PALAIOS
Emphasizing the impact of life on Earth's history

PALAIOS, 2017, v. 32, 678–688
Research Article
DOI: http://dx.doi.org/10.2110/palo.2017.033

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Society for Sedimentary Geology

ASSESSING THE EFFECTS OF ANTHROPOGENIC EUTROPHICATION ON MARINE BIVALVE LIFE HISTORY IN THE NORTHERN GULF OF MEXICO

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ABSTRACT: **Natural and anthropogenic eutrophication can increase food supply to basal consumers in aquatic food webs. All else being equal, increased food supply is expected to relax life history trade-offs between egg size and number, resulting in a reduction in egg size over time as individuals that produce more numerous, small eggs exhibit greater fitness. We tested this hypothesis by comparing the sizes of larval shells (PI) of the marine bivalve *Nuculana acuta* in living and death assemblages collected from surficial seafloor sediments on the Alabama continental shelf; PI size is positively correlated with egg size and can be measured from adult shells. We found that the mean PI size of living *N. acuta* was approximately three microns smaller than that of the associated death assemblage and that this difference was robust to potential taphonomic biases. This life history shift occurred relatively recently as no trend exists in PI size over the past 3100 years. The live-dead disagreement that we observed is consistent with the history of anthropogenic eutrophication in the Mississippi Bight. These data provide a baseline for comparison with other regions in the Gulf of Mexico that have more sustained histories of anthropogenic eutrophication. More broadly, live-dead comparisons of molluscan life history coupled with age dating of molluscan shells can complement community-level metrics when assessing the impacts of anthropogenic eutrophication on coastal ecosystems, and offer a unique study system for investigating life history adaptation in a field context.**

INTRODUCTION

The delivery of nitrogen and phosphorous to coastal ecosystems has increased markedly in recent centuries through deforestation and erosion, fertilizer production and application, wastewater management, and other human activities (Rabalais 2002; Smith 2003; Rabalais et al. 2007). Rates of primary production are commonly limited by the availability of these nutrients (Elser et al. 2000), and consequently have increased as a result of anthropogenic nutrient enrichment (Smith 2006). How have these changes in the abundance and taxonomic composition of primary producers propagated upward through marine food webs? Has increased nutrient availability led to the relaxation of life history trade-offs and, if so, how have the life history traits of organisms in eutrophic environments changed (Snell-Rood et al. 2015)? Has anthropogenic nutrient-enrichment weakened natural habitat gradients and, if so, what effect has this had on functional diversity (Alexander et al. 2017)? Our expectations for how eutrophication will affect these and other ecological and evolutionary processes are primarily informed by laboratory studies and theory (see recent reviews by Snell-Rood et al. 2015; Alexander et al. 2017). To date, few studies have considered these questions in a field context, in part because of a dearth of long-term biological data sets that predate the onset of eutrophic conditions.

Surficial death assemblages preserved in marine soft sediments can yield biological data that predate anthropogenic eutrophication and thereby offer time-averaged baselines for comparison with living assemblages (Kidwell 2013, 2015; Dietl et al. 2015; Kosnik and Kowalewski 2016). These historical baselines may be particularly valuable in regions that lack "pristine" control sites (National Academies of Sciences, Engineering, and Medicine 2017). Meta-analyses of live-dead studies have shown that anthropogenic eutrophication can result in live-dead disagreement in the composition and relative abundance of molluscan communities (Kidwell 2007, 2008, 2009), though benthic trawling and other human activities can also affect live-dead agreement (Kidwell 2013; Casey et al. 2014; Negri et al. 2015). Living assemblages in areas affected by anthropogenic eutrophication may be enriched in deposit-feeding bivalves and depleted in seagrass-dwelling species relative to the frequencies of these taxa in associated death assemblages (Kidwell 2007, 2009; Leshno et al. 2015; Negri et al. 2015).

