

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



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## ABSTRACT

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., 2006; Halpern et al., 2008, 2012; Waycott et al., 2009). 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 et al., 2006). Therefore, the assessment of human modifications to marine environments is essential for informing effective mitigation, conservation, and restoration efforts. However a primary challenge

for biological conservation is recognizing what represents a pre-anthropogenic 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). 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). Death assemblages may preserve a record of the ecosystem prior to the onset of local anthropogenic pressures (Kidwell, 2013), 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). 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). 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). 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). 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). 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); 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). 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 et al., 1992; Best, 2008; Kidwell, 2008). 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). Varying reproductive rates of species and random colonization and mortality events may also affect live–dead fidelity (Kidwell, 2009, 2013).

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 Kidwell, 2007). 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), 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).

## 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) 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

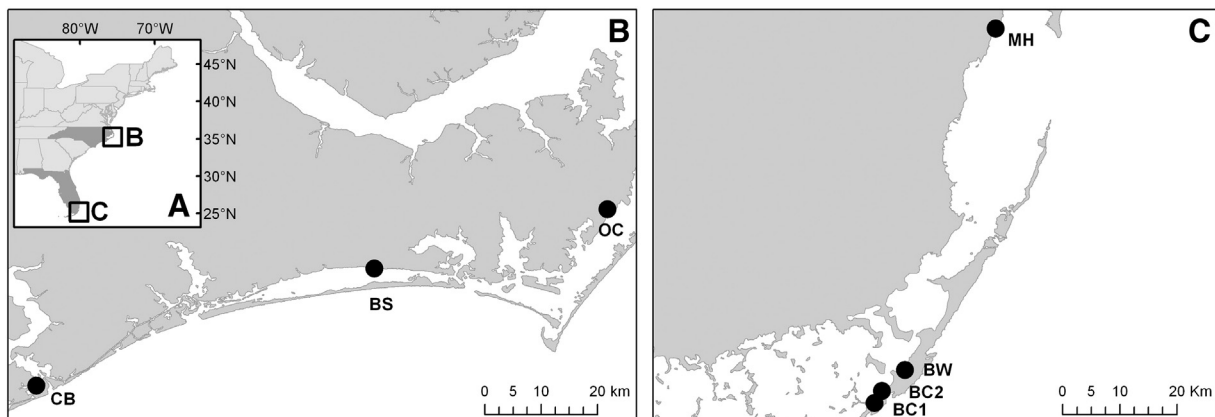


Fig. 1. A) Locations of study sites along the southeastern coast of the United States. B) Siliciclastic sites, North Carolina: Chadwick Bay, CB; Bogue Sound, BS; Oyster Creek, OC. C) Carbonate sites, Florida: Bay Cove 1, BC1; Bay Cove 2, BC2; Blackwater, BW. Siliciclastic–carbonate transition site: Matheson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

terrestrial runoff site due to the high potential of nutrient and sediment input from local land use. Whereas Google Earth images reveal increasing agricultural use of the region over the last two decades, historical maps indicate that farming and land modification and clearance have occurred in the vicinity of Oyster Creek since the mid-1800s (North Carolina Maps). Inland irrigation canals have also traversed the modern agricultural area since at least 1935 (North Carolina Maps).

Chadwick Bay (CB) represents a seagrass habitat subjected to physical substrate disturbance by periodic dredging of the adjacent Atlantic Intracoastal Waterway (AICW), a 1200-mile natural and manmade channel running from Virginia to the Florida Keys used for commercial and recreational purposes (Pickel, 2011). The construction and usage of the AICW through Chadwick Bay began around 1917, facilitating frequent and year-round boat traffic (Lewis, 2011; Pickel, 2011). To prevent shoaling, the channel (which is located <0.1 mi from our study site) is dredged every few years by the US Army Corps of Engineers, resulting in likely increased turbidity, substrate instability, and incidental burial of nearby benthic assemblages (Lewis, 2011; Pickel, 2011). Google Earth images show minor variations of the AICW channel width and morphology over the last 20 years.

All of these siliciclastic seagrass localities are intertidal and are exposed at low tide. The sediment at all of these sites contains subangular, fine quartz sand. The seagrass species that we observed at the North Carolina localities primarily include *Halodule wrightii* and *Zostera marina* with some appearances of *Ruppia maritima*.

## 2.2. Subtidal carbonate, Florida

Within Florida Bay, the carbonate localities comprise Blackwater Sound, Bay Cove 1, and Bay Cove 2 (Fig. 1C). Blackwater Sound (BW) is designated as a freshwater runoff site due to its position next to a nearly entirely impervious shoreline: a large clubhouse associated with a marina runs parallel to the shore and is surrounded by pavement that extends to the edge of the water. According to Google Earth imagery, this highly developed and impervious coastline has changed very little (minor infrastructure changes) in the last 20 years; thus anthropogenic increase in freshwater runoff at the site has likely occurred for at least that long. Bay Cove 1 (BC1) is interpreted as a nutrient and sediment runoff site because at the time of sampling the adjacent coastline was deforested, the soil exposed, and construction was taking place along the shore. Google Earth images reveal that this is a relatively recent change of the landscape, which was forested until 2008 when it was cleared and left with the soil exposed up to the time of sampling in 2012. Bay Cove 2 (BC2) is deemed a physical substrate disturbance locality due to the presence of numerous propeller scar paths across the site. Created when boat propellers physically disturb and uproot seagrass, the propeller scar paths at BC2 provide direct evidence of localized physical disturbance. Google Earth images indicate that the number of scar paths have increased over the last 20 years.

Tide is negligible in Florida Bay, so all three sites are consistently submerged. The sediment is primarily a fine carbonate mud at each of the localities; coarser material (pebbles and gravel) is common at BW and BC1. We observed *Thalassia testudinum* to be the dominant seagrass species at all sites, with lesser contributions of *Syringodium filiforme* and *Halodule wrightii*.

## 2.3. Subtidal siliciclastic-carbonate transition, Florida

Located south of Miami at Coral Gables, FL, the transition locality (Matheson Hammock, MH) is classified as a freshwater runoff site (Fig. 1C). Directly onshore of our study site is a large paved parking lot that runs parallel to the coastline and comes within 1 m of the edge of the water. Google Earth images show that this impervious surface has been in place at MH since at least 1994, suggesting the potential for consistently higher than natural freshwater runoff at this site during the last two decades.

Like the Florida Bay localities, MH is subtidal and primarily characterized by *Thalassia testudinum*. The sediment at the transition locality is composed primarily of subangular, poorly sorted quartz sand with ~15% of fine carbonate sediments.

## 3. Methods

### 3.1. Field methods

At all study sites, sediment samples containing both living and dead bivalves and gastropods were collected at 10-m intervals along three 30-m transects for a total of 12 collecting holes per site. Collection techniques differed between the North Carolina (siliciclastic) and Florida (carbonate and transition) sites due to differences in tidal ranges, water depth, and amount of sediment present. In North Carolina, the siliciclastic bulk samples were collected at low tide using a shovel and a custom-built coring tool – a 75-cm tall, 30-cm diameter PVC pipe with handles and a serrated bottom edge – to stabilize the sides of collection holes. Bulk sediment samples were removed from within the coring device in 20-cm depth intervals: 0–20 cm and 20–40 cm. All bulk samples were sieved using 5 mm mesh, which is generally the coarsest mesh size used for such molluscan studies.

