine spatial grain (sites 50 m distant from the posts in unaltered seagrass beds were compositionally distinct, non-eutrophied baselines). The modern world is full of opportunities for this kind of taphonomic field experiment, taking advantage post hoc of known human perturbations of natural systems.

LD MISMATCH IN SPECIES THAT ARE DISTURBANCE-SENSITIVE AS EVIDENCE OF BOTTOM-TRAWLING (BT)

Bottom-trawling (BT) here includes all methods of harvesting demersal fin-fish and shell-fish (*sensu lato*, i.e., mollusks, crustaceans, sea cucumbers and urchins) that disturb the sediment-water interface. Thus dredging and raking as well as bottom-trawling s.s. are included, whereas hook-and-line, pot- or trap-catching, and various mid-column netting efforts are excluded. BT tends to produce significant benthic bycatch (species other than the target species) and can do considerable damage to the physical habitat. Trawling heavy gear across

a soft-sedimentary seafloor is analogous to clear-cutting or plowing land surfaces. It causes strong declines particularly in attached epifauna but also in free-living epifauna and in long-lived and/or relatively sessile infauna (e.g., low capacity to re-establish themselves in burrows), and favors the establishment and survival of short-lived, mostly soft-bodied species (e.g., Thrush et al., 1998; Gray et al., 2006; NRC, 2002). These observations provide specific predictions for LD mismatch in areas subject to bottom-trawling.

BT has a long history but was largely limited to shallow coastal waters until engines replaced sails. Mechanized harvesting methods were developed for oysters by the late 1800's, causing massive destruction of reef habitats in estuaries (e.g., Rothschild et al., 1994; Kirby, 2004). Exploitation using heavy gear expanded to increasingly deeper (shelf) waters in the early 20th century (e.g., Cranfield et al., 1999; Edgar and Sampson, 2004). The global extent and magnitude of effect of "industrial" extraction of wild fish stocks is increasingly appreciated as are the deep historical roots of "fishing down" marine foodwebs and the resulting trophic cascades and impacts on ecosystem services (e.g., Pauly, 1995; Jackson et al., 2001; Myers and Worm, 2003; Lötze et al., 2006; Lötze and Worm, 2009; Worm et al., 2006; Baum and Worm, 2009), even when bottom-trawling is not involved.

Analytic findings

Analysis includes both open shelves (covered in Kidwell, 2008) and coastal embayments (work first reported here). No LD study has included oyster-reefs s.s. although several have sampled shell-rich sediments from the flanks of reefs, which are included here. Because of uncertainty in commercial efforts in some embayments, I've added a BT0.5 category for Tomales, Galveston, and West Bays (significant oyster fisheries in the area, but not relevant to the habitats sampled for LD data). I have also shifted the Patagonian shelf to this category, out of BT0. BT scores for shelves are otherwise as used in Kidwell (2008). For a complete listing of study areas and meta-data on trawling, see Kidwell (2007).

As already reported (Kidwell, 2008), shelf datasets are notable for *not* showing a significant correlation between BT and LD agreement in species composition (JC, rho). In crossplots of taxonomic similarity (JC

and rank-abundance agreement (rho), LD agreement datasets from BT2 areas show the same high values as those from BT0 areas, and thus no significant correlation exists even though some BT1 datasets exhibit low LD agreement (Fig. 6.2). I find the same lack of association among datasets from coastal embayments (Fig. 6.1). A significant correlation of LD agreement with BT fails to emerge even if analysis of BT is restricted to areas that are otherwise pristine (AE0 areas; not displayed).

Virtually all trawled areas in the database were subject to commercial exploitation for decades before being sampled for LD data, which might explain the lack of a trawling signal in these general (JC, rho) measures of LD agreement. Another factor—probably equal or more important than the long history of BT—is that many datasets are from sand and mud bottoms, which tend to have few epifaunal or byssate species even when undisturbed and thus exhibit only modest changes in response to trawling. Based on before-after-control studies of living communities and comparisons of trawled and untrawled seafloors (e.g., Thrush et al., 1998; Tillin et al., 2006; Hiddink et al., 2007; Hinz et al., 2009), benthic communities that are dominated naturally by short-lived and/or free-living infaunal species (mobile sands, soft muds) undergo less change and recover faster than do communities that include species that live freely on the seafloor (mobile epifauna), live attached to the seafloor (cementing and byssate epifauna), and/or live partly or fully burrowed into the sediment but stabilized using byssal threads (endo-byssate infauna and semi-infauna).

When analysis is focused exclusively on the 25 LD datasets from gravel or gravelly habitats whose communities are most likely to be sensitive to trawling, BT still leaves no distinct signal in terms of JC and rho (Fig. 6). However, significant LD mismatches exist in the proportional *abundance* and proportional *richness* of the subset of bivalve species that should be most sensitive to bottom disturbance (Fig. 7). This subset includes all epifaunal species regardless of attachment and all species that are either facultatively or obligately byssate as adults, regardless of life position (see list in caption of Fig. 7). Spearman rank correlation tests find that the difference in proportional abundance of these species in the DA versus the LA is significantly positively correlated with the BT score (rho = 0.564, p