Live-dead discordance at the community-level is a conservative measure of the impacts of human activities on marine benthos as approximately 40% of data sets in areas affected by anthropogenic eutrophication exhibit levels of live-dead agreement that are statistically indistinguishable from sites with little or no history of anthropogenic eutrophication (Kidwell 2007). Live-dead agreement in environments affected by anthropogenic eutrophication may result from rapid rates of shell loss and/or high sedimentation rates, both processes which would decrease the temporal offset between living and time-averaged death assemblages (Kidwell 2007). Alternatively in environments that were characterized by meso- or eutrophic conditions prior to human arrival, anthropogenic eutrophication may not be an ecological disturbance for resident benthos (Kidwell 2007).

Aspects of life history (e.g., egg size and growth rate) can change quite rapidly and may offer additional indicators of the effects of anthropogenic eutrophication on marine benthos that would complement existing community-level ecological metrics such as the Jaccard-Chao index of taxonomic similarity (Chao et al. 2005) and Spearman correlation of species rank-abundance (e.g., Kidwell 2007; Kidwell 2013 and references therein). However there have been relatively few live-dead studies of organismal traits (though see Cummins et al. 1986; Tomašových 2004; Miller et al. 2014), and none that have specifically examined live-dead

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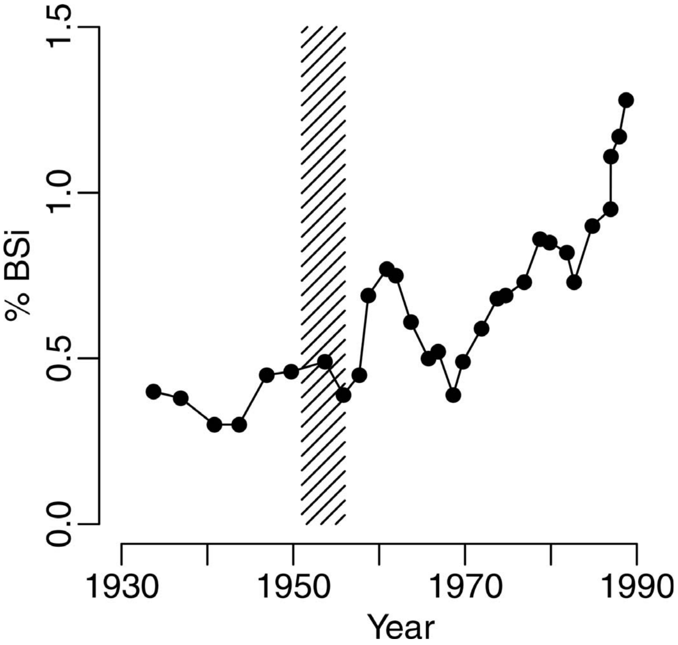

FIG. 1.—Timing of anthropogenic eutrophication in the northern Gulf of Mexico. Concentrations of biologically bound silica (% BSi) in sedimentary cores indicate increasing primary production in the Louisiana Bight through the twentieth century as a result of anthropogenic nutrient enrichment (data replotted from Turner and Rabalais 1994, fig. 3b). In the Mississippi Bight, core top foraminiferal assemblages indicate occurrence of seasonal hypoxia (hatched lines) in the 1950s as a result of enhanced primary production and seasonal stratification of the water column (Brunner et al. 2006).

concordance in life history in the context of recent changes in primary production.

All else being equal, increased rates of phytoplankton production provide additional food to basal consumers such as suspension- and deposit-feeding benthic marine mollusks, and life history theory predicts that increased resource availability will result in relaxed natural selection on life history traits such as egg size (Snell-Rood et al. 2015). Whereas food limitation is expected to cause an increase in mean egg size over time as offspring developing from larger eggs experience greater probabilities of survival (Moran 2004), enhanced food supply in eutrophic settings may lead to a reduction in mean egg size due to the weakening effects of egg size on juvenile survival probability and overall enhanced survival rates. The effects of enhanced food supply on egg size may be compounded by the effects of hypoxia commonly associated with eutrophication. Oxygen limitation can directly affect the survival rates of eggs of varying size (Einum et al. 2002), and can also indirectly affect egg size through the exclusion of predators (Robb and Abrahams 2003; Hedges and Abrahams 2015). Predatory release can lead to reduced investment in egg size among prey populations and fecundity selection (Heath et al. 2003).

