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COMPARATIVE TAPHONOMY OF MOLLUSCAN DEATH ASSEMBLAGES FROM THE GULF OF MEXICO

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INTRODUCTION

Biodiversity in our world is unequivocally linked to climate. Due to anthropogenic climate change, ecosystems are changing at rates that are affecting the continuity of ecosystem services we depend upon, creating a greater need for biomonitoring and restoration efforts. Since the Industrial Revolution, there have been increasing changes in marine ecosystems, leading to growing concern about potential losses in marine biodiversity. This is largely due to factors such as habitat loss, pollution, overfishing, introduction of invasive species, eutrophication, and acidification (Harnik et al., 2012). Live-dead studies provide one approach for assessing recent changes in ecosystems in response to human activities. Live-dead comparisons typically focus on the taxonomic composition and relative abundance of species in samples of the living community versus the occurrence and abundance of species in associated death assemblages (Kidwell, 2009). Death assemblages refer to the accumulation of skeletal remains such as bones, teeth, and shells. Live-dead studies have been used to assess discordance in disturbed ecosystems pre- and post-human impacts, which can help inform conservation and restoration decisions (Terry, 2009; Kidwell, 2009). However, before death assemblages can be used to reconstruct past communities, or be used as reference points for pre-impact communities, we have to understand the ways in which post-mortem taphonomic processes potentially bias the biological and ecological information contained in these assemblages. Post-mortem taphonomic biases can include both abiotic and biotic factors such as transport, corrosion, predation, and digestion, that work to destroy skeletal materials before they have a chance to be incorporated into stratigraphic records (Denys, 2002). Post-mortem processes could result in live-dead mismatch that is not representative of recent or historical biological changes.

Past studies have examined taphonomic variation associated with factors such as substrate, life habit, pore water geochemistry, and shell mineralogy (Best, 2008; Best and Kidwell, 2002; Hauser and Gischler, 2008; Kowalewski and Flessa, 2008; Leonard-Pingel, 2005; Lockwood and Work 2006; Parsons-Hubbard, 2005). These studiesfound recognizable signatures of taphonomic variation across environments. In particular, Best and Kidwell (2002) found that the quality of preservation varied among siliciclastic versus carbonate settings in the tropics. Using a similar scoring protocol, we can compare Best and Kidwell's model from Panama with a higher latitude setting such as the Gulf Mexico.

In this study, I addressed two main questions about the variation in types and intensities of damage on bivalve shells from the Northern Gulf of Mexico:

1. How does the taphonomic signature (as measured by a variety of post-mortem damage types) vary regionally between habitats characterized by siliciclastic sedimentation (i.e., Louisiana and Alabama) and habitats characterized by carbonate and/or mixed carbonate-clastic sedimentation (i.e., Florida)?

2. How much variation exists in taphonomic damage among localities within each region (e.g. within Alabama)?

GEOLOGIC SETTING

The Gulf of Mexico (GOM) is a 1.5-million km^2 semi-enclosed body of water that is bordered by the United States, Mexico and Cuba. It is a passive margin and in most regions is comprised of a wide, shallowly dipping continental shelf, almost 40% of which is 20 meters deep or less (Ellis and Dean, 2012). Over 150 rivers in North America drain into the GOM, influencing the hydrodynamics of the basin. Of these rivers, the Mississippi River is the largest, both in terms of average flow and sediment input (Ellis and Dean, 2012). There are a wide range of substrates in the Gulf, from sand to fine clays. A majority of the sediment inputs in the northern Gulf are fluvial, however the eastern Gulf is dominated by reworked carbonate from the regional karst bedrock and carbonate sediments produced by modern organisms (Ellis and Dean, 2012).

My study area (Fig. 1) focuses on a siliciclastic-to-carbonate transect across the northern and eastern GOM from Louisiana to western Florida. Samples were collected over two field seasons off the coast of Alabama, Louisiana, and northern and central Florida. I participated in the collection of death assemblages offshore of Alabama and Louisiana in the summer of 2016. The sampled geographic locations represent a range of substrate types and nutrient conditions. The sites from offshore Tampa (FL) are strictly carbonate settings with relatively low nutrient levels. In contrast, the sites from the panhandle offshore St. Teresa (FL) are mixed carbonate-clastic. Coastal Alabama is a siliciclastic setting with considerably higher nutrient content. Louisiana is also a siliciclastic environment and given its location adjacent to the mouth of the Mississippi River, has the highest nutrient inputs and likely the highest sedimentation rates of any of the regions studied.