Similar methods were intended to be used in Florida with the substitution of an airlift device to extract and sieve shell material from the same depths in the substrate (0–20 cm and 20–40 cm). However, upon preliminary investigation of the nearshore Florida Bay localities, we discovered that there is a relatively thin sediment veneer (ranging from <5 cm to ~15 cm) over the limestone bedrock. Because sediment samples could not be collected consistently from 0 to 20 cm, an alternative approach was devised. In order to gather enough live and dead shell material to conduct statistical analyses, the airlift was used to collect shells and sediment from three “holes” at each 10-m interval along three 30-m transects for a total of 12 samples per site. A “hole” was defined by placing the coring device on/in the substrate and using the airlift to extract whatever sediment was present on top of the bedrock within the coring device. For consistency, the period of airlifting in each “hole” at all sites was limited to 30 s. The same methods used in Florida Bay were employed at the transition zone site near Miami, FL. All the samples collected in Florida were sieved using a 5 mm mesh.

### 3.2. Laboratory methods

In the laboratory, bivalve and gastropod specimens were identified to the species level if possible (Abbott and Sandström, 1996; Mikkelsen and Bieler, 2008; The Bailey Matthews Shell Museum, 2011). Living (i.e. alive at the time of collection) and dead specimens were also distinguished. A specimen was defined as a single bivalve valve with the beak preserved or a gastropod with an intact apex. An individual represents a complete organism, e.g. a bivalve individual = two valves; the number of live bivalve specimens was calculated by multiplying the total number of live individuals by two. Total specimen counts per site were calculated by pooling data from all transects within a site.

### 3.3. Data analyses

We used a variety of statistical analyses to compare the living and dead molluscan assemblages within and between sites, sedimentary environments, and types of anthropogenic stress. Analyses were completed for the total molluscan assemblage as well as separately for each molluscan class (bivalves and gastropods).

#### 3.3.1. Richness

Because changes in community richness may coincide with environmental changes and/or suggest the magnitude of time averaging (Kidwell, 2009), rarefaction curves were generated using Holland's

**Analytical Rarefaction 1.3.** (2013) in order to compare richness of samples differing in size. Using sample-size standardized richness values from rarefaction, the ratio of the death assemblage richness to the life assemblage richness (Delta-S) was calculated for each locality to determine live–dead fidelity in terms of richness (Olszewski and Kidwell, 2007; Kidwell, 2009). Delta-S equals 1 when the richness of the living and death assemblages are the same, <1 when the death assemblage is less rich than the living assemblage, and >1 when the death assemblage is richer than the living.

### 3.3.2. Evenness

If environmental stress escalates, fewer taxa may be able to tolerate the conditions, potentially leading to a change in community evenness. Taxonomic evenness was calculated in PAST for each assemblage, and live–dead agreement in evenness was measured for each locality by subtracting the life assemblage evenness from the death assemblage evenness (delta-PIE; Olszewski and Kidwell, 2007; Kidwell, 2009). Delta-PIE values are positive when the death assemblage is more even than the living assemblage and negative when the death assemblage is less even. A delta-PIE value of zero arises when the death and living assemblages are equally even (Kidwell, 2009).

### 3.3.3. Rank-order correlation

Changes in relative abundances of particular taxa can be early indications of environmental change (Kidwell, 2007). Thus, we used the Spearman rank-order correlation analysis (Sokal and Rohlf, 1995) to compare the fidelity of rank-order abundances between assemblages and among sites. Spearman's correlation coefficient ( $\rho$ ) can range from  $-1$  to  $1$ , with positive values indicating similar ranking of species abundances and negative values indicating reverse rankings between assemblages. Spearman analysis is most sensitive to fairly large shifts in rank (i.e. from a high ranking to a middle or bottom rank), rather than minor shuffling of ranks (Kidwell, 2009). Spearman rank correlation was completed using the number of individuals per taxon at [www.wessa.net/rankcorr.wasp](http://www.wessa.net/rankcorr.wasp).

### 3.3.4. Taxonomic similarity

Changes in environmental conditions may lead to local extirpations and immigrations depending on the preferences and tolerances of specific species (Kidwell, 2009). The Jaccard–Chao index of taxonomic similarity measures the agreement of living and dead assemblages by dividing the number of taxa shared by both the living community and death assemblage by the total number of taxa observed in both assemblages (Chao et al., 2005; Kidwell, 2007). To calculate the Jaccard–Chao similarity index, raw abundance specimen data were uploaded to EstimateS 9.0.0. Jaccard–Chao results can range from 0 to 1, where 0 represents no shared taxa between the assemblages being compared and 1 indicates that 100% of the taxa in both assemblages are found in the other (Chao et al., 2005).

By plotting Jaccard–Chao against Spearman rho values in a scatter plot, fidelity can be further assessed (Kidwell, 2007). The greater the taxonomic similarity and rank-order agreement of living and dead assemblages, the higher a site plots in the upper right quadrant of the scatter plot. In a meta-analysis of ~100 live–dead datasets, Kidwell (2007) found that low stress sites (“pristine”) yield high live–dead agreement and plot within the upper right quadrant of scatter plots. In contrast, high-stressed areas tended to yield low live–dead agreement with Jaccard–Chao values <0.05 and low Spearman rho values.

### 3.3.5. Multidimensional scaling

In order to view the gradients in taxonomic composition between samples, global non-parametric multidimensional scaling (MDS) was created in Primer 6.1.5. The MDS creates an ordination of the ranks of the distances between samples in  $n$  dimensions, with the number of dimensions accounting for and satisfying all comparisons and conditions from a Bray–Curtis dissimilarity matrix (Clarke and Warwick, 2001).

To account for differences in sample sizes, the data to be used in the Bray–Curtis dissimilarity matrix were first standardized by dividing the number of specimens of a taxon at a site by the total number of specimens for that taxon among all the sites. Using the standardized data, a Bray–Curtis dissimilarity matrix was produced by comparing each sample (each study site) to every other sample to determine their similarity to one another. The significance of sample similarities illustrated by MDS was tested using ANOSIM (the analysis of similarities), a nonparametric analysis also derived from the Bray–Curtis dissimilarity matrix and conducted in Primer 6.1.5.

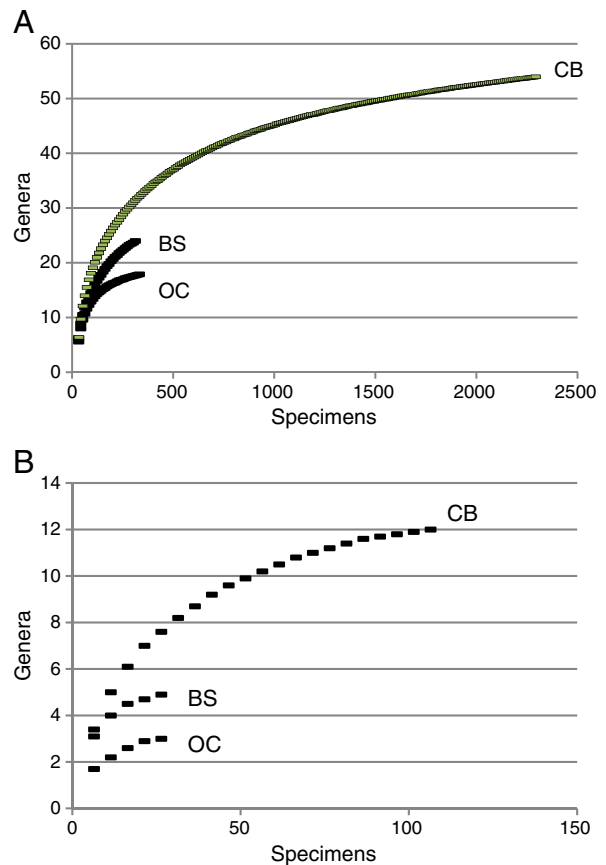
## 4. Results

Results are reported only for the total assemblages (bivalves and gastropods pooled per site), except when patterns are different for analyses of bivalves and gastropods separately.