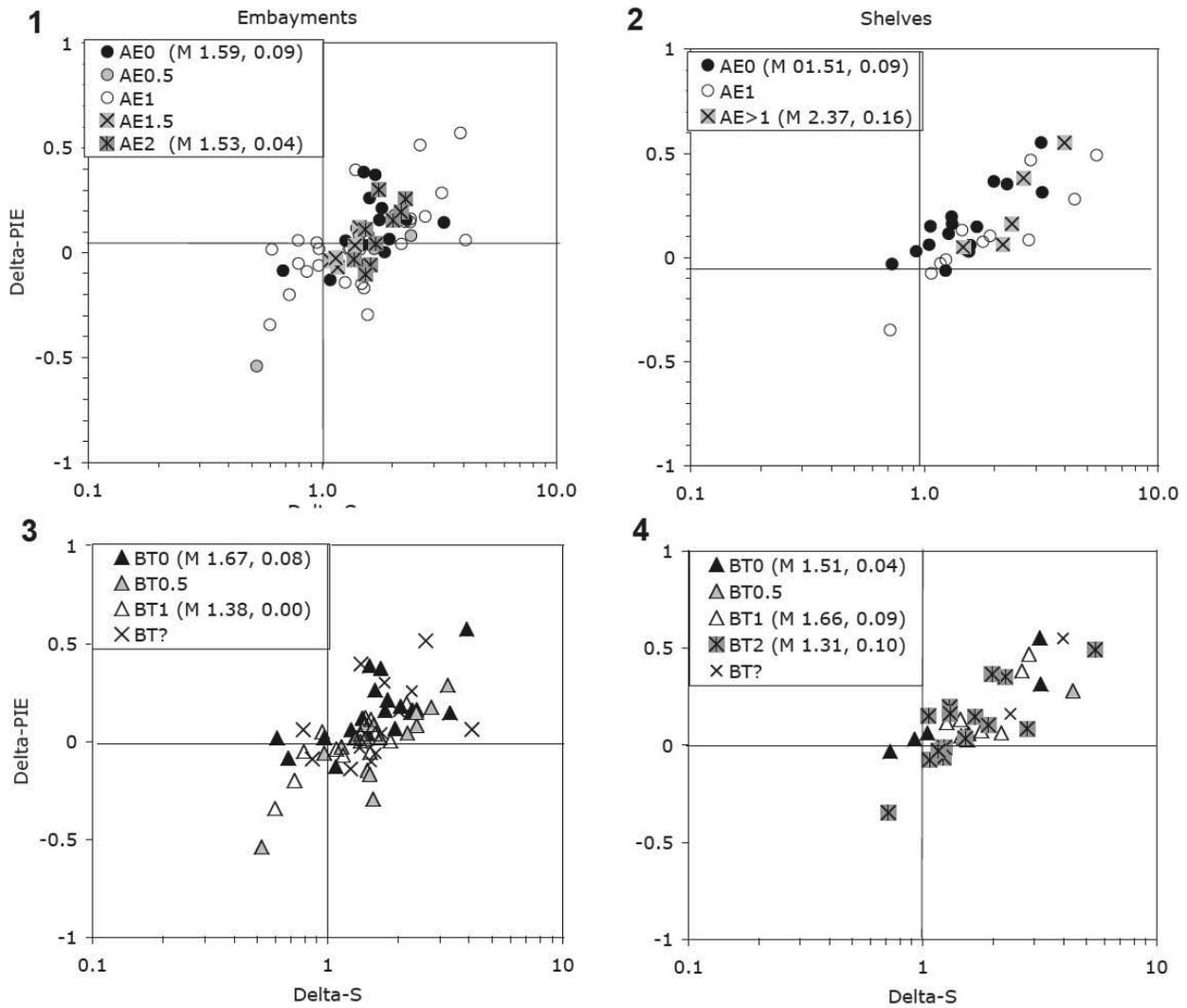


FIGURE 8.—Scatterplots of LD agreement in species richness (sample-size standardized delta-S; x-axes) and evenness (delta-PIE, y axes) in either embayments (1, 3) and open shelves (2, 4) for datasets scored by AE (1, 2; M = median value for AE0 and AE>1) or scored for BT (3, 4). DAs from areas impacted by either AE or BT are not significantly more enriched in species than are DAs from natural areas, nor do they exhibit more even abundance distributions, with the exception of shelves under strong AE (AE>1).

= 0.002), and that the difference in proportional richness of these species in the DA versus the LA is also significantly positively correlated with the BT ($\rho = 0.714, p < 0.001$; 25 gravel datasets from all environments and states of AE).

The difference in proportional richness is particularly striking: with one exception, disturbance-sensitive species are ~30 percentage-points more abundant in BT2 DAs than in counterpart LAs, which contrasts quite cleanly with BT0 datasets where DAs tend to

match their counterpart LAs quite closely (compare trend lines in Fig. 7.2).

The same patterns result if the analysis focuses exclusively on gravel datasets from areas that are otherwise pristine. Among gravels in AE0 areas, LD mismatches in the proportional *abundance* of sensitive species are still positively correlated with BT albeit no longer significant ($\rho = 0.41, p = 0.10$). The effect of BT on proportional *richness* remains significantly positive ($\rho = 0.728, p < 0.001$; 17 datasets).

Implications for conservation biology

There is a pressing need for methods that (1) permit recognition of BT in areas with little regulation and/or enforcement and (2) identify species that need recovery. There is also a need for methods to retrospectively (3) estimate pre-BT community composition in regions where bottom disturbance from even legal fishing is so extensive that it is difficult or impossible to identify “baseline” areas to set recovery targets (e.g., de Juan et al., 2009).

The positive results reported here indicate that LD mismatch, focusing on the subset of species whose life habits make them most sensitive to physical disturbance, would be a useful new tool for all three needs. Habitats subject to BT, especially intense BT, yield DAs that are significantly richer in disturbance-sensitive species than co-sampled LAs, indicating historical declines in the populations of these species within the scale of time averaging. Species occurring dead-only and especially those having more than trace abundance in the DA are the species that have suffered the strongest declines, and thus provide targets for judging recovery. LD analytic results are for gravelly habitats only, but biologists have already discovered that these communities undergo the strongest change and have the slowest recovery times of all soft-sedimentary seafloors.

The scatterplots provide additional insights into the biology of these settings and guidelines for recognizing human disturbance. (1) Disturbance-sensitive species can constitute anywhere up to ~80% of *individuals* in the LAs of BT0 gravels, but with one exception do not constitute more than 20% of *living* individuals in trawled gravels and in all eight intensely trawled (BT2) gravels constitute <10% of living individuals. Epifaunal and byssate infaunal mollusks thus definitely do “see” trawling and even small LA samples such as found in LD datasets can recognize the scarcity of these species (Fig. 7.1). Mollusks thus provide a reasonable surrogate for the response of the entire macrobenthos. (2) Disturbance-sensitive species constitute at least 10% of total species richness in the LAs of BT0 gravels but commonly are entirely absent in the LAs of trawled gravels. In five of the 12 trawled gravels (BT0.5 to BT2) sensitive species occurred exclusively as empty shells (Fig. 7.2). Thus epifaunal and byssate taxa do not consistently dominate gravel bivalve communities taxonomically even under completely natural condi-

tions, but they are consistently present alive.

AE AND BT HAVE LITTLE EFFECT ON LD AGREEMENT IN COMMUNITY STRUCTURE (RICHNESS AND EVENNESS)

The richness (count of species) and evenness (degree of dominance by a few species) of benthic communities might respond in a variety of ways to human impacts. For example, richness might *decrease* owing to extermination of species by overexploitation or habitat destruction, might *increase* owing to non-native species being introduced either intentionally (e.g., transplantation for exploitation) or unintentionally (ballast water, cryptic species hitchhiking on exploited species, escapees from aquaria), or might be *unchanged* (a net balance of local extinction and introduction). Evenness is generally expected to *decrease* because human intervention commonly leads to *fewer competitors* (loss of redundancy within trophic levels or functional groups as some species are driven to functional extinction), *more stress* (narrower range of species capable of tolerating conditions of pollution, nutrient over-loading, or physical disturbance), and *more static conditions* (held at a particular level by human pressure, thereby suppressing stochastic variability and small-scale natural fluctuations in the community, allowing single species to dominate).

Analytic findings

Datasets analyzed here include all but five of the *subtidal* habitats analyzed by Olszewski and Kidwell (2007). Datasets from Mannin Bay are excluded because the richness of the death assemblage was originally under-counted in a way that cannot be corrected retrospectively, affecting delta-S but not delta-PIE.