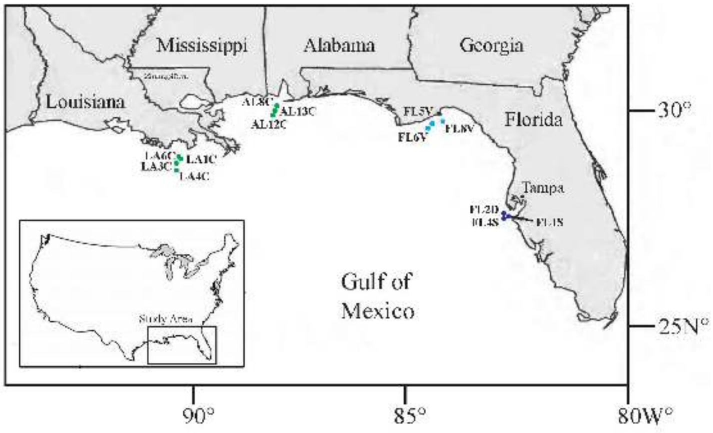

Figure 1. The Northern Gulf of Mexico; dots indicate the location of my sampling sites. Sampling sites in siliciclastic depositional environments are marked in green; mixed siliciclastic-carbonate environments are marked in light blue; carbonate environments are marked in dark blue.

METHODS

Field. We collected mollusk shells for this study using three different types of equipment: sediment grabs and box cores (in Alabama, Louisiana, and the Florida panhandle) and dredging (in central Florida). The dredge was used offshore Tampa, Florida because the carbonate substrate was too hard to use the box core and there was a relatively thin layer of surficial sediments. Although we have fairly good geographic coverage across the central and eastern edge of the GOM, within any given geographic area we sampled relatively few sites. This was not a substantial limitation given the scope of my project, but does present a possibility for future studies to expand sampling efforts in each of these regions. We processed our sediment samples on the boat, sieving all material through a 2 mm mesh and then separating live and dead molluscan (bivalves and gastropods) material. We did not retain the smallest size fraction of shelly material (< 2mm). Death assemblages were shipped back to Franklin and Marshall College where they were rinsed with fresh water and dried in a hood. Replicate sampling was used to increase the live count and provide a more robust understanding of the current live population.

Laboratory. In characterizing the taphonomic conditions of each site, all molloscan shell material in the death assemblage was emptied onto a grid consisting of 2x2 inch squares. I then used a random number generator to identify which grid cell was to be analyzed. This was done in order to identify an unbiased sub-sample that would be characteristic of the taphonomic damage at each site. This method was repeated until at least 50 bioclasts, which included whole shells and fragments, had been analyzed. This was usually accomplished using material from 1-2 squares. Of the 34 sites sampled over the two

		Taphonomic Grade (Rank)			
Taphonomic Variable	**Description**	**0 (good)**	**1 (fair)**	**2 (poor)**	**Study/Reference**
articulation	Presence or absence of articulated valves	valves articulated	valves disarticulated	-	Best and Kidwell 2000 Lockwood and Work 2006 Parsons-Hubbard 2005
fragmentation	Describes the degree of shell breakage	none	>20% of the shell remains (large fragment)	<20% of the shell remains (small fragment)	Kowalewski et al. 1994 Leonard-Pingel 2005 Best and Kidwell 2000 Lockwood and Work 2006 Parsons-Hubbard 2005
edge modification	Describes the degree of abrasion affecting the edges of the shell	not modified	angular-subangular or chipped edges	rounded-subrounded edges	Kidwell et al. 2001 Leonard-Pingel 2005 Best and Kidwell 2000 Lockwood and Work 2006
encrustation	Describes the extent of encrusting organisms on the shell surface. The location of the encruster is also specified as I (inside), O(outside), B(both sides)	none	<10% of total shell area covered	>10% of total shell area covered	Kidwell et al. 2001 Kowalewski et al. 1994 Leonard-Pingel 2005 Best and Kidwell 2000
internal and external luster	Describes the degradation of the surface of the shell. Loss of internal or external luster were scored separately	shiny- well preserved original luster	dull- original luster partially lost	chalky- original luster completely lost	Kowalewski et al. 1994 Parsons-Hubbard 2005
bioerosion	Quantifies the degradation to the shell surface due to biological activity such as sponge borings, gastropod borings, root etching, algal traces, etc.	none	<10% shell area covered	>10% shell area covered	Parsons-Hubbard 2005 Kowalewski et al. 1994 Leonard-Pingel 2005
dissolution	Describes the degree to which the shell has been modified chemically through dissolution and is characterized by pitting	none	moderate	extreme	Leonard-Pingel 2005
thickness	Quantifies the robustness of shells and shell fragments	<1mm thick	1-2 mm thick	>2mm thick	-