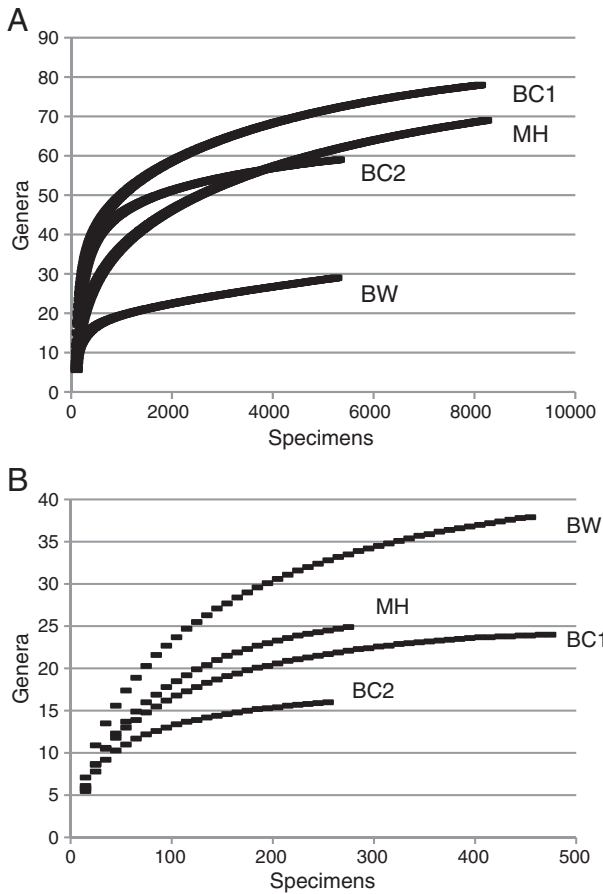
### 4.1. Richness and rarefaction

The total death assemblages are enriched compared to their corresponding total living assemblages at all sites except Blackwater (BW) (Figs. 2, 3). Delta-S values also indicate that the death assemblages at the siliciclastic sites are more highly enriched than are the death assemblages at the carbonate and transition sites (Table 1).

Among the siliciclastic sites, Chadwick Bay (CB, physical disturbance) contains the greatest abundance and diversity (number of genera) of dead and living assemblages (Fig. 2), whereas Oyster Creek (OC, nutrient runoff) has the lowest abundance and diversity of both assemblages. Among carbonate sites, Bay Cove 1 (BC1, nutrient runoff) contains the greatest dead diversity and abundance but the lowest diversity of living



**Fig. 2.** Rarefaction curves for the siliciclastic total A) dead and B) living assemblages in which bivalves and gastropods are pooled per site. Abbreviations for sites as in Fig. 1.



**Fig. 3.** Rarefaction curves for the carbonate and transition total A) death and B) living assemblages in which bivalves and gastropod are pooled per site. Abbreviations for sites as in Fig. 1.

individuals (Fig. 3). In contrast, Blackwater (freshwater runoff) has the least diverse and abundant death assemblage but the most diverse living assemblage. When carbonate bivalves and gastropods are analyzed separately, the gastropod data vary slightly from the total assemblage and

bivalve assemblage trends. Specifically, BW contains the greatest richness of dead and living gastropods (yet the lowest abundance among gastropod death assemblages), whereas BC2 yields the lowest diversity of dead and living gastropods as well as the lowest abundance of living gastropods. In comparison to the carbonate sites, the transition locality Matheson Hammock (MH, freshwater runoff) contains a highly diverse and abundant death assemblage, similar to BC1 (Fig. 3). However, the living assemblage at MH is less diverse and abundant than at any of the carbonate sites.

4.2. Evenness

At all localities the living assemblages are more even than the death assemblages (Table 1). Delta-PIE values reveal that evenness is slightly more similar between the living and dead assemblages at the carbonate localities than those at the siliciclastic sites. The transition locality reveals the lowest live–dead fidelity in terms of evenness.

4.3. Spearman rank-order correlation

Rank-order abundances are positively and significantly correlated for total, bivalve and gastropod assemblages within each site, with very few exceptions (Table 2). Total assemblage live–dead Spearman rho values at siliciclastic sites range from 0.28 to 0.4288 (Table 2A). Rank-order fidelity is highest for the total assemblage at BS (freshwater) and lowest at CB (disturbance). When analyzed separately, rank-order fidelity is highest for bivalves at CB and gastropods at BS, whereas bivalve fidelity is lowest at BS and OC (nutrient runoff) and gastropod fidelity is lowest at CB.

Among carbonate sites, total assemblage Spearman rho values are consistently positive and range from 0.4555 to 0.6908 (Table 2B). BC1 (nutrient runoff) yields the greatest rank-order fidelity for the total assemblages, whereas BC2 (disturbance) yields the lowest rank-order fidelity. When molluscan classes are analyzed separately, BC1 yields the highest bivalve rank-order fidelity and BC2 the highest gastropod rank-order fidelity, whereas BC2 is the lowest for bivalves and BW (freshwater runoff) the lowest for gastropods. MH shows positive, significant live–dead rank-order fidelity for the pooled, bivalve, and gastropod assemblages (Table 2C).

The disturbance sites (total assemblages) yield the lowest rank-order fidelities in both siliciclastic and carbonate environments (rho values of

**Table 1**

Live–dead fidelity of richness (Delta-S) and evenness (Delta-PIE) for the total, bivalve, and gastropod assemblages at each site per sedimentary environment: A) siliciclastic, B) carbonate, and C) transition. Abbreviations for sites as in Fig. 1.

Live–dead fidelity of richness (Delta-S) and evenness (Delta-PIE)						
Sedimentary environment	Stress	Locality	Assemblage	Delta-S	Delta-PIE	
A	Siliciclastic	Freshwater	BS	Total	1.4122	–0.3336
			Bivalves	2.3223	–0.4884	
			Gastropods	1.4243	–0.1919	
	Nutrient runoff	OC	Total	1.9545	–0.0832	
			Bivalves	1.8012	–0.3163	
			Gastropods	Undetermined	–0.292	
	Disturbance (dredging)	CB	Total	1.2286	–0.2754	
			Bivalves	1.3181	–0.2444	
			Gastropods	1.3949	–0.2376	
B	Carbonate	Freshwater	BW	Total	0.7828	–0.2129
			Bivalves	1.0906	–0.3603	
			Gastropods	1	–0.6013	
	Nutrient runoff	BC1	Total	1.1862	–0.1719	
			Bivalves	1.3243	–0.3895	
			Gastropods	1.091	–0.4271	
	Disturbance (propeller scarring)	BC2	Total	1.1053	–0.1315	
			Bivalves	1.2341	–0.1635	
			Gastropods	0.8418	–0.55	
C	Transition	Freshwater	MH	Total	0.918	–0.45
			Bivalves	1.2405	–0.3858	
			Gastropods	0.8937	–0.5182	

**Table 2**  
Live–dead fidelity of rank-order abundance (Spearman's rho) and taxonomic similarity (Jaccard–Chao) for total, bivalve, and gastropod assemblages at each site per sedimentary environment: A) siliciclastic, B) carbonate, and C) transition. Abbreviations for sites as in Fig. 1. \* denotes that rho is statistically significant at  $p < 0.05$ .

