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Molluscan live–dead agreement in anthropogenically stressed seagrass habitats: Siliciclastic versus carbonate environments

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Molluscan live–dead fidelity studies investigate the influences of anthropogenic activities on marine ecosystems by comparing the taxonomic composition of a living community to its corresponding death assemblage. Environments subjected to intense anthropogenic stresses tend to yield low fidelity (high discordance) in rank-order abundance and taxonomic similarity between living and dead assemblages. This project assesses the sensitivity of the live–dead approach by applying various fidelity metrics – community richness (Delta-S), evenness (Delta-PIE), rank-order correlation (Spearman rho), and taxonomic similarity (Jaccard–Chao) – to molluscan assemblages in seagrass habitats exposed to anthropogenic stresses in different sedimentary environments. Our study sites include siliciclastic sites in North Carolina, carbonate sites in Florida Bay, and a siliciclastic–carbonate transition locality along the coast of southern Florida. The dominant forms of human stresses at these seagrass sites consist of increased freshwater runoff, increased nutrient runoff, and physical substrate disturbance by dredging (North Carolina) and propeller scarring (Florida Bay). As a result of such anthropogenic stresses, we expected to find low live–dead fidelity results at all of our study sites. We also anticipated variations in the results between sedimentary environments, reflecting intrinsic differences in how molluscan material accumulates and is preserved in siliciclastic versus carbonate settings. Using bulk sediment samples, fidelity analyses consistently yield greater live–dead disagreement at the

siliciclastic sites. Despite well-documented historical human stresses to Florida Bay and sediment cores indicating multiple ecological shifts in response to human impacts over time, results from carbonate localities yield higher fidelity and provide little evidence for ecological change. We argue that greater time averaging allows for the death assemblages at the siliciclastic sites to retain a longer memory of the local communities, thus preserving evidence of local ecological changes. In contrast, less time averaging and more rapid live–dead equilibration in carbonate sediments reduces the signal of community changes. Thus we propose that the live–dead fidelity approach is more sensitive at detecting recent ecological changes in siliciclastic versus carbonate environments, confirming the conservative nature of the approach and demonstrating the role of taphonomic bias in live–dead methodology.

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1. Introduction

Globally and historically, human settlement in coastal regions has led to centuries of overexploitation, habitat alteration, species invasions, pollution and eutrophication of coastal environments [\(Lötze et al.,](#page--1-0) [2006; Halpern et al., 2008, 2012; Waycott et al., 2009\)](#page--1-0). Over time the cumulative effects of these actions have had the most impact on densely populated coastal environments, transforming ecosystem dynamics and degrading local biodiversity ([Jackson et al., 2001; Lötze et al., 2006; Orth](#page--1-0) [et al., 2006\)](#page--1-0). Therefore, the assessment of human modifications to marine environments is essential for informing effective mitigation, conservation, and restoration efforts. However a primary challenge

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for biological conservation is recognizing what represents a preanthropogenic ecosystem.

Live–dead fidelity research, in which fidelity refers to the similarity of life and death assemblages, has been used for decades to detect post-mortem bias ([Kidwell, 2013\)](#page--1-0). More recently, live–dead research has been applied to determine the impact of anthropogenic perturbations to environments by assessing whether community composition and structure (richness, evenness, rank-order abundance of species, taxonomic composition) have changed over time ([Kidwell, 2007\)](#page--1-0). Death assemblages may preserve a record of the ecosystem prior to the onset of local anthropogenic pressures [\(Kidwell, 2013](#page--1-0)), whereas the life assemblage will represent a snapshot of the modern ecology and current environmental conditions. "Pristine" environments experiencing relatively little to no anthropogenic stresses maintain high fidelity between the living and death assemblages ([Kidwell, 2001, 2007, 2008, 2009](#page--1-0)). In contrast, localities that suffer from anthropogenic stresses on average

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yield significantly lower fidelity, presumably because the composition of the death assemblage lags behind any changes in the living community — a process known as taphonomic inertia ([Kidwell, 2008\)](#page--1-0). Where lower fidelity exists, the life assemblage suggests a shift in molluscan community composition in response to some environmental modification, and the death assemblage may be interpreted to reflect the community state prior to the onset of anthropogenic stressors and used to establish an ecologic baseline ([Kidwell, 2007, 2009, 2013](#page--1-0)). From this baseline, the molluscan community composition and structure preceding anthropogenic impacts can be interpreted, thus providing implications for mitigation and restoration.