Table 1. Damage types used to characterize the taphonomic signature of each sampling site. The taphonomic condition of all bivalve shells and shell fragments in each sample was determined using a dissecting microscope.

years, I compared the taphonomic signature of 13 sites, representing a range of sedimentary facies: 3 from Alabama, 6 from Florida (3 from Tampa and 3 from St. Teresa), and 4 from Louisiana. One notorious problem with assessing taphonomic profiles is the subjectivity of the scorer as well as the lack of standardization of scoring guides used between different studies (Best and Kidwell, 2000). Before starting to collect my data, I created a taphonomic scale, based on descriptions and techniques from various other studies, with representative pictures of each category and used it to, as objectively as possible, categorize the bioclasts.

Each shell was scored using a semi-quantitative scale for eight different taphonomic variables; articulation, fragmentation, edge modification, encrustation, internal and external luster, bioerosion, dissolution, and thickness. See Table 1 for a description of each taphonomic variable. A handheld caliper was used to measure the length of the long axis as well as the longest axis perpendicular to the first measurement. These two measurements helped differentiate the geometric shape (round versus elongate) of the bioclast. The caliper was also used to differentiate between categories of thickness.

RESULTS

Articulation. In ten of the thirteen sites, 100% of the shells occurred as disarticulated valves. At two sites in Alabama (AL8C and AL12C), articulated valves comprised 0.05% and 2% of specimens, respectively, and at one site in Louisiana (LA1C), 4.5% of specimens were articulated (Fig. 2A). Although taxonomic identifications were beyond the scope of my project, the articulated shells in these samples tended to be either *Nuculana* or *Abra*. These

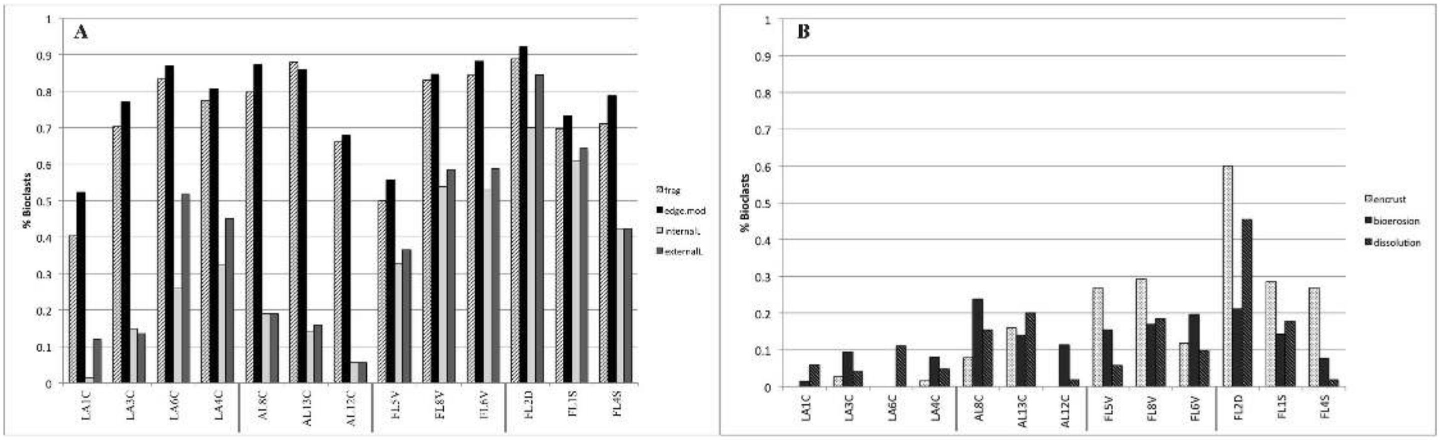

Figure 2. Taphonomic signature of bivalve death assemblages across the Northern Gulf of Mexico based on the percentage of bioclasts in a sample that were assigned a damage score of 1 or 2 (on a 3 point scale). A: Percent fragmentation, edge modification, internal luster, and external luster at individual sampling sites. B: Percent encrustation, bioerosion, and dissolution at individual sampling sites. Taphonomic variables in the legend (top to bottom) are plotted for each site (left to rigth).