Live–dead fidelity of rank-abundance (Spearman's rho) and taxonomic similarity (Jaccard–Chao)						
Sedimentary environment	Stress	Locality	Assemblage	Spearman rho	Jaccard–Chao	
A	Siliciclastic	Freshwater	BS	Total	0.4288*	0.558
				Bivalves	0.2266*	0.5
				Gastropods	0.7953*	0.561
		Nutrient runoff	OC	Total	0.3492*	0.368
				Bivalves	0.2262*	0.042
				Gastropods	0.5791*	0.472
		Disturbance (dredging)	CB	Total	0.2800*	0.451
				Bivalves	0.3775*	0.453
				Gastropods	0.1757	0.618
B	Carbonate	Freshwater	BW	Total	0.5652*	0.565
				Bivalves	0.7147*	0.917
				Gastropods	0.4101*	0.706
		Nutrient runoff	BC1	Total	0.6908*	0.857
				Bivalves	0.7211*	0.872
				Gastropods	0.6272*	0.834
		Disturbance (propeller scarring)	BC2	Total	0.4555*	0.626
				Bivalves	0.2485	0.655
				Gastropods	0.6886*	0.689
C	Transition	Freshwater	MH	Total	0.4923*	0.286
				Bivalves	0.4888*	0.627
				Gastropods	0.4914*	0.923

0.28 and 0.4555, respectively). Overall, siliciclastic environments yield lower rho values (average of ~0.35) than the carbonate sites (average of ~0.57). The transition site yields an intermediate rho value of 0.49.

Dead–dead and live–live rank-order agreement were also determined for all assemblages at every site (Table 3). In both siliciclastic and carbonate environments, dead–dead rank-order fidelity between sites within each environment is high and significant for all total assemblage comparisons (Table 3A). Within each sedimentary environment, comparisons between freshwater and nutrient runoff sites yield the highest dead–dead correlations, and freshwater–disturbance comparisons yield the lowest correlations. Live–live rank-order correlations between siliciclastic sites are primarily negative and nonsignificant, whereas live–live rank-order correlations between carbonate sites are all positive and mostly significant (Table 3B). The greatest significant carbonate live–live rank-order correlation is between the nutrient runoff and disturbance sites.

Spearman analyses for dead–dead and live–live agreement between siliciclastic and carbonate sites consistently yield negative rank-order correlations, few of which are statistically significant. Dead–dead analyses between MH and siliciclastic sites yield negative correlations, whereas death assemblages at MH and carbonate sites are significantly and

positively correlated for total and gastropod assemblages. All live–live analyses between MH and siliciclastic and carbonate sites are negative.

#### 4.4. Taxonomic similarity

The cross-plots in Fig. 4 illustrate the variation in live–dead agreement as a function of the Jaccard–Chao index of similarity (Table 2) and rank-order abundance of taxa (Spearman rho). Analyses of the total assemblages reveal that carbonate sites yield greater taxonomic similarity and slightly greater rank-order fidelity than the siliciclastic and transition sites (Fig. 4A). Due to low taxonomic similarity, two siliciclastic sites (CB and OC) and the transition site (MH) plot outside the “pristine” upper right quadrant. When bivalve and gastropod assemblages are analyzed separately, the siliciclastic bivalve assemblages exhibit greater live–dead taxonomic difference than do the siliciclastic gastropod assemblages (Fig. 4B, C). In contrast, the carbonate total, bivalve, and gastropod assemblages show little difference in live–dead taxonomic agreement and rank-order correlations, consistently plotting in the upper right quadrant (Fig. 4A, B, C). Although rho values vary little among the total, bivalve, and gastropod assemblages at the transition site, taxonomic agreement differs considerably among these three assemblages at MH (Fig. 4A, B, C).

**Table 3**  
A) Dead–dead and B) live–live fidelity of rank-order abundance (Spearman's rho) for total, bivalve, and gastropod assemblages within siliciclastic and carbonate environments. Types of anthropogenic stress include: F = freshwater runoff, N = nutrient runoff, D = physical substrate disturbance. Abbreviations for sites as in Fig. 1. \* denotes that rho is statistically significant at  $p < 0.05$ .

Sedimentary environment	Stress	Localities	Total assemblage	Bivalves only	Gastropods only			
A	Siliciclastic	Dead–dead fidelity of rank-abundance (Spearman's rho) between sites						
		F–N	BS–OC	0.6962*	0.7236*	0.6402*		
		F–D	BS–CB	0.3212*	0.4633*	0.0678		
		N–D	OC–CB	0.4438*	0.5093*	0.2294		
		F–N	BW–BC1	0.7145*	0.6912*	0.7802*		
		F–D	BW–BC2	0.4546*	0.4402*	0.6371*		
		N–D	BC1–BC2	0.6502*	0.6161*	0.7565*		
		B	Carbonate	Live–live fidelity of rank-abundance (Spearman's rho) between sites				
				F–N	BS–OC	–0.0894	–0.2485	–0.2582
F–D	BS–CB			0.0395	0.1830	0.0000		
N–D	OC–CB			–0.6495	–0.5837	–0.7746		
F–N	BW–BC1			0.4933*	0.5553*	0.3442		
F–D	BW–BC2			0.3755*	0.4358	0.3733*		
N–D	BC1–BC2			0.5856*	0.7331*	0.7062*		