Regardless of the type or intensity of human impacts in the study area, the majority of LD datasets have DAs that are both richer and more even than counterpart LAs—that is, most fall in the upper-right quadrant of a cross-plot of delta-PIE against delta-richness (Fig. 8, Table 3). In estuaries, AE has no significant effect on community structure. Datasets from areas with $AE \geq 1$ are centered on the cloud of AE0 datasets but show greater dispersion in both delta-richness and delta-PIE (especially datasets from AE1 areas; Fig. 8.1). On shelves, DAs from areas with $AE \geq 1$ tend to be more inflated in richness on average than are DAs from AE0

TABLE 3.—Live-Dead (LD) agreement in molluscan composition and structure, based on 109 habitat-level datasets globally (left columns) and on the subset of 40 datasets from areas with no anthropogenic eutrophication (AE0; right columns). Interquartile ranges in boldface. Mean with 95% confidence intervals calculated on the standard error.

Measure of LD agreement	All areas		Pristine (AE0) areas only	
	Median Min/ Q1/ Q3/ Max	Mean	Median Min/ Q1/ Q3/ Max	Mean
Taxonomic similarity (JC)	0.80 0/ 0.61/ 0.93 / 1	0.73 ± 0.05	0.90 0.14/ 0.79/0.95 /1	0.85 ± 0.04
Rank-abundance correlation (rho)	0.36 -0.58/ 0.25/ 0.51 / 0.86	0.37 ± 0.05	0.47 0.14/ 0.32/ 0.60 / 0.85	0.46 ± 0.06
Raw ratio of DA richness to LA richness	3.23 0.58/ 2.14/ 4.92 / 18.4	3.94 ± 0.53	2.94 1.02/ 2.17/ 5.21 / 10.75	3.91 ± 0.86
Delta-richness (standardized)	1.53 0.52/ 1.26/ 2.07 / 5.46	1.76 ± 0.17	1.52 0.68/ 1.30/ 1.81 / 3.31	1.65 ± 0.21
Delta-PIE	0.06 -0.54/ -0.03/ 0.17 / 0.57	0.08 ± 0.04	0.06 -0.35/ 0.00/ 0.16 / 0.55	0.10 ± 0.05

areas (Fig. 8.2; see median values in key). There is no significant change in average delta-PIE among shelf datasets as a function of increasing AE. Arguably, the environmental distinctions in delta-richness arise because shelves have more richness to lose when environmental conditions deteriorate under AE, and are less likely than estuaries and lagoons to include species that are tolerant of hypoxic intervals and other stresses related to temporary nutrient pulses (see Kidwell, 2007, 2008, for discussion of mesh-size effects).

When the same datasets are evaluated for variation with trawling intensity, no significant effect emerges for either delta-richness or delta-PIE in either environment (Fig. 8.3, 8.4). Datasets from trawled (BT1) areas—even datasets from intensely trawled areas (BT2)—plot basically on top of datasets from untrawled areas (BT0). Datasets with less certain (BT0.5) or unknown trawling intensity (BT?) also occupy the same portion of the crossplots.

Implications for conservation biology

The finding here that DA richness is generally not significantly more inflated in impacted than in pristine settings suggests at first glance that there is a basic trade-off in molluscan species gained and lost with AE and BT. However, this result should *not* be interpreted

as evidence of community saturation. It arises instead from comparing time-averaged DAs with non-averaged, snapshot samples of LAs. DAs are usually richer than local LAs even in pristine settings and even when sample-size standardized (Figs. 2, 8; Table 3) because the coarser temporal resolution of the DA leads to a flatter abundance distribution (the qualitative expectation of Fürsich and Aberhan, 1990) and also allows a long tail of rare species to develop (Tomasovych and Kidwell, in prep).

The results indicate that, notwithstanding changes in the identities and relative abundances of species that occur with AE and BT (earlier sections), the magnitude of effect on LD agreement in richness and evenness is not substantively different than what is observed in pristine habitats, somewhat contrary to intuition. Within fully natural settings, natural volatility of (mostly small) populations continuously shifts species back and forth between the alternative states of being dead-only and being present both alive and dead (and see Tomasovych and Kidwell, 2009c, and Kidwell and Tomasovych, 2009, for comparisons of LD agreement with “live-live” agreement among spatially and temporally replicate samples of LAs). In addition, environmental conditions can vary considerably within the window of time averaging (see Fig. 1). These changing conditions

bring additional species into the local LA (and thus also into the local DA) from the regional species pool and force some species out of the local LA (but not out of the local DA, whose richness simply continues to ratchet upward). In any single random sampling of a natural system, the richness of the LA may be seasonally low (including zero) but the DA will remain consistently higher from the inclusion of relicts from earlier natural but quite different conditions. Delta-richness can thus be naturally high. Neither AE nor BT pushes systems outside this natural range, which is quite large. Even under human stresses, the local LA and thus the local time-averaged DA continue to draw on the same regional species pool.

Recognizing AE and BT using LD mismatch thus requires an analysis of species composition—the identities and relative abundances of species, especially of functionally sensitive species, as discussed in earlier sections—and not a simple comparison of species counts or abundance structures.

DETERMINING THE COMPOSITION OF NATURAL “BASELINE” COMMUNITIES AS TARGETS FOR RESTORATION: THE NEXT FRONTIER

The high degree of LD agreement observed in pristine settings (Table 3; Fig. 4) provides the best current estimate for the reliability of DAs as time-averaged complements to the data generated by conventional biological surveys. It also represents the best current estimate, albeit an optimistic one, for the reliability of DAs from buried historic layers, from which paleoecologists try to acquire deeper-time perspectives on modern communities, both natural and human-modified. How reasonable are these two applications?

In habitats from pristine areas, LD agreement is quite high. LD agreement is not perfect—both similarity in species presence/absence (JC) and rank-abundance (ρ) are less than 1 (Table 3; Fig. 4). However, focused empirical analysis and modeling of these pristine datasets now underway indicate that, although DAs and LAs differ in part because of significant post-mortem bias in some instances, most of the mismatch in composition owes to spatial and temporal variability in the living community (Tomasovych and Kidwell, 2009c; Kidwell and Tomasovych, 2009). High within-habitat variability in LA composition—among sites at a

single moment and from season to season over multiple years—creates a large range of species compositions in natural settings, which makes a large (easier) target for DA composition to hit. For example, the multivariate centroid of sampled DAs within a habitat does not always fall precisely on the centroid of LA samples from that habitat, but is almost always inside the multivariate dispersion of LA samples (Tomasovych and Kidwell, in prep.).

The time-averaged nature of DAs is thus a good means of estimating average LA composition in natural settings, as anticipated by Peterson (1977) in his early treatment of the issue. Our new findings using spatial and temporal replicates of LAs, as well as the high average LD agreement summarized here from meta-analysis at the habitat-scale (Table 3; Fig. 4), indicate that LD agreement in mixed-layer sediments can be used to identify which regions might best serve as restoration baselines. Such spatial baselines—habitat similar to the impacted one but in a nearby region that has escaped or been resilient to human activities—can be difficult to identify in regions with long histories of heavy trawling or coastal development (e.g., Caddy et al., 1995; de Juan et al., 2009). Ideally, LD agreement would not be the only method used to judge the status of a given habitat or multi-habitat region, but this new approach deserves a rigorous trial via case studies.