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two species were the majority of what was found at LA1C (see Grimmelbein, this volume). There were no articulated valves found in the subsamples from any of the locations sampled in Florida.

Fragmentation. Levels of fragmentation were generally very high across all settings (50-89% of bioclasts) with the exception of LA1C in which only 40% of shells were fragmented (Fig. 2A). There was no apparent difference between carbonate and clastic settings. Fragmentation can be a difficult taphonomic variable to interpret because it can be due to mechanical breakage (e.g., wave energy), biotic processes (e.g., predation), or simply the processing of skeletal material in the field or lab (Best and Kidwell, 2000; Leonard-Pingel, 2005; Zuschin and Stanton Jr., 2003).

Edge Modification. The occurrence of rounding or chipping of shells was uniformly high across all sites (52-92%) (Fig. 2A). Similar to fragmentation, edge modification can be attributed to a number of factors including abrasion, dissolution, and/or predation. The degree of rounding versus chipped edges could indicate the amount of energy in the system or possibly the time the bioclast has spent in the "taphonomically active zone" (Leonard-Pingel, 2005). Edge modification does not vary markedly between localities in the northern versus eastern Gulf.

Encrustation. The amount of encrustation varied distinctly among regions, and appears to reflect differences in substrate type. The percent of encrusted shells in Louisiana ranged between 0-3% and in Alabama between 0-16%. In the Panhandle of Florida, 12-29% of shells were encrusted whereas offshore Tampa had the highest percentages of encrusted bioclasts (ranging from 27-60%) (Fig. 2B). These numbers represent the occurrence of encrustation on either the outside or the inside of the shell. This means that the organisms encrusting the shells could have done so during the lifetime of the bivalve, which would not reflect post mortem processes affecting the death assemblages. When the comparison is limited to encrustation frequencies on only the inside of shells, the trend remains: Louisiana has the lowest occurrence of encrustation on the inside of bioclasts (0-2%), followed by Alabama (0-6%), then the Florida Panhandle (6-21%), and finally Tampa (17-47%).

Luster. Both the internal and external luster was scored during data collection. However, as with encrustation, external luster can change over the lifetime of a specimen or post-mortem, whereas the extent of loss of internal luster is indisputably tied to taphonomic processes. Loss of luster can occur quickly after the death of the bivalve and can therefore be a good indication of early degradation (Parsons-Hubbard, 2005). Only shells that are buried relatively quickly after death retain their original luster (Parsons-Hubbard, 2005). Loss of internal luster was variable among regions. Louisiana varied between 1-32%. The rates in Alabama ranged between 6-19% loss. The Florida Panhandle had high rates of loss ranging from 33-54%, and Tampa had the highest loss, between 42-70% (Fig. 2A). In Louisiana, the loss of original luster had a characteristic flakey pattern, which may reflect water chemistry.

Bioerosion. Bioerosion across all regions was generally low, ranging between 0-24% (Fig. 2B). Bioerosion is an all-encompassing category of factors that includes predatory boring, algal traces, sponge boring, and other unidentified damage traces that were attributed to biologic origins (Leonard-Pingel, 2005; Kowalewski et al.,1994; Parsons-Hubbard, 2005). Alabama had the highest frequencies and Louisiana had the lowest frequencies of bioerosion, which differs from the geographic trends seen in some of the other damage categories in which Florida had the highest damage profile.

Dissolution. The moderate and extreme dissolution of shell material visible with a dissecting microscope was relatively uncommon across all regions. In Louisiana, dissolution rates were lowest, ranging between 4-11%. In Alabama, between 2-20% of shells were pitted. In the Panhandle, dissolution rates ranged between 6-18% and in Tampa 2-46% of shells were noticeably dissolved (Fig. 2B).

Thickness. Most bioclasts were less than a millimeter thick. In Louisiana, 3-22% of bioclasts were thicker than a millimeter. A majority of these shells were between one and two millimeters, with a few exceptions that were thicker than two millimeters. Bioclasts thicker than a millimeter in both Alabama and the Panhandle ranged between 2-12%. In Tampa, 10-24% of shells were thicker than one millimeter.

