Learning Science Through Research
Published by Keck Geology Consortium

Short Contributions
30th Annual Symposium Volume
29th April, 2017
ISBN: 1528-7491

HISTORICAL ECOLOGY OF MARINE MOLLUSKS IN THE NORTHERN GULF OF MEXICO

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INTRODUCTION

The Mississippi River watershed drains 40% of the continental United States and is home to approximately 70 million people (National Research Council, 2008). The river's delivery of nutrients has supported tremendous primary production in the marine ecosystems of the Northern Gulf of Mexico for millennia; evident today by the network of offshore oil and gas wells that mine the region's hydrocarbon-rich sedimentary deposits (Darnell, 2015). Human activities have enhanced nutrient delivery to the Northern Gulf of Mexico through farming, urbanization, and surface run-off and, as in terrestrial ecosystems, these additions of nitrogen and phosphorous have spurred coastal primary production (Rabalais et al., 2007; Darnell, 2015 and references therein). Phytoplankton blooms in the Northern Gulf have led to the growth of one of the largest oxygen-limited zones in the world (Rabalais et al., 2007; Diaz and Rosenberg, 2008). How has anthropogenic eutrophication affected the marine species that live in the Northern Gulf of Mexico?

Answering this question requires a historical perspective, yet long-term biomonitoring is rare and where such data exist they often postdate the environmental changes that are of interest. Live-dead analysis – the comparison of living communities with the skeletal remains of past communities - has emerged as a valuable tool for evaluating historical changes in marine and terrestrial ecosystems that occurred before biomonitoring began (Kidwell, 2007; Terry, 2010; Miller, 2011; Kidwell and Tomasovych, 2013; Casey et al., 2014).

Many marine live-dead data sets exhibit significant similarities between the taxonomic composition and relative abundance of mollusk species living today and time-averaged samples of skeletal remains (Kidwell, 2002; Lockwood and Chastant, 2006; Kidwell, 2007). Yet, such live-dead agreement can break down as a result of human activities. In the Northwestern Gulf of Mexico, for example, the magnitude of live-dead disagreement in species relative abundance and taxonomic composition varies as a function of anthropogenic eutrophication (Kidwell, 2007), with live communities in eutrophic settings characterized by an overabundance of organic-loving species and a scarcity of seagrass-dwelling species relative to associated death assemblages (Kidwell, 2009). Although live-dead disagreement in taxonomic composition and abundance can reveal some of the biotic consequences of anthropogenic eutrophication, such comparisons may be conservative; some live-dead comparisons exhibit little difference despite documented histories of human impacts (Kidwell, 2009).

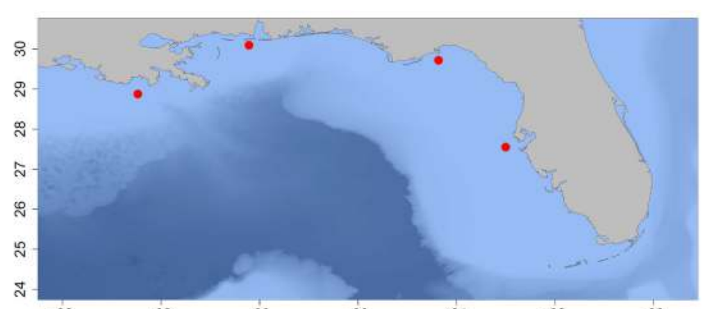

Figure 1. Regions of live-dead sampling in the Gulf of Mexico. Red dots indicate areas on the continental shelf in which live-dead molluscan samples were collected in 2015 and 2016.

This project focused on present and historical marine bivalve communities distributed along a nutrient gradient in the Gulf of Mexico that extended from the nutrient-rich Louisiana shelf to the nutrient-poor west Florida shelf (Fig. 1). The overarching aims of the project were to assess: (1) taphonomic variation between regions characterized by siliciclastic versus carbonate sedimentation; (2) live-dead agreement in community composition and species relative abundance; and (3) live-dead agreement in life history characteristics.

Previous studies indicate that the median age of dead mollusk shells recovered from surficial sediments on the continental shelf date to approximately 2000 years before present (YBP), though can range from the present-day to >10,000 YBP (Flessa and Kowalewski, 1994). Radiocarbon dates for dead specimens of the bivalve *Nuculana acuta* collected offshore Dauphin Island record a median age of approximately 600 YBP, with individual specimens ranging from post-bomb to 3100 YBP. As such, molluscan death assemblages may provide a pre-Industrial baseline for benthic communities in the Gulf of Mexico.

METHODS

Live-dead samples were collected in June 2016 on the continental shelf offshore Cocodrie, Louisiana and Dauphin Island, Alabama (Fig. 1). Surficial seafloor sediments were collected from approximately -20 meters water depth using box corers (average penetration depth to -20cm) deployed from research vessels operated by the Dauphin Island Sea Lab and Louisiana Universities Marine Consortium. In each region, samples were collected over two consecutive days, with the first day focused on the collection of numerous (>50) replicate samples from a single locality and the second day focused on less intensive sampling (3-5 replicates/locality) at multiple localities. Intensive sampling at individual localities was necessary to generate a robust collection of live material for live-dead analyses in each region. Sampling at multiple localities was necessary for taphonomic comparisons within and among regions. While offshore, participants documented and sieved sediment samples and sorted live and dead molluscan material > 2mm for further study (Fig. 2).

For their individual research projects, participants also worked with samples collected offshore Alabama and Florida in 2015. These live-dead samples were collected by the Project Director, Franklin and Marshall College undergraduate students, and the staff at the Dauphin Island Sea Lab, Florida State University Coastal and Marine Laboratory, and Florida Institute of Oceanography. Collection protocols in 2015 were comparable to those in 2016 with the exception that a greater variety of benthic sampling equipment was employed (i.e., sediment grab samplers, box corers, and dredge) due to regional variation in substrates and equipment availability at each marine lab.