It is generally assumed that a life history tradeoff exists between the size and number of eggs that a mother can produce (Vance 1973; Moran 2004). Consequently, increased food availability and greater juvenile survival should result in greater fitness for individuals that produce more numerous small eggs. A study of salmon populations raised in captivity found that enhanced juvenile survival can lead to fecundity selection and the rapid evolution of smaller eggs (Heath et al. 2003), though greater juvenile survivorship in this case was due to the exclusion of predators and not increasing food supply. Analyses of marine mollusks have shown that egg size can also vary over much longer time scales. For example, the development of oligotrophic conditions in the Caribbean following the closure of the Central American Seaway approximately three million years ago led to an increase in egg size among Caribbean bivalves relative to their sister species in the more nutrient-rich east Pacific (Moran 2004). It is possible to track the egg sizes of mollusks over millennia because egg size is positively correlated with the diameter of the first phase of growth of the bivalve larval shell (Prodissoconch I, PI) (Malchus and Sartori 2012). Because bivalves grow by accretion of calcium carbonate along their shell margins, their shells preserve a rich ontogenetic history which can be used to investigate changes in life history in response to natural and anthropogenic eutrophication.

Our goals for this study were to assess: (1) live-dead agreement in PI size; (2) temporal variation in PI size over past millennia; and (3) taphonomic biases that might affect live-dead comparisons of PI size. We focus on a region of the northern Gulf of Mexico with a relatively limited history of anthropogenic eutrophication (Brunner et al. 2006). Determining how PI size varies when anthropogenic eutrophication is weak or absent is important because PI size can vary in response to temperature as well as nutrients (Lutz and Jablonski 1978). The data we present here offer a live-dead baseline that we intend to use in assessing live-dead agreement in bivalve egg size at other sites in the northern Gulf of Mexico with more sustained cultural histories of eutrophication.

NORTHERN GULF OF MEXICO

Anthropogenic eutrophication and associated hypoxia have been monitored annually in the northern Gulf of Mexico since the 1970s (Rabalais and Turner 2001; Osterman et al. 2005), with an emphasis on regions of coastal Louisiana affected by Mississippi River discharge. The Mississippi River drains approximately 40% of the continental United States and delivers tremendous quantities of nutrients, sediment, and freshwater to the northern Gulf (National Research Council 2008). Analyses of sedimentary cores indicate that anthropogenic eutrophication has increased in the Louisiana Bight since the 1950s (Turner and Rabalais 1994; Rabalais et al. 2007; Osterman et al. 2011) (Fig. 1). Hypoxic conditions have also increased over time in the Louisiana Bight since they were first reported in the 1970s (Diaz and Rosenberg 2008). Hypoxic conditions on the Louisiana shelf result from the decomposition of organic matter and the seasonal stratification of the water column (Rabalais et al. 2002). Today this region hosts one of the largest ‘dead zones’ in the world (Rabalais et al. 2002).

In contrast to the Louisiana Bight, eutrophic conditions have historically been more spatiotemporally restricted in the Mississippi Bight seaward of the Mississippi-Alabama barrier islands (Brunner et al. 2006 and references therein). Areas of the Mississippi Bight are affected by Mobile Bay outflow, yet the Mobile Bay watershed is less than 5% the size of the Mississippi River watershed, and consequently the delivery of freshwater, nutrients, and sediments to the adjacent continental shelf are markedly less (Van Der Zwaan 2000). Circulation seaward of the Mississippi-Alabama barrier islands is generally from east to west (Darnell 2015), yet years of high Mississippi River discharge bring freshwater plumes to the Mississippi-Alabama shelf (Brunner et al. 2006). These large, but infrequent, freshwater fluxes from the Mississippi River have been associated with spatially restricted hypoxic conditions in the Mississippi Bight since at least the 1950s (Brunner et al. 2006) (Fig. 1). As in coastal Louisiana, hypoxic conditions on the Mississippi-Alabama shelf are caused by nutrient delivery and enhanced primary production as well as stratification of the water column (Brunner et al. 2006). In contrast to the Mississippi-Alabama shelf, Mobile Bay has a much longer history of hypoxia; hypoxic conditions were first reported in the estuary in the nineteenth century and continue to the present-day (May 1973; Rabalais et al. 1985).