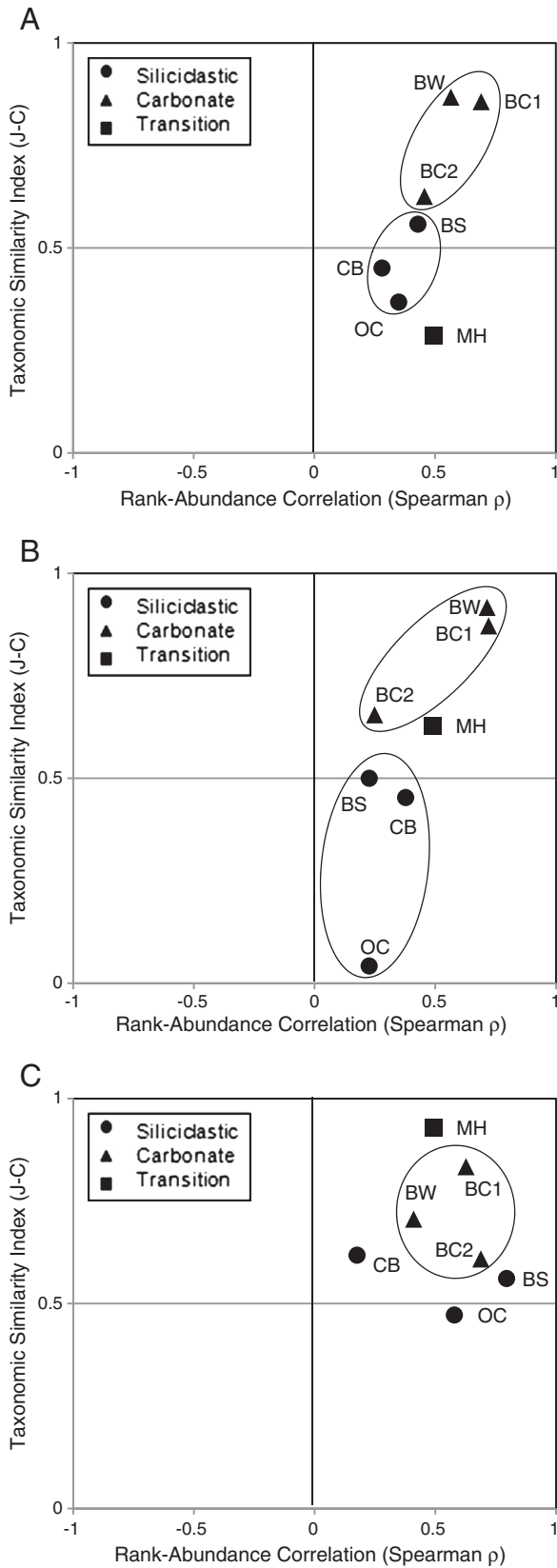


Fig. 4. Live–dead taxonomic agreement (Jaccard–Chao similarity index) plotted against live–dead rank–order correlation (Spearman rho) for A) total assemblages, B) bivalve assemblages, and C) gastropod assemblages per site. Abbreviations for sites as in Fig. 1.

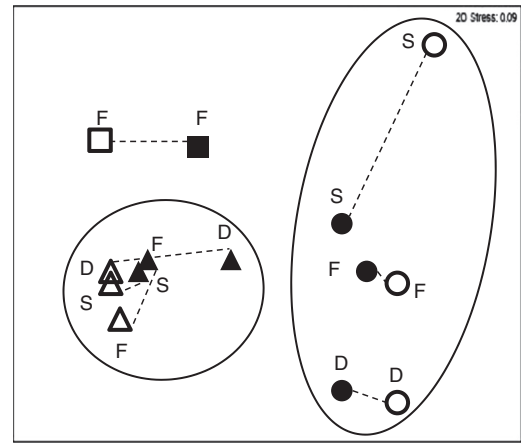


Fig. 5. Multidimensional scaling (MDS) plot of total molluscan assemblages, living and dead, per sedimentary environment and type of anthropogenic stress. Circles = siliciclastic sites. Triangles = carbonate sites. Squares = transition site. Closed symbols represent death assemblages, whereas open symbols represent living assemblages. The letter beside each symbol denotes the type of stress associated with that site and assemblage: F = freshwater runoff, N = nutrient runoff, D = physical substrate disturbance. Dashed lines connect living and dead assemblages from the same site.

#### 4.5. Multidimensional scaling

Multidimensional scaling (MDS) illustrates gradients in taxonomic composition among assemblages based on species proportional abundance (Fig. 5). All sites (living and dead assemblages) separate primarily by sedimentary environment. For all siliciclastic, carbonate, and transition sites, corresponding living and dead assemblages generally show good similarity to one another, i.e. are near-neighbors, nearer than others with few exceptions. Greater spread (greater differences) occurs among the siliciclastic sites than among carbonate sites, indicating that the carbonate assemblages are more similar to one another than siliciclastic sites are to each other. The transition site plots separately from the other assemblages and is closer to the carbonate sites than the siliciclastic on the y-axis, but not on the x-axis. The results of the ANOSIM assessments confirm the statistical significance of the relationships between assemblages illustrated by MDS.

#### 4.6. Characteristic taxa

The siliciclastic sites are characterized by an abundance of “dead-only” taxa (i.e. taxa found in the death assemblage but not in the living communities; Kidwell, 2002, 2007). These dead-only genera are among the most abundant bivalves and gastropods in the death assemblages. At most siliciclastic sites, dead-only bivalves include *Mulinia lateralis* and *Tellina* sp., which are opportunists (Mikkelsen and Bieler, 2008). The low-diversity siliciclastic living assemblages contain oysters and generally very few other bivalves and gastropods, all of which are typical of intertidal environments (NMiTA Database). The CB living community is dominated by *Solemya velum*, an organic-loving, chemosymbiotic bivalve (NMiTA Database; Abbott and Sandström, 1996).

The carbonate and transition sites also contain numerous moderately abundant dead-only taxa as well as a few relatively rare live-only taxa. Many of these dead-only taxa belong to the bivalve family Tellinidae, of which many species are considered to be opportunistic (Mikkelsen and Bieler, 2008). The live-only taxa include the tellinid bivalve *Angulus robins* and the fragile yet typical seagrass gastropod *Haminoea* sp. at BW, and the mussel *Amygdalum papyrium*, which can tolerate a wide range of salinities (Paleobiology Database), at MH. Many taxa that are found both living and dead tolerate stressful conditions – such as salinity fluctuations, brackish conditions, and reduced water quality – and are considered to be opportunists (Brewster-Wingard et al., 2001). For example, the bivalves *Brachidontes exustus*,

*Arcopsis adamsi* and *Modiolus squamosus* have wide salinity tolerances (Paleobiology Database) and are highly abundant at most sites. Also common in all living and death assemblages are the bivalve *Chione cancellata* (well-adapted to survive in difficult conditions; Abbott and Sandström, 1996) and tellinid species of the genera *Angulus*, *Eurytellina*, *Macoma*, and *Tellina* (opportunists; Mikkelsen and Bieler, 2008). In general, living and death assemblages at BW are characterized by several taxa with wide salinity ranges; the living and death assemblages at BC1 also contain opportunistic tellinids and a few chemosymbiotic lucinids. As with the siliciclastic disturbance site CB, disturbance site BC2 contains greater abundances of living chemosymbiotic lucinid bivalves (*Codakia orbicularis*, *Lucina* sp., *Parvilucina multilineata*) than the other carbonate sites. BC2 also contains the common salinity-tolerant and opportunistic genera found at BC1 and BW. The transition locality death assemblage contains various opportunistic, wide salinity tolerant, and chemosymbiotic taxa. The transition locality living assemblage is largely characterized by tellinids, *Brachidontes exustus*, and the live-only mussel *Mygdalum papyrium*. Full taxa lists and abundances are in Appendix.

## 5. Discussion

The various metrics we used to assess live–dead fidelity – richness, evenness, rank-order correlation, taxonomic similarity – reveal agreement between the living and dead assemblages at most study sites. This live–dead agreement could be interpreted to mean that the anthropogenic stresses we have observed and inferred are not severe enough to bring about significant ecological changes, or that the metrics we are using to detect anthropogenically induced changes are not sensitive enough (Kidwell, 2009). Alternatively, anthropogenic stresses may be so deeply rooted that taphonomic inertia has been overcome, causing death assemblages to resemble their ecologically altered living communities. Comparison of the fidelity results among sites indicates that the magnitude of time averaging, and thus the sensitivity of the live–dead approach, varies with sedimentary environment. Despite high live–dead fidelity at most sites, subtle live–dead variations and data from previous studies suggest that our sites have not been immune to recent ecological changes.