An alternative and usually preferable baseline for setting targets for restoration is information on what the local community was like before human modification—that is, a historical perspective on the impacted habitat at hand. In the absence of a strong history of local biomonitoring, historical ecologists use past scientific surveys, interviews with elderly fishermen and other residents, archeological middens, and sedimentary cores. The mixed-layer DAs in the impacted area may show poor LD agreement, but at some depth one should encounter DAs from historic layers of sufficient geologic age that they time-averaged exclusively natural LAs.

To what extent can we trust that DAs from *historic* layers will be as faithful in composition to LAs from that past time as modern mixed-layer DAs are to modern-day LAs? This topic is a current research frontier. Part of the reason that *mixed-layer* DAs agree so well with LAs—in fact, perhaps a very large part—is that mixed-layer DAs are still open systems that receive input of dead individuals from the local LA (Fig. 3). If rates of

postmortem destruction are indeed highest in the initial postmortem interval—and experiments suggest this, particularly for newly settled juvenile mollusks and other meiofauna (e.g., Cummins et al., 1986a, b; Green et al., 1998, 2004; Best et al., 2008; Best, 2009)—then the tendency of mixed-layer DAs to be dominated by recently dead shells may well be transformed into normal and even flat shell-age frequency distributions with burial down-core (e.g., as seen in shelly beach ridges positioned increasingly far from the active shoreline, Kowalewski et al., 1998). Such a change should shift the composition of the DA toward species having the highest preservation rates. To the extent that these rates correlate with species' original abundances in the LA and are not counter-balanced by variation in population turnover rates, the relative abundances of species will be either preserved or shifted (erroneously biased) toward rare species.

To test the reliability of historic-layer DAs explicitly we need, first, down-core tests of the shape of the shell age frequency-distribution. These tests must penetrate *below* the uppermost age-homogeneous mixed layer (as Terry, 2008, has done for small mammals in the stratigraphic records of rock-shelters). This can be expensive and logistically challenging given the thickness of some mixed layers, but is conceptually straightforward (e.g., Flessa et al., 1993; Kosnik et al., 2007). Second, we need down-core tests of how well DAs retain species composition and community structure. Down-core tests of fidelity present a considerable logistical challenge because we need to know, from independent evidence, the history of the living community (strongest test, based on long-term monitoring of living communities) or at the least need to know the regional environmental and cultural history quite well. We would otherwise have to assume that past LAs were *not* substantively different from those sampled locally today, which would in turn force us to (perhaps erroneously) conclude that all down-core changes in DA composition are taphonomic in origin.

One very encouraging implicit test of the compositional fidelity of historical molluscan DAs is that of Edgar and Samson (2004). Based on 13 replicate Pb-210-dated cores along a ~100 km stretch of the eastern Tasmanian shelf, they documented a ~50% decline in sample-size standardized richness over the last 60 years, coincident with an historically documented collapse of the scallop trawling industry, including a time-lag in

the onset of decline in the portion of the shelf where commercial operations began later. Because only living scallops had been directly monitored, the overall decline in regional diversity had been unappreciated.

MOVING FROM PROMISE TO APPLICATION

The findings of global meta-analysis suggest some protocols for incorporating LD analysis of seafloor sediments as a standard approach to recognizing whether and how local benthic communities have changed in response to human stressors.

1. Evidence of strong recent ecological change

Analysis of a global database of ~100 molluscan live-dead (LD) datasets indicates that LD mismatch in species composition can indeed be used to retrospectively recognize strong, recent shifts in ecosystems.

In applying this approach to conservation biology, two provisos are important. First, this method is not a silver bullet. About 40% of datasets from areas that were definitely subject to anthropogenic eutrophication at the time of LD sampling yield LD mismatches in species composition that are statistically indistinguishable from those observed in pristine areas (see overlap of scatterplots in Figs. 4 and 6). LD comparison is thus a conservative means of recognizing recent ecological changes, prone to false negatives rather than false positives. The approach is still valuable, however, especially given the dearth of even a decadal-scale temporal perspective on benthic communities in most regions. Moreover, it is possible that the LD analysis is correct that no significant change occurred within the scale of time averaging represented by the mixed-layer death assemblage in some AE areas, and/or that the DA record of pre-impact LAs is now buried (resides in historic layers, accessible only from sediment cores). In areas that are naturally eutrophic, biologists regularly find “no change” in response to significant input of new nutrients. DAs from embayments show the highest failure rate (e.g., AE2 datasets with high LD agreement), and these are in fact the settings most prone to having naturally high nutrient inputs, long histories of AE, and high rates of sedimentation, all of which would promote *minimal* LD mismatch in mixed-layer DAs even in the face of significant present-day AE.

Second, “recent ecological change” means change

that has occurred within the scale of time averaging—“recent” does not have a universal absolute value when working with time-averaged DAs. In coastal embayments, direct-dating of molluscan DAs indicates that most shells reflect input over the most recent few decades, with some shells dating to the past few centuries (and maximum shell ages of several millennia in some cases; Fig. 1; and see Kowalewski, 2009). Fewer open-shelf DAs have been analyzed as rigorously, but taphonomists generally suspect that scales of time averaging tend to be longer, with most shells reflecting input over the last few decades to centuries (and maximum shell ages of a few tens of thousands of years). Change in the species composition of the LA over these time scales, implied by LD mismatch, can still easily be anthropogenic (Fig. 1). However, in applying this LD approach to the ecological history of a given study area, direct dating of species that are anomalously abundant in the DA should be conducted to quantify how deeply in the past these former populations existed and thus to determine the absolute time-frame of significant ecological change.

2. Evidence of particular drivers of change and of how composition has changed

Although regions vary greatly in the human stressor(s) that are most important locally—for some lagoons it will be changes in salinity arising from modified inlets, and in others it might be toxic runoff or dredge-spoil dumping—eutrophication from urban, agricultural, and industrial nutrient loading leaves the strongest signal in the global molluscan database of live-dead studies (Kidwell, 2007, 2008). Meta-analysis also indicates that the impact of AE on molluscan communities in shallow coastal embayments is via the decline of seagrass as a habitat and an increased abundance of opportunistic species in all bottom types, whereas on open shelves the signature is a decline in the relative abundance of suspension-feeders and rise in chemosymbiotic, hypoxia-tolerant, and deposit-feeding species, at least where conditions are most severe. Commercial harvesting of benthos using heavy gear leaves a distinct signature only in gravelly habitats, which are more likely to have included disturbance-sensitive epifaunal and byssate infaunal species when in a natural state (Fig. 7). Declines in the proportional abundance and richness of these species are significant and evident even when the habitat has also been subject to

anthropogenic eutrophication. Using LD mismatch to assess possible change and identify unknown stresses is thus reasonable but will require surveying multiple habitats within a region because habitats differ in the sensitivity of their LAs to different kinds of stress, as is well known from biological studies. The basic protocol should be, for example, a bay-wide or cross-shelf sampling effort of LAs and DAs to intersect with a variety of seafloor types.