Time Averaging. A subset of *Nuculana acuta* shells that were collected from Alabama during the first year of this project were sent to Woods Hole Oceanographic Institution for radiocarbon dating in order to understand the time averaging of GOM death assemblages. Out of the 100 dated specimens, 17 of them were post-bomb (1950s to present) and the median age of the remaining shells was 646 years before present, but ranged between 83-3192 YBP.

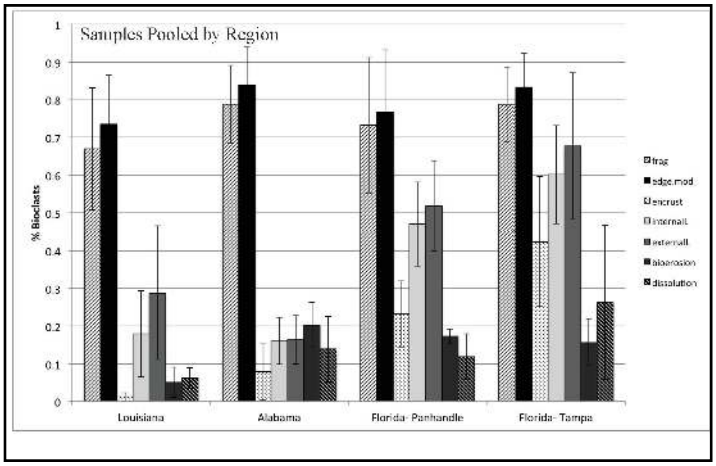

Figure 3. Taphonomic signatures of bivalve death assemblages across the northern Gulf of Mexico based on the percentage of bioclasts in a region that were assigned a damage score of 1 or 2. Error bars are 95% confidence intervals.

Specimens collected in Louisiana and Florida are currently being dated by Northern Arizona University and University of California, Irvine; results are forthcoming.

DISCUSSION AND CONCLUSION

Taphonomic results can be difficult to compare among studies because of the lack of a standardized scoring method, the subjectivity of some of the scores, and different sampling techniques (Best and Kidwell, 2000; Rothfus, 2004; Kidwell et al., 2001). That being said, our results mirror some of Best and Kidwell's (2000) results for tropical taphofacies, which showed "superb" preservation in siliciclastic substrates and higher frequencies of more damaged shells in carbonate settings. The taphonomic differences observed between death assemblages found in carbonate and siliciclastic settings may be attributed to differences in residence time on the seafloor. In Louisiana and Alabama, it is likely that sedimentation rates are much higher and therefore shells are buried more quickly which removes them from the taphonomically active zone, whereas in Florida, reduced sedimentation rates lead to longer exposure times of shells at the sediment-water interface, giving them more time to accumulate certain damage types such as encrustation and bioerosion (Best, 2008; Best and Kidwell, 2000).

The taphonomic characteristics that appear to be most variable between regions are encrustation, bioerosion, dissolution, and loss of luster (Fig. 3). Of these variables, encrustation and luster are noticeably higher in the carbonate and mixed carbonate-siliciclastic settings in Florida. The other damage categories (bioerosion and dissolution) that vary between regions may reflect differing environmental conditions such as water chemistry or sedimentation rates, or biological factors such as shell microstructure or life habit (Best, 2008; Lockwood and Work, 2006). Other taphonomic features, such as articulation, fragmentation, and edge modification seem to be consistently high across all regions and do not vary by substrate type.

As documented by Laurent et al. (2016), summer hypoxic cycles in the GOM are directly linked to high nutrient inputs from the Mississippi River which cause eutrophication-induced acidification. Our samples from LA1C are from the middle of this hypoxic “dead zone” and therefore show some different trends in preservation. The flakey texture of many of the *Nuculana* shells at LA1 could be a product of this acidification, although a more in-depth study would need to be done to confirm that hypothesis. Such a study could focus on field samples that span a range of pH levels or could experimentally examine shell degradation under different pH treatments.

The benthic communities of bivalves in the GOM are experiencing multiple stressors that could possibly drive changes in species abundance and diversity. These include habitat change, climate change, exploitation of native species, biological invasions, biogeochemical disturbances, and natural disasters such as hurricanes (Dietl et al., 2015). From our data we cannot necessarily disentangle the causes of shifting communities, but from this study we can at least recognize the potential biases that are introduced post mortem and incorporate that knowledge into interpretations of past community structures.

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