### 5.1. Fidelity metrics across sedimentary environments

#### 5.1.1. Richness

Because death assemblages represent the time-averaged accumulation of living communities over a period of years, death assemblage richness typically is greater than that of the living community collected during a single year (Kidwell, 2002). A death assemblage that is enriched compared to its corresponding living assemblage may be time averaged sufficiently to preserve the pre-stress death assemblage (Kidwell, 2008). Although the death assemblages are enriched at all of our study sites, the siliciclastic death assemblages show greater enrichment than do the carbonate death assemblages compared to their respective living communities. The difference in Delta-S between sedimentary environments suggests that siliciclastic sites experienced greater time averaging and thus possess a longer memory of the local molluscan assemblage, potentially retaining material from the pre-stress community. In contrast, less time averaging and faster live–dead equilibration may lead to loss of the pre-stress community in carbonate settings.

Kidwell et al. (2005) and Best et al., (2007) linked live–dead equilibration in carbonate sediments to greater shell loss related to boring and encrusting organisms during exposure of shells on the seafloor and to dissolution just below the sediment–water interface. Greater shell destruction by bioerosion may be a factor at our Florida Bay localities due to greater exposure of the shell material, partially owing to the thin sediment veneer overlying the bedrock and evidenced by more shell fragments in carbonate bulk samples. Although seasonal shell dissolution occurs in temperate siliciclastic sediments (Green and Aller,

1998), year-round shell dissolution has been found to occur in Florida Bay (Ku et al., 1999). Loss of older shell material would allow taxa in the living communities to quickly become dominant in the death assemblages (Kidwell, 1998), causing more similar richness in living and dead assemblages at the carbonate sites.

Aside from time averaging, the richness of death assemblages can be inflated by input of allochthonous material (Kidwell, 2008). However, based upon sediment and site observations as well as other research (Tourney and Perkins, 1972; Miller et al., 1992), we do not believe that transport is a significant concern at our study areas. Conversely, loss of thin- or fragile-shelled taxa from the death assemblage due to taphonomic processes may increase the richness of the living community relative to the death assemblage. Examination of the taxa present in corresponding living and dead assemblages indicate that this process does not pose a significant bias.

#### 5.1.2. Evenness

Regardless of depositional environment or sediment grain size, evenness has been found to differ little between corresponding living and death assemblages (Olszewski and Kidwell, 2007). Lower evenness in the death assemblage – as found at all of our sites – has been attributed to input of low-evenness allochthonous material or time averaging over an environmental change (Olszewski and Kidwell, 2007). With postmortem transport unlikely in our study areas, it is possible that lower evenness in our death assemblages reflects recent changes (toward more even living communities) that have not yet been recorded in the death assemblages. More similar live–dead evenness (Delta-PIE) at carbonate sites may again reflect more rapid live–dead equilibration in carbonate sediments compared to siliciclastic sites. In both sedimentary settings, however, natural variation and volatility of the living assemblage could account for greater evenness in the living communities as random colonization events may lead to a cohort of juveniles dominated by a particular species.

#### 5.1.3. Rank-order correlation and taxonomic similarity

Kidwell (2007) found that as the severity of anthropogenic stresses increases there is generally first a drop in live–dead rank-order agreement followed by a decline in taxonomic similarity. Such live–dead discordances are due to the death assemblages lagging behind taxonomic changes in the living community that are within the window of time averaging (Kidwell, 2007). Greater live–dead difference occurs in taxonomic composition and rank-order abundance at the siliciclastic sites than at the carbonate sites, suggesting that ecological changes may be more severe or are captured better by time averaging in siliciclastic sediments. More rapid condensation and equilibration of living and dead assemblages in carbonate sediments could be responsible for dampening the appearance of ecological changes in both rank-order and taxonomic agreement at those sites. Ferguson and Miller (2007) recognized such capacity for rapid, decadal-scale live–dead equilibration in carbonate environments, reporting that high live–dead rank-order agreement has been maintained in Smuggler's Cove, St. Croix for over 20 years despite major taxonomic changes in the molluscan community composition. However, at both siliciclastic and carbonate localities, the presence of numerous moderately abundant, dead-only taxa indicates that ecological changes may be taking place in which those dead-only taxa are fading from the communities (Kidwell, 2013). Furthermore, by considering the ecological traits and tolerances of taxa limited to the death assemblage or the living assemblage, we can discern subtle differences between living and dead assemblages and between sites that may indicate anthropogenic stresses.

### 5.2. Interpretations regarding anthropogenic stress

#### 5.2.1. Siliciclastic sites

The combination of numerous dead-only taxa and relatively low diversity of the living assemblage at the siliciclastic sites might indicate

ecological changes that favor the survival of only those taxa that tolerate or prefer the modified conditions (Kidwell, 2009). Although the inferred primary environmental stresses vary among our three siliciclastic sites, the survival of oysters (*Crassostrea virginica*, *Ostrea equestris*), among very few other taxa, at each of these localities suggests that these genera are the most tolerant of ecological changes. Dead–dead and live–live rank–order correlations between sites also suggest that the siliciclastic localities preserve evidence of recent ecological changes. Although rank–order abundance is generally not correlated between live assemblages at the three sites, positive correlations exist for the dead assemblages between sites. These results suggest that the death assemblages, and consequently former living communities, along the coast of North Carolina were at one point more similar to one another. Although this current discordance between sites may be the result of natural variation in living assemblages, it is also possible that differences in living communities reflect recent ecological changes, given our knowledge of anthropogenic stresses at our study sites.

The low diversity of living assemblages at all sites makes it difficult to characterize precisely the ecological consequences associated with the three forms of anthropogenic stresses examined. However, the unique abundance of the chemosymbiotic bivalve *Solemya velum* at CB potentially reflects a fundamental difference between substrate disturbance stresses versus nutrient or freshwater runoff stresses. Although we might expect organic-loving taxa such as *S. velum* to be more dominant at our nutrient runoff locality OC, it is possible that nutrient enrichment is not as significant at OC as we inferred, or that CB represents a nutrient-enriched environment, possibly due to significant coastal development around Chadwick Bay.

Because native and European settlement in coastal North Carolina began centuries prior to the onset of the stresses delineated by us at our study sites (Hendricks and Hendricks, 1995), there is high probability for very deeply-rooted human pressures at these localities that go beyond the current stresses we have inferred and observed. High sedimentation rates typical of coastal embayments such as our North Carolina sites may be limiting the temporal scope of our samples due to potential for permanent burial of the pre-stress communities below the sediment mixing zone (Kidwell, 2009). As a result, the death assemblages we have sampled in the siliciclastic environments may not represent the pre-stress community. To investigate this possibility, it was our intention to sample every site to a depth of 60 cm, collecting bulk samples at every 20-cm interval. However, this sampling could not be conducted at our carbonate sites, and deeper samples (20–40 cm and 40–60 cm) at our siliciclastic sites contained little to no shell material. From these results, we can assume that older shell material (including a pre-stress community) is 1) buried deeper than 60 cm, 2) present in the 0–20 cm samples we collected and analyzed, or 3) lost to taphonomic processes. If the pre-stress community is buried deeper than our sampling efforts, it is possible that the death assemblages we collected represent a post-stress community. Our measurements of fidelity may then be falsely positive (Kidwell, 2009). Even if the pre-stress communities were not sampled at our siliciclastic sites, the probability of greater time averaging in the siliciclastic sediments suggests that these sites better preserve the memory of older assemblages than do carbonate sediments.