3. Seeing through multiple stressors

The finding here that bottom-trawling is secondary in importance to AE in creating LD mismatch does not contradict global meta-analyses using other kinds of data, where harvesting of animal populations is the anthropogenic factor that usually *initiates* significant marine ecosystem decline and is most important in explaining the depletion of commercial populations (e.g., Jackson et al., 2001; Myers and Worm, 2003; Lötze et al., 2006; the productivity of many fisheries is unaffected or improves with low-level AE, e.g., Caddy et al., 1995; Breitburg et al., 2009). As stressed by most workers (*ibid.*, plus Halpern et al., 2008; Orth et al., 2006; and many others), coastal ecosystems are in duress from multiple significant stressors, usually acting in rapid succession or simultaneously, and commonly having additive or even synergistic effects. By all accounts, AE has been hugely important in ecosystem deterioration, especially since World War II, even though many species had been depleted or driven to functional extinction by then in many regions (e.g., Lötze et al., 2006). Climate change has emerged more strongly in the last few decades, becoming recognizable as a force in an increasing number of regions, along with disease and introduced species, which are linked also with the rapid global transport of goods.

The emergence of AE as the most important factor in compositional changes in *molluscan* communities probably reflects several factors. First, most LD study areas are from embayments or nearshore shelf habitats, where AE is most likely to be strong in absolute terms and even point-sourced. The signature of LD mismatch created by AE is thus likely to overwhelm the signatures of other stressors, particularly if their effect was more deeply rooted historically and largely past (like now-collapsed fisheries) or indirect (via habitat disruption or trophic cascades associated with harvesting other species; e.g., Myers et al., 2007, on cascading

effects of over-harvesting of sharks on the population increases in rays and consequent declines of their molluscan prey). Second, the vast majority of molluscan species in LD datasets are bycatch rather than targets of commercial fisheries. For example, demersal fish and shrimp are the primary targets of bottom-trawling in shelf LD study areas here, and shrimp and single bivalve species are the primary targets in most of the embayments (oysters, marsh clams; see study area descriptions in Kidwell, 2007). The strength of the signal that does emerge from bottom trawling in LD mismatch, even in areas that are also subject to AE, is thus impressive. Trawling only fails to leave a signature of LD compositional mismatch in soft mud seafloors and mobile sands where the impact of BT on the community can be difficult for biologists to recognize even using the entire macrobenthos.

4. LD mismatches in richness and evenness can be large even in natural settings

Despite their impact on the relative abundances and identities of species, neither AE nor BT are effective in themselves in explaining variation in LD agreement in richness and evenness. This lack of relationship has several practical implications. First, “taxon-free” characterizations of species diversity—simple counts of species, dominance metrics, and descriptions of the shape of the species abundance-distribution—will fail to reliably detect baseline shifts. This absence of an effect on richness and evenness does not belittle the importance of the ecological change, but rather stresses that even communities modified by human activities draw on the same regional species pool as do unimpacted communities at that site. Also, in both situations—natural and impacted—temporally acute “snapshot” samples of LAs are being compared to a time-averaged DA. These LAs will thus generally tend to be less rich than local DAs regardless of environmental conditions at the time of sampling (ongoing modeling and analytic effort with A. Tomasovych). DAs are typically 50% richer than LAs even under fully natural conditions and sample-size standardization (Table 3; 3x richer using raw data), with wide variation among individual datasets, providing a large target for impacted datasets to fall inside.

Second, the insensitivity of LD mismatch in richness and evenness to AE and BT underscores the importance of bringing taxonomic and autecologic expertise to LD analysis in the service of conservation biology. It

is not the loss (or gain) of some critical number of molluscan species or the degree to which any single species dominates locally that signifies AE or BT. Instead, it is significant change(s) in *particular* species that reveals human impacts via LD mismatch.

5. Determining the composition of natural “baseline” communities as targets for restoration

Molluscan DAs show remarkably high average agreement in composition and structure to LAs in natural settings considering the range of postmortem processes that act on DAs and the natural temporal variability in LAs encompassed by time averaging over decades to centuries (Table 3; Fig. 1). This agreement is encouraging for using mixed-layer DAs to acquire a time-averaged perspective on habitat-level communities in areas where conventional live-collected samples are sparse or unavailable. The strong spatial and temporal variability that exists *among replicate samples of LAs* under natural conditions is in itself a sobering take-home for conventional benthic surveys, underscoring the need for the averaged information captured by DAs. LD agreement in mixed-layer samples from natural settings also constitutes the best current estimate—albeit a liberal, best-case one—for the ecological fidelity of DAs from *historic* layers to the time-averaged LA of those past times in that same habitat. Moving beyond the recognition of recent ecological change in an environment (points 1 thru 4 above) to being able to recognize the composition of pre-impact baseline communities, retrospectively, from Holocene sedimentary records is a current research frontier in taphonomy applied to conservation biology.

It is thus time to add LD analysis of seafloor samples to the basic protocol of biological environmental assessment. Benthic biologists already collect mixed-layer DAs as a byproduct of sampling soft-sedimentary seafloors for LAs—DAs are simply the residual debris on sieves after living animals have been picked out. Adding LD analysis would thus entail no additional sampling, only the time to pick, identify, and count the DA already on hand. Given the scarcity of relevant and especially quantitative historical data on benthic communities globally and the pressing need to assess and rank habitats and regions for conservation or restoration, time-averaged death assemblages represent an important under-exploited resource for rapid retrospec-

tive identification of the magnitude and nature of recent community change.