Previous studies suggest that the live–dead fidelity approach is conservative in that not all cases of anthropogenic stress result in low fidelity ([Kidwell, 2013](#page--1-0)). In some instances taphonomic inertia may be overcome, yielding high fidelity as an artifact of long-established environmental change and biologic responses [\(Kidwell, 2007, 2009, 2013\)](#page--1-0). High fidelity may also result if anthropogenic stresses are relatively mild, intermittent, or spatially diffuse, producing ecological changes that are not beyond the natural range of variability of the pre-stress community [\(Kidwell, 2013](#page--1-0)); in such cases, the life assemblage does not change appreciably from the pre-stress death assemblage. Ecological and taphonomic factors can also influence live–dead data. Rapid sedimentation may bury the pre-stress death assemblage below the sampling level, producing high fidelity between a more recent death assemblage and the living community ([Kidwell, 2013](#page--1-0)). Minimal sedimentation may lead to greater exposure of dead material on the sea floor and increase the chances for postmortem transport, although several studies conclude that out-of-habitat postmortem transportation is not a significant concern for most shallow marine environments ([Miller](#page--1-0) [et al., 1992;](#page--1-0) [Best, 2008; Kidwell, 2008\)](#page--1-0). Greater exposure of dead material on the sea floor also may reduce shell preservation potential due to taphonomic processes (e.g. bioeroders, encrusters); the composition of molluscan living and dead assemblages then may diverge due to differential preservation of species based on shell mineralogy, size, and life mode ([Best et al., 2007\)](#page--1-0). Varying reproductive rates of species and random colonization and mortality events may also affect live– dead fidelity ([Kidwell, 2009, 2013](#page--1-0)).

In order to investigate the variables influencing live–dead fidelity, in this study we examine how fidelity is captured in different sedimentary environments. Although previous live–dead meta-analyses have differentiated sites by habitat (marsh, intertidal, coastal embayment, open shelf) and grain size (muddy versus sandy substrate), these studies have found that the effects of grain size vary and depend upon the metrics and datasets tested [\(Kidwell, 2001, 2002, 2008; Olszewski and](#page--1-0) [Kidwell, 2007\)](#page--1-0). To further examine the effect of sedimentological differences and various anthropogenic stresses on live–dead fidelity within a habitat, we assessed the sensitivity of the live–dead approach by sampling nearshore seagrass environments located in both siliciclastic and carbonate settings subjected to different human activities. Applying several fidelity metrics, we analyzed how molluscan communities respond to different modes of habitat modification in seagrass habitats and how the responses compare in different sedimentary environments. Following the results of [Kidwell \(2007\)](#page--1-0), we hypothesized that overall our study sites would yield low rank-order and taxonomic fidelity as a result of anthropogenic modifications to the environments and consequent ecological responses. Moreover, we expected fidelity results to vary among the types of impacts as well as between sedimentary environments, reflecting intrinsic consequences relating to specific forms of stress and of the sedimentary conditions [\(Best et al., 2007\)](#page--1-0).

2. Study areas

Marine molluscan communities were sampled and evaluated at three seagrass sites in both siliciclastic (North Carolina) and carbonate (northeastern Florida Bay) environments (Fig. 1). Additionally, a seagrass habitat located near the transition between siliciclastic and carbonate zones was sampled (near Miami, FL). The sites were selected based upon evidence of anthropogenic stresses observed or inferred from local experts, property owners, published literature, and time series photographs from [Google Earth \(2012\)](#page--1-0) which are available for the last 20 years (1993–2013). Each site is designated by the dominant form of stress occurring. The three sites within each sedimentary environment include a seagrass bed subjected to: 1) freshwater runoff increased beyond that expected under natural conditions, 2) nutrient and terrestrial runoff, and 3) physical substrate disturbance by boat traffic, propeller scarring and/or channel dredging.

2.1. Intertidal siliciclastic, North Carolina

The siliciclastic sites consist of Bogue Sound, Oyster Creek, and Chadwick Bay (Fig. 1B). Bogue Sound (BS) is delineated as a freshwater runoff site, initially based upon observations by local property owners who have witnessed substantial deforestation and development of the coastline surrounding their property over the last forty years. Coinciding with the increase in nearby impervious surfaces (housing developments with multiple tennis courts and paved roads and driveways adjacent to the shore), the property owners have observed an unprecedented increase in the abundance of freshwater-tolerant vegetation along their shoreline. Google Earth images confirm significant land clearance and construction of impervious surfaces particularly over the last 15 years, supporting the potential for an anthropogenic increase in freshwater runoff in the area.

Located within an embayment surrounded by predominantly agricultural land, the Oyster Creek (OC) locality is deemed a nutrient and

Fig. 1. A) Locations of study sites along the southeastern coast of the United States. B) Siliciclastic sites, North Carolina: Chadwick Bay, CB; Bogue Sound, BS; Oyster Creek, OC. C) Carbonate sites, Florida: Bay Cove 1, BC1; Bay Cove 2, BC2; Blackwater, BW. Siliciclastic–carbonate transition site: Matheson Hammock, MH.

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