### 5.2.2. Carbonate sites

Although there is greater live–dead taxonomic similarity and rank–order agreement among the carbonate sites, examination of the taxa rank abundances and comparison of the data with previous studies provide evidence of recent ecological changes at these sites. As with the siliciclastic sites, multiple dead-only genera indicate that there has been some shift in the community structure (Kidwell, 2013). Many of these dead-only taxa are opportunistic tellinid genera with relatively rapid reproduction and turnover rates; their presence only in the death assemblages could merely reflect the natural volatility of the living communities over time. The appearance of a few rare live-only

taxa also may signify recent ecological changes as they represent new arrivals to the local community (Kidwell, 2013). Differential preservation could account for the absence of these live-only taxa in the death assemblages, especially as the shells of these taxa are fairly fragile. However, because the live-only taxa are relatively rare ( $n \leq 9$ ) and there are a variety of similarly fragile organisms preserved in the death assemblages, the effects of this bias are probably not overwhelming.

The ecological preferences and tolerances of taxa at the carbonate sites may be used to infer anthropogenic stresses. The abundance of several taxa with tolerance for wide salinity ranges in all of the carbonate living and dead assemblages likely reflects the impact of long-term anthropogenic modifications to the Florida Bay area. As early as the late 1880s, freshwater was diverted away from Florida Bay, while coastal and marine development progressed in the surrounding region (Brewster-Wingard and Ishman, 1999; Fourqurean and Robblee, 1999; Brewster-Wingard et al., 2001). It was suspected that these anthropogenic stresses, combined with years of drastic rainfall fluctuations, increased the salinity in Florida Bay, particularly in the northeastern portion (Brewster-Wingard et al., 2001). Extensive sediment cores taken throughout Florida Bay by Brewster-Wingard et al. (2001) reveal that molluscan and foraminiferan faunas have fluctuated over the last century in response to salinity changes. Thus, resembling molluscan assemblages established by the 1980s, the current communities dominated by salinity-tolerant taxa represent an ecological shift in response to historical anthropogenic stresses. Positive, significant live–live and dead–dead rank–order fidelity between all of the carbonate sites support the regional ubiquity of anthropogenic impacts to Florida Bay as well as the taphonomic tendency for rapid live–dead equilibration in carbonate environments (Ferguson and Miller, 2007).

In addition to the abundance of salinity-tolerant taxa reflecting historical bay-wide anthropogenic stress, we believe that subtle taxonomic differences among the carbonate sites yield greater evidence for more recent and site-specific ecological changes and environmental conditions. For BC1, we propose that the abundance of opportunistic tellinids and chemosymbiotic lucinids may signify a recent relative increase in nutrient runoff at the site associated with recent land clearance along the nearby shoreline. At BW, nearly exclusive dominance by euryhaline taxa may reflect increased freshwater runoff due to extensive impervious surfaces along the adjacent coast. Although the abundance of opportunistic taxa at BC2 may reflect stressful conditions associated with physical substrate disturbance, the occurrence of several organic-loving, chemosymbiotic lucinids may reflect the proximity of the site to nutrient-rich mangrove environments. However, the greater abundance of organic-loving taxa in both the siliciclastic and carbonate disturbance sites may suggest a common consequence for substrate disturbance areas; displacement and re-suspension of sediment may increase the amount of suspended organic material. Overall, given our higher live–dead fidelity results along with evidence for historical ecological changes in Florida Bay, we argue that rapid live–dead equilibration in carbonate sediments decreases the sensitivity of the live–dead approach alone in detecting recent ecological change.

### 5.2.3. Transition site

Due to its location in the transition zone, we expected MH to yield relatively moderate live–dead fidelity results, reflecting a taphonomic middle ground between siliciclastic and carbonate conditions. Although highly similar live–dead richness and evenness values are reminiscent of live–dead equilibration found at our carbonate sites, relatively low live–dead taxonomic similarity and moderate rank–order agreement provide clues to community changes preserved by time averaging (Kidwell, 2009). As found at the siliciclastic and carbonate sites, numerous dead-only taxa imply ecological changes that removed many genera from the living community (Kidwell, 2013). These dead-only taxa include bivalves and gastropods with various life modes, indicating no shift toward a particular life mode or feeding habit. However, the moderately abundant live-only species *Amygdalum papyrium*, which

tolerates a wide range of salinities and is generally rare in seagrass environments (Paleobiology Database; Mikkelsen and Bieler, 2008), may indicate changing salinity conditions. Likewise, the abundance of opportunistic taxa and other euryhaline genera further suggests that environmental changes have occurred at MH. Given these ecological characteristics and tolerances, we argue that the suspected anthropogenic increase in freshwater runoff at MH may be responsible for the abundances of these taxa. Because the living and death assemblages are dominated by similar taxa, it seems that taphonomic inertia has largely been overcome at MH, excepting for the variety of rare dead-only specimens. Without sediment samples deeper than 20 cm and data from other studies, it is difficult to ascertain if and when community changes have taken place at MH. However, considering the close proximity of an extensive impervious surface to our sampled environment as well as community compositions similar to those impacted by known anthropogenic stresses in Florida Bay, we propose that biotic changes have occurred at MH, although their detection is hampered by live–dead equilibration. Thus, the degree of time averaging at MH may be more similar to that at the carbonate sites. This likeness may be influenced by several factors that were more comparable between the transition and carbonate sites, such as 1) generally finer grain size and more similar sediment composition, 2) similar taxa due to adjacent and overlapping ecoregions (Spalding et al., 2007), and 3) similar environmental conditions (water depth, tidal influence, geographic and latitudinal location).

## 6. Conclusions

Our results indicate that the live–dead approach is most sensitive to detecting recent ecological changes in siliciclastic environments because the death assemblages show greater time averaging. As a result

of more rapid live–dead equilibration in carbonate sediments, live–dead analyses conducted in carbonate environments may be more prone to yielding false positive assessments of live–dead fidelity. Although various environmental, biologic, and taphonomic factors may alter taxonomic similarity and relative abundance data, we argue that our results reaffirm the conservative nature of the live–dead approach. Future live–dead studies conducted in carbonate environments should consider the effect of rapid live–dead equilibration when examining the impact and magnitude of anthropogenic stresses. If possible, future studies should also collect death assemblages from greater depths in the substrate (>20 cm) to ensure sampling of buried, pre-stress communities. Such a practice in any sedimentary environment would not only aid the study at hand, but also further develop our collective understanding of the sensitivity of the live–dead approach in detecting ecological changes over time, in different sedimentary conditions, and in response to various types of anthropogenic stresses.

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**Appendix. List of living (L) and dead (D) bivalve and gastropod taxa found at all sites. Siliciclastic sites: BS, Bogue Sound; OC, Oyster Creek; CB, Chadwick Bay. Carbonate sites: BW, Blackwater; BC1, Bay Cove 1; BC2, Bay Cove 2. Transition site: MH, Matheson Hammock.**