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REFERENCES

- AIROLDI, L., AND M.W. BECK. 2007. Loss, status and trends for coastal marine habitats of Europe. *Oceanography and Marine Biology: An Annual Review*, 45:345-405.
- BAUM, J. K., AND B. WORM. 2009. Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, 78:699-714.
- BEHRENSMEYER, A. K., S. M. KIDWELL, AND R. GASTALDO. 2000. Taphonomy and paleobiology, p. 103-147. *In* D. H. Erwin and S. L. Wing (eds.). *Deep Time: Paleobiology's Perspective*. *Paleobiology, Supplement to Vol. 26*(4).
- BEST, M. M. R. 2009. Shell taphonomy experiments across latitudes: Contrasts in net preservation, processes, and pathways. 9th North American Paleontological Convention Abstracts, Cincinnati Science Museum Scientific Contributions No. 3:220.
- BEST, M. M. R., A. MLOSZEWSKA, Z. HUANG, K. BIBEAU, M. ROUGH, AND T. BROWN. 2008. Latitudinal contrasts in the net preservation of skeletal carbonate. *Geological Society of America Abstracts with Programs*, 40(7).
- BOUCHET, P., P. LOZOUET, P. MAESTRATI, AND V. HEROS. 2002. Assessing the magnitude of species richness in tropical marine environments: Exceptionally high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society*, 75:421-436.
- BOURCIER, M. 1980. Evolution récente des peuplements macrobenthiques entre la Ciotat et les îles des Embiez (Côtes de Provence). *Processus de contamination du benthos entre bassins côtiers voisins*. *Tethys*, 9:197-206.
- BREITBURG, D. L., D. W. HONDORP, L. A. DAVIAS, AND R. J. DIAZ. 2009. Hypoxia, nitrogen, and fisheries: Integrating effects across local and global landscapes. *Annual Review of Marine Science*, 1: 329-349.
- BREWER, P. G., AND E. T. PELTZER. 2009. Limits to marine life. *Science*, 324(5925):347-348.
- CADDY, J.F., R. REFK, AND T. DO-CHI. 1995. Productivity estimates for the Mediterranean: Evidence of accelerating ecological change. *Ocean and Coastal Management*, 26:1-18.
- CHAN, F., J. A. BARTH, J. LUBCHENCO, A. KIRINCICH, H. WEEKS, W.T. PETERSON, AND B. A. MENGE. 2008. Emergence of anoxia in the California Current Large Marine Ecosystem. *Science*, 319(5865): 920.
- CHAO, A., R. L. CHAZDON, R. K. COLWELL, AND T.-J. SHEN. 2005. A new statistical approach for assessing compositional similarity based on incidence and abundance data. *Ecology Letters* 8:148-159.
- COLLIE, J. S., S. J. HALL, M. J. KAISER, AND I. R. POINER. 2000. A quantitative analysis of fishing impacts on shelf-sea benthos. *Journal of Animal Ecology*, 69:785-798.
- CRANFIELD, H. J., K. P. MICHAEL, AND I. J. DOONAN. 1999. Changes in the distribution of epifaunal reefs and oysters during 130 years of dredging for oysters in Foveaux Strait, southern New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 9:461-483.
- CUMMINS, H., E. N. POWELL, R. J. STANTON, AND G. M. STAFF. 1986a. The size frequency distribution in palaeoecology: Effects of taphonomic processes during formation of molluscan death assemblages in Texas Bays. *Palaeontology*, 29:495-518.
- CUMMINS, H., E. N. POWELL, R. J. STANTON, AND G. M. STAFF. 1986b. The rate of taphonomic loss in modern benthic habitats: How much of the potentially preservable community is preserved? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 52: 291-320.
- DAVIS, F. M. 1923. Quantitative studies on the fauna of the sea bottom. No. 1. Preliminary investigation of the Dogger Bank. Ministry of Agriculture and Fisheries, Fishery Investigations. Series II, Vol VI(2), 54 p.
- DE JUAN, S., M. DEMESTRE, AND S. THRUSH. 2009. Defining ecological indicators of trawling disturbance when everywhere that can be fished is fished: A Mediterranean case study. *Marine Policy*, 33(3):472-478.
- DIAZ, R. J., AND R. ROSENBERG. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology: An Annual Review*, 33:245-303.
- DIAZ, R. J., AND R. ROSENBERG. 2008. Spreading dead zones and consequences for marine ecosystems. *Science*, 321(5891): 926-929.
- EDGAR, G.J., AND C.R. SAMSON. 2004. Catastrophic decline in mollusk diversity in eastern Tasmania and its concurrence with shellfish fisheries. *Conservation Biology*, 18: 1579-1588.
- EKDALE, A. A. 1977. Quantitative paleoecological aspects of modern marine mollusk distribution, northeast Yucatán coast, Mexico, p. 195-207. *In* S. H. Frost, M. P. Weiss, and J. B. Saunders (eds.). *Reefs and Related Carbonates: Ecology and Sedimentology*. American Association of

- Petroleum Geologists, Studies in Geology, 4.
- FERGUSON, C. A. 2008. Nutrient pollution and the molluscan death record: Use of mollusc shells to diagnose environmental change. *Journal of Coastal Research*, 24:250-259.
- FERGUSON, C. A., AND A. I. MILLER. 2007. A sea change in Smuggler's Cove? Detection of decadal-scale compositional transitions in the subfossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 254(3-4): 418-429.
- FISCHER, A. G. 1961. Stratigraphic record of transgressing seas in light of sedimentation on Atlantic coast of New Jersey. *American Association of Petroleum Geologists Bulletin*, 45:1656-1666.
- FLESSA, K. W. 1998. Well-traveled cockles: Shell transport during the Holocene transgression of the southern North Sea. *Geology*, 26:187-190.
- FLESSA, K. W., AND M. KOWALEWSKI. 1994. Shell survival and time-averaging in nearshore and shelf environments: Estimates from the radiocarbon literature. *Lethaia*, 27:153-165.
- FLESSA, K. W., A. H. CUTLER, AND K. H. MELDAHL. 1993. Time and taphonomy: Quantitative estimates of time-averaging and stratigraphic disorder in a shallow marine habitat. *Paleobiology*, 19: 266-286.
- FÜRSICH, F. T., AND M. ABERHAN. 1990. Significance of time-averaging for paleocommunity analysis. *Lethaia*, 23:143-152.
- GRAY, J. S., AND M. ELLIOTT. 2009. *Ecology of Marine Sediments: From Science to Management* (2nd edition). Oxford University Press, Oxford, 225 p.
- GRAY, J. S., P. DAYTON, S. THRUSH, AND M. J. KAISER. 2006. On effects of trawling, benthos and sampling design. *Marine Pollution Bulletin*, 52: 840-843.
- GREEN, M. A., R. C. ALLER, AND J. Y. ALLER. 1998. Influence of carbonate dissolution on survival of shell-bearing meiobenthos in nearshore sediments. *Limnology and Oceanography*, 43: 18-28.
- GREEN, M. A., M. E. JONES, C. L. BOUDREAU, R. L. MOORE, AND B. A. WESTMAN. 2004. Dissolution mortality of juvenile bivalves in coastal marine deposits. *Limnology and Oceanography*, 49(3): 727-734.
- GREENSTEIN, B. J., A. H. CURRAN, AND J. M. PANDOLFI. 1998. Shifting ecological baselines and the demise of *Acropora cervicornis* in the western North Atlantic and Caribbean Province: A Pleistocene perspective. *Coral Reefs*, 17(3):249-261.
- HALLAM, A. 1967. The interpretation of size-frequency distributions in molluscan death assemblages. *Palaeontology*, 10:25-42.
- HALPERN, B. S., S. WALBRIDGE, K. A. SELKOE, C. V. KAPPEL, F. MICHELI, C. D'AGROSA, J. F. BRUNO, K. S. CASEY, C. EBERT, H. E. FOX, R. FUJITA, D. HEINEMANN, H. S. LENIHAN, E. M. P. MADIN, M. T. PERRY, E. R. SELIG, M. SPALDING, R. STENECK, AND R. WATSON. 2008. A global map of human impact on marine ecosystems. *Science*, 319(5865):948-952.
- HEWITT, J.E., S. F. THRUSH, J. HALLIDAY, AND L. DUFFY. 2005. The importance of small-scale habitat structure for maintaining beta diversity. *Ecology*, 86(6):1619-1626.
- HIDDINK, J. G., S. JENNINGS, AND M.J. KAISER. 2007. Assessing and predicting the relative ecological impacts of disturbance on habitats with different sensitivities. *Journal of Applied Ecology*, 44: 405-413.
- HINZ, H., V. PRIETO, AND M. J. KAISER. 2009. Trawl disturbance on benthic communities: Chronic effects and experimental predictions. *Ecological Applications*, 19: 761-773.
- JACKSON, J. B. C. 1997. Reefs since Columbus. *Coral Reefs*, Supplement to Vol. 16:23-32.
- JACKSON, J. B. C., M. X. KIRBY, W. H. BERGER, K. A. BJORN-DAL, L. W. BOTSFORD, B. J. BOURQUE, R. H. BRADBURY, R. COOKE, J. ERLANDSON, J. A. ESTES, T. P. HUGHES, S. KIDWELL, C. B. LANGE, H. S. LENIHAN, J. M. PANDOLFI, C. H. PETERSON, R. S. STENECK, M. J. TEGNER, AND R. R. WARNER. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293: 629-637.
- JOHNSON, R. G. 1965. Pelecypod death assemblages in Tomales Bay, California. *Journal of Paleontology*, 39: 80-85.
- KIDWELL, S. M. 2001. Preservation of species abundance in marine death assemblages. *Science*, 294:1091-1094.
- KIDWELL, S. M. 2002a. Time-averaged molluscan death assemblages: Palimpsests of richness, snapshots of abundance. *Geology*, 30:803-806.
- KIDWELL, S. M. 2002b. Mesh-size effects on the ecological fidelity of death assemblages: A meta-analysis of molluscan live-dead studies. *Geobios Mémoire Special*, 24:107-119.
- KIDWELL, S. M. 2005. Brachiopod versus bivalve radiocarbon ages: Implications for Phanerozoic trends in time-averaging and productivity. *Geological Society of America Abstracts with Programs*, 37(7):117.
- KIDWELL, S. M. 2007. Discordance between living and death assemblages as evidence for anthropogenic ecological change. *Proceedings of the National Academy of Sciences of the United States of America*, 104:17701-17706.
- KIDWELL, S. M. 2008. Ecological fidelity of open marine molluscan death assemblages: Effects of post-mortem transportation, shelf health, and taphonomic inertia. *Lethaia*, 41(3):199-217.
- KIDWELL, S. M., AND D. W. J. BOSENCE. 1991. Taphonomy and time-averaging of marine shelly faunas, p. 115-209. *In* P. A. Allison and D. E. G. Briggs (eds.). *Taphonomy, Releasing the Data Locked in the Fossil Record*. Plenum Press, New York.