Figure 2. A representative molluscan death assemblage collected on the continental shelf offshore Cocodrie, Louisiana in 2016. Tweezers for scale.

For comparison with previously-dated bivalve remains from offshore Alabama, a subsample of bivalve shells from other Gulf localities were sent to Northern Arizona University's Geochronology Lab and UC Irvine's AMS lab for radiocarbon dating. Dates for *Nuculana acuta* and *Lirophora sp.* from Louisiana death assemblages, and *N. acuta* from death assemblages from the Florida panhandle were pending at the time of this publication.

RESEARCH

Taphonomic characterization

Anik Regan (Macalester College) examined taphonomic variation in death assemblages from across the Northern and Eastern Gulf of Mexico. Although differences between life and death assemblages can reflect recent changes in benthic communities in response to human activities (e.g., Kidwell, 2007; Casey et al., 2014), post-mortem processes such as shell dissolution and fragmentation can also result in live-dead disagreement (Kidwell and Flessa, 1995 and references therein). Understanding the nature of these post-mortem filters, and specifically how they differ among depositional environments, is essential for interpreting the ecological information recorded by death assemblages. Previous work on tropical marine environments found that the condition of molluscan remains varied markedly between carbonate and siliciclastic depositional settings (Best and Kidwell, 2000). Regan gathered data on the taphonomic grades of bivalve shells and shell fragments from multiple localities across the Gulf to assess whether similar differences existed between carbonate and siliciclastic settings in higher latitude, subtropical shelf environments.

Live-dead comparison

Luke Grimmelbein (Beloit College) examined live-dead agreement in bivalve communities at two localities in the Northern Gulf of Mexico. Previous work found that live-dead agreement can break down in regions affected by anthropogenic eutrophication in part because of the enrichment of organic-loving species in the living community relative to the associated death assemblage (Kidwell, 2007). Grimmelbein gathered data on the taxonomic composition and relative abundance of bivalve species offshore Louisiana and Alabama to determine the effects of anthropogenic eutrophication on live-dead agreement in the Northern Gulf, and specifically if live-dead disagreement varied with proximity to the Mississippi River.

Morgan Torstenson (Franklin and Marshall College) examined live-dead agreement in bivalve life history characteristics at two localities in the Northern Gulf. Life history theory predicts that egg size will vary inversely with food availability (Snell-Rood et al., 2015). Anthropogenic eutrophication results in increased phytoplankton production which, all else being equal, would increase food supply for basal consumers such as marine bivalves (Snell-Rood et al., 2015; Alexander et al., 2017). The size of the earliest larval shell of marine bivalves is correlated with egg size (Malchus and Sartori, 2012) and previous studies have shown that larval shell size can track variation in primary production over millennia (Moran, 2004). Torstenson gathered data on live and dead larval shell size for the marine bivalve *Nuculana acuta* to test the hypothesis that populations today have smaller larval shells than historical populations. Torstenson focused on samples from offshore Louisiana and Alabama and hypothesized that the magnitude of live-dead disagreement in larval shell size would increase with proximity to the Mississippi River.

IMPLICATIONS OF THIS WORK AND NEXT STEPS

As the footprint of human activities on Gulf marine ecosystems continues to increase, biological baselines that pre-date these activities become more critical. Biological baselines are needed to evaluate the impacts of anthropogenic eutrophication, industrial fishing, and other stressors on marine benthos, and to establish meaningful targets for ecosystem restoration following environmental disasters (National Academies of Science, Enginnering, and Medicine, 2016). Molluscan death assemblages can provide such baselines provided that potential taphonomic biases are taken into account.

Future work will expand the scope of live-dead comparisons and provide further age constraints on Gulf death assemblages. Additional radiocarbon dates are needed to assess the validity of different putative drivers of live-dead disagreement in the Northern Gulf of Mexico. Live-dead analyses at additional localities are also needed to determine the extent to which live-dead disagreement varies as a function of the magnitude of anthropogenic eutrophication. Because of the relatively poor preservation of *N. acuta* larval shells offshore Louisiana, additional live and dead specimens are needed to assess the robustness of live-dead life history results. More broadly, expanding these live-dead comparisons to include additional species and additional traits (e.g., body size) will provide a more comprehensive understanding of the effects of anthropogenic eutrophication on Gulf marine benthos.

ACKNOWLEDGEMENTS

Funding for this project was provided by the Keck Geology Consortium, the National Science Foundation (NSF-REU1358987), ExxonMobil Corporation, and Franklin and Marshall College. This research would not have been possible without the assistance of the research crews at the Louisiana Universities Marine Consortium, Dauphin Island Sea Lab, Florida State University Coastal and Marine Laboratory, and Florida Institute of Oceanography. Radiocarbon dates were generated by Woods Hole Oceanographic Institution NOSAMs facility and Northern Arizona University's Geochronology Lab working in collaboration with UC Irvine's AMS lab. Many students have assisted in the field and in the lab over the past two years. In addition to the three 2016 Keck participants (Luke Grimmelbein, Anik Regan, and Morgan Torstenson), I would like to thank Mario Williams, Danielle Moloney, Kevin Cerna, Jared Brush, Sophia Gigliotti, and Rachel Clifford for their assistance in the field. Mario Williams also helped to develop the SEM workflows that he and Torstenson used to gather *N. acuta* larval shell data. Lastly, I would like to thank Ray Rogers (Macalester College) and Carl Mendelson (Beloit College) for advising Anik and Luke's projects.

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