Taxon – bivalves	BS		OC		CB		BW		BC1		BC2		MH	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D
<i>Abra aequalis</i>		2		3		111								
<i>Aequipecten muscosus</i>						1								
<i>Amygdalum papyrium</i>													10	
<i>Anadara transversa</i>					3	15					2			
<i>Anatina anatine</i>						1								
<i>Angulus agilis</i>										1			88	758
<i>Angulus merus</i>								3		97		26		1
<i>Angulus robins</i>							8							
<i>Angulus sp.</i>								1				4		835
<i>Angulus tampaensis</i>										2		33		
<i>Angulus texanus</i>								1	2	54	2	46		33
<i>Anomalocardia cuneimeris</i>								1	2	51	4	21	10	294
<i>Anomia simplex</i>				1		19		17		1				24
<i>Arcopsis adamsi</i>							52	1100	14	225	12	91		5
<i>Argopecten concentricus</i>		9	2	5		35								
<i>Argopecten gibbus</i>								63		26		46		32
<i>Barbatia cancellaria</i>								1						1
<i>Brachidontes exustus</i>							44	1519	94	1402	94	977	42	92
Bivalve sp. FL								1						
Bivalve sp. 1 NC		1												
Bivalve sp. 2 NC						1								
<i>Callista eucymata</i>										9		2		2
<i>Cardita floridana</i>							86	356	76	1153	24	194	2	578
<i>Chione cancellata</i>		2		10		40	46	536	46	674	32	99	8	126
<i>Chione grus</i>						6								
<i>Codakia orbicularis</i>							36	316	96	216	48	50		1
<i>Corbula dietziana</i>						4								
<i>Crassostrea virginica</i>			2	6	1	19								7
<i>Ctena orbiculata</i>								1						
<i>Cumingia tellinoidea</i>		2		4		5		18		78		69		1
<i>Cyrtopleura costata</i>						1								
<i>Diplodonta punctata</i>					1	4		4		3		2		7

## Appendix (continued)

Taxon – bivalves	BS		OC		CB		BW		BC1		BC2		MH	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D
<i>Diplodonta?</i>						3								
<i>Divaricella quadrisulcata</i>					1	13								
<i>Donax variabilis</i>						2								
<i>Dosinia discus</i>						8								
<i>Ensis directus</i>		1				76								
<i>Eurytellina angulosa</i>												5		
<i>Eurytellina nitens</i>							8	29		120		50	2	29
<i>Ischadium recurvum</i>								1		1				3
<i>Isognomon alatus</i>										2				2
<i>Laevicardium mortoni</i>		2		15		5	4	210	8	200		94		96
<i>Lima scabra</i>														1
<i>Limaria pellucid</i>							2	52		5		58		1
<i>Lioberus castanea</i>										1		9		
<i>Lucina sp. 1</i>										2	10	13		
<i>Lyonsia floridana</i>						2							34	24
<i>Macoma breviformis</i>										1		1		2
<i>Macoma cerina</i>										2		14	20	142
<i>Macoma constricta</i>						79						7		4
<i>Macoma tenta</i>								1		53		7		21
<i>Mactra fragilis</i>		1		3		8								
<i>Martesia cuneiformis</i>						5								
<i>Mercenaria mercenaria</i>	8	47		25	9	196		2				1		4
<i>Modiolus squamosus</i>							20	358		14		3		1
<i>Mulinia lateralis</i>		37		11	2	427		1		1				
<i>Mya arenaria</i>						23								
<i>Noetia ponderosa</i>						91								
<i>Nucula proxima</i>						3	6	20	52	102	4			
<i>Orobitella floridana</i>						1								
<i>Ostrea equestris</i>	10	2			8	14								10
<i>Oyster sp.</i>														1
<i>Parvilucina multilineata</i>		3				66				3	2	1		6
<i>Pecten sp.</i>														1
<i>Perna viridis</i>										2				1
<i>Pinctada imbricate</i>								185		75		208		
<i>Pitar fulminates</i>							46	335	16	241	6	30		8
<i>Scissula similis</i>							2	7		4				
<i>Semele proficua</i>						7				1				
<i>Solemya velum</i>				2	22	63								
<i>Spisula solidissima</i>		3		1										
<i>Sportella depressa</i>						7								
<i>Tagelus sp.</i>	4	31		25	1	231						114		4
<i>Tellina sp.</i>		13		8		571				11		32		
<i>Trachycardium muricatum</i>						4								
<i>Transennella conradina</i>								22		116	2	49		
<i>Taxon – gastropods</i>														
<i>Acteocina sp.</i>						5	1							
<i>Anachis avara</i>					2	10		3						
<i>Batillaria minima</i>								6		43			5	2699
<i>Bittium varium</i>						5	1	24		20	1	10		36
<i>Boonea impressa</i>						1								
<i>Boonea seminude</i>								7						1
<i>Bulla striata</i>							6	41	5	271	9	996	8	327
<i>Busycotypus spiratus</i>										1				
<i>Calotrophon ostrearum</i>								1					1	
<i>Cantharus multangulus</i>								3		7			5	
<i>Cerithidea scalariformis</i>								2		2				
<i>Cerithiopsis sp.</i>								2						2
<i>Cerithium muscarum</i>							4	162	7	378	3	109	17	966
<i>Cerodrilla thea</i>							1	4	2	2		2		
<i>Columbella rusticooides</i>							4	51		43		4		1
<i>Conus sp.</i>							2	27	2	34		1		1
<i>Crassispira sanibelensis</i>												1		
<i>Crepidula sp.</i>	11	49		73	1	50		15		71		1008	1	708
<i>Daphnella sp.</i>								3		23		15		2
<i>Dentimargo aureocinctus</i>								6		14		9		1
<i>Diadora cayenensis</i>								2		77		104		3
<i>Eupleura sp.</i>						1		1		2				
<i>Fasciolaria tulipa</i>						1	2	64	4	94	2	19		3
<i>Gastropod sp. 1</i>								4						2
<i>Gastropod sp. 2</i>										8				
<i>Haminoea sp.</i>								9		14	4	31		2
<i>Hyalina avena</i>										3		1		2

(continued on next page)

## Appendix (continued)

Taxon – gastropods	BS		OC		CB		BW		BC1		BC2		MH	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D
<i>Hyalina veliei</i>							10	5	2	3		8		
<i>Ilyanassa</i> sp.	1	9	23	95		2		10		2				
<i>Littorina angulifera</i>									3		2			
<i>Marginella</i> sp.									2					3
<i>Melanella</i> sp.		1				1					3			
<i>Mitrella lunata</i>						2								
<i>Modulus modiolus</i>							3	29	16	126	3	253		66
<i>Nassarius acutus</i>						1								
<i>Nassarius</i> sp.							8	36	10	82	3	47		23
<i>Nassarius vibex</i>	4	19		32	9	8								
<i>Neverita delessertiana</i>												1		
<i>Olivella pusilla</i>		1					1	64	2	846	1	89		15
<i>Patelloida pustulata</i>								4		1				1
<i>Pazionotus stimpsoni</i>								1		1				
<i>Persicula lavalleana</i>							10	38	7	173	6	84	2	17
<i>Pilsbryspira leucocyma</i>							2	34	2	173		29	3	23
<i>Pisania tinctoria</i>										1				
<i>Prunum apicinum</i>				1			10	53	8	248	2	68		11
<i>Puperita pupa</i>														1
<i>Pyramidella crenulata</i>						12					8			
<i>Pyrgocythara plicosa</i>						2								
<i>Pyrgospira tampaensis</i>								2						
<i>Rissoina angeli</i>								98	1	76	1	21		2
<i>Seila adamsi</i>								18		15				
<i>Stellatoma stellata</i>								16		23		2		11
<i>Suturoglypta iontha</i>										2				
<i>Tegula fasciata</i>								84		95		6		2
<i>Terebra</i> sp.		5												
<i>Thala floridana</i>							2	24		5				4
<i>Truncatella caribaeensis</i>								2		4				
<i>Turbo castanea</i>							1	184	3	56	1	13		9
<i>Turbonilla</i> sp.							1	1		4		2		27
<i>Turritella</i> sp.								2						
<i>Urosalpinx cinerea</i>						2	2	6		4				2
<i>Urosalpinx tampaensis</i>							3	3						

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