- KIDWELL, S. M., AND D. JABLONSKI. 1983. Taphonomic feedback: Ecological consequences of shell accumulation, p. 195-248. *In* M. J. S. Tevesz and P. L. McCall (eds.), *Biotic Interactions in Recent and Fossil Benthic Communities*. Plenum Press, New York.
- KIDWELL, S. M., AND K. W. FLESSA. 1995. The quality of the fossil record: Populations, species, and communities. *Annual Review of Ecology and Systematics*, 26:269-299.
- KIDWELL, S. M., M. M. R. BEST, AND D. KAUFMAN. 2005. Taphonomic tradeoffs in tropical marine death assemblages: Differential time-averaging, shell loss, and probable bias in siliciclastic versus carbonate facies. *Geology*, 33:729-732.
- KIDWELL, S. M., AND A. TOMASOVYCH. 2009. Nobody's perfect: Assessing modern death assemblages as historical recorders using "live-live" comparisons. 9th North American Paleontological Convention Abstracts, Cincinnati Science Museum Scientific Contributions, 3:379-380.
- KIRBY, M. X. 2004. Fishing down the coast: Historical expansion and collapse of oyster fisheries along continental margins. *Proceedings of the National Academy of Sciences of the United States of America*, 101:13096-13099.
- KOSNIK, M., Q. HUA, G. JACOBSEN, D. S. KAUFMAN, AND R. A. WÜST. 2007. Sediment mixing and stratigraphic disorder revealed by the age-structure of *Tellina* shells in Great Barrier Reef sediment. *Geology*, 35: 811-814.
- KOSNIK, M. A., Q. HUA, D. S. KAUFMAN, AND R. A. WÜST. In press. Taphonomic bias and time-averaging in tropical molluscan death assemblages: Differential shell half-lives in Great Barrier Reef sediment. *Paleobiology*.
- KOWALEWSKI, M. 2009. The youngest fossil record and conservation biology: Holocene shells as eco-environmental recorders. *In* G. P. Dietl, and K. W. Flessa (eds.), *Conservation Paleobiology: Using the Past to Manage for the Future*. The Paleontological Society Papers, 15 (this volume).
- KOWALEWSKI, M., G. A. GOODFRIEND, AND K. W. FLESSA. 1998. High-resolution estimates of temporal mixing within shell beds: The evils and virtues of time-averaging. *Paleobiology*, 24:287-304.
- KRAUSE, R. A., JR., S. L. BARBOUR WOOD, M. KOWALEWSKI, D. S. KAUFMAN, C. S. ROMANEK, M. G. SIMÕES, AND J. F. WEHMILLER. In press. Quantitative estimates and modeling of time averaging in bivalve and brachiopod shell accumulations. *Paleobiology*.
- LADD, H. S., J. W. HEDGPETH, AND R. POST. 1957. Environments and facies of existing bays on the central Texas coast. *Geological Society of America Memoir*, 67:599-640.
- LÖTZE, H. K., AND B. WORM. 2009. Historical baselines for large marine animals. *Trends in Ecology and Evolution*, 24:254-262.
- LÖTZE, H. K., H. S. LENIHAN, B. J. BOURQUE, R. BRADBURY, R. G. COOKE, M. KAY, S. M. KIDWELL, M. X. KIRBY, C. H. PETERSON, AND J. B. C. JACKSON. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas worldwide. *Science*, 312:1806-1809.
- MELDAHL, K. E., K. W. FLESSA, AND A. H. CUTLER. 1997. Time-averaging and postmortem skeletal survival in benthic fossil assemblages: Quantitative comparisons among Holocene environments. *Paleobiology*, 23:207-229.
- MILLER, A. I. 1988. Spatial resolution in subfossil molluscan remains: Implications for paleobiological analyses. *Paleobiology*, 14:91-103.
- MYERS, R. A., AND B. WORM. 2003. Rapid worldwide depletion of predatory fish communities. *Nature*, 423:280-283.
- MYERS, R. A., J. K. BAUM, T. D. SHEPHERD, S. P. POWERS, AND C. H. PETERSON. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, 315:1846-1850.
- NRC (NATIONAL RESEARCH COUNCIL). 2002. *Effects of Trawling and Dredging on Seafloor Habitats*. National Academies Press, Washington, D.C., 136 p.
- NRC (NATIONAL RESEARCH COUNCIL). 2005. *The Geological Record of Ecological Dynamics*. National Academies Press, Washington, D.C., 200 p.
- OLSZEWSKI, T. A., AND S. M. KIDWELL. 2007. The preservational fidelity of evenness in molluscan death assemblages. *Paleobiology*, 33:1-23.
- ORTH, R. J., T. J. B. CARRUTHERS, W. C. DENNISON, C. M. DUARTE, J. W. FOURQUREAN, K. L. HECK, A. R. HUGHES, G. A. KENDRICK, W. J. KENWORTHY, S. OLYARNIK, F. T. SHORT, M. WAYCOTT, AND S. L. WILLIAMS. 2006. A global crisis for seagrass ecosystems. *Bioscience*, 56:987-996.
- PALACIOS, R., D. A. ARMSTRONG, AND J. ORENSANZ. 2000. Fate and legacy of an invasion: Extinct and extant populations of the soft-shell clam (*Mya arenaria*) in Grays Harbor (Washington). *Aquatic Conservation: Marine and Freshwater Ecosystems*, 10:279-303.
- PANDOLFI, J. M., R. H. BRADBURY, E. SALA, T. P. HUGHES, K. A. BJORNNDAL, R. G. COOKE, D. MACARDLE, L. MCCLENANHAN, M. J. H. NEWMAN, G. PAREDES, R. R. WARNER, AND J. B. C. JACKSON. 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science*, 301: 955-958.
- PAULY, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution*, 10:430.
- PETERSON, C. H. 1976. Relative abundance of living and dead molluscs in two California lagoons. *Lethaia*, 9:137-148.
- PETERSON, C. H. 1977. The paleoecological significance of undetected, short-term temporal variability. *Journal of*

- Paleontology, 51:976-981.
- POWERS, S. P., C. H. PETERSON, R. R. CHRISTIAN, E. SULLIVAN, M. J. POWERS, M. J. BISHOP, AND C. P. BUZZELLI. 2005. Effects of eutrophication on bottom habitat and prey resources of demersal fishes. *Marine Ecology Progress Series*, 302:233-243.
- RABALAIS, N. N., AND R. E. TURNER. 2001. Coastal Hypoxia: Consequences for Living Resources and Ecosystems. *Coastal and Estuarine Sciences*, American Geophysical Union, 463 p.
- RICK, T. C., AND J. M. ERLANDSON. 2009. Coastal exploitation. *Science*, 325:952-953.
- ROTHSCHILD, B. J., J. S. AULT, P. GOULLETQUER, AND M. HÉRAL. 1994. Decline of the Chesapeake Bay oyster population: A century of habitat destruction and overfishing. *Marine Ecology Progress Series*, 111:29-39.
- SADLER, P. M. 1993. Models of time-averaging as a maturation process: How soon do sedimentary sections escape reworking?, p. 169-187. *In* S. M. Kidwell and A. K. Behrensmeier (eds.), *Taphonomic Approaches to Time Resolution in Fossil Assemblages*, Short Course in Paleontology, 6.
- SMITH, S. D. A. 2008. Interpreting molluscan death assemblages on rocky shores: Are they representative of the regional fauna? *Journal of Experimental Marine Biology and Ecology*, 366:151-159.
- STAFF, G. M., AND E. N. POWELL. 1999. Onshore-offshore trends in community structural attributes: Death assemblages from the shallow continental shelf of Texas. *Continental Shelf Research*, 19:717-756.
- STAFF, G. M., R. J. STANTON, JR., E. N. POWELL, AND H. CUMMINS. 1986. Time averaging, taphonomy and their impact on paleocommunity reconstruction: Death assemblages in Texas bays. *Geological Society of America Bulletin*, 97:428-443.
- TERRY, R. C. 2008. The scale and dynamics of time-averaging quantified through AMS ¹⁴C dating of kangaroo rat bones. *Geological Society of America, Abstracts with Programs*, 40(7).
- THRUSH, S. F., J. E. HEWITT, V. J. CUMMINGS, P. K. DAYTON, M. CRYER, S. J. TURNER, G. A. FUNNELL, R. G. BUDD, C. J. MILBURN, AND M. R. WILKINSON. 1998. Disturbance of the marine benthic habitat by commercial fishing: Impacts at the scale of the fishery. *Ecological Applications*, 8:866-879.
- TILLIN, H. M., J. G. HIDDINK, S. JENNINGS, AND M. J. KAISER. 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Marine Ecology-Progress Series*, 318:31-45.
- TOMASOVYCH, A. 2004. Postmortem durability and population dynamics affecting the fidelity of brachiopod size-frequency distributions. *Palaaios*, 19:477-496.
- TOMASOVYCH, A., AND S. M. KIDWELL. 2009a. Preservation of spatial and environmental gradients by death assemblages. *Paleobiology*, 35:119-145.
- TOMASOVYCH, A., AND S. M. KIDWELL. 2009b. Fidelity of variation in species composition and diversity partitioning by death assemblages: Time-averaging transfers diversity from beta to alpha levels. *Paleobiology*, 35:97-121.
- TOMASOVYCH, A., AND S. M. KIDWELL. 2009c. Discriminating effects of natural and sampling variation from effects of postmortem variation on compositional fidelity of death assemblages. 9th North American Paleontological Convention Abstracts, Cincinnati Science Museum Scientific Contributions, 3:155-156.
- TWILLEY, R. R., W. M. KEMP, K. W. STAVER, J. C. STEVENSON, AND W. R. BOYNTON. 1985. Nutrient enrichment of estuarine submersed vascular plant communities. 1. Algal growth and effects on production of plants and associated communities. *Marine Ecology-Progress Series*, 23:179-191.
- WARME, J. E. 1971. Paleocological aspects of a modern coastal lagoon. *University of California Publications in Geological Sciences*, 87:1-110.
- WARWICK, R.M., AND J. LIGHT. 2002. Death assemblages of molluscs on St. Martin's Flats, Isles of Scilly: A surrogate for regional biodiversity? *Biodiversity and Conservation*, 11: 99-112.
- WHITE, E. P., P. B. ADLER, W. K. LAUENROTH, R. A. GILL, D. GREENBERG, D. M. KAUFMAN, A. RASSWEILER, J. A. RUSAK, M. D. SMITH, J. R. STEINBECK, R. B. WAIDE, AND J. YAO. 2006. A comparison of the species-time relationship across ecosystems and taxonomic groups. *Oikos*, 112:185-195.
- WORM, B., E. B. BARBIER, N. BEAUMONT, J. E. DUFFY, C. FOLKE, B. S. HALPERN, J. B. C. JACKSON, H. K. LOTZE, F. MICHELI, S. R. PALUMBI, E. SALA, K. A. SELKOE, J. J. STACHOWICZ, AND R. WATSON. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science*, 314:787-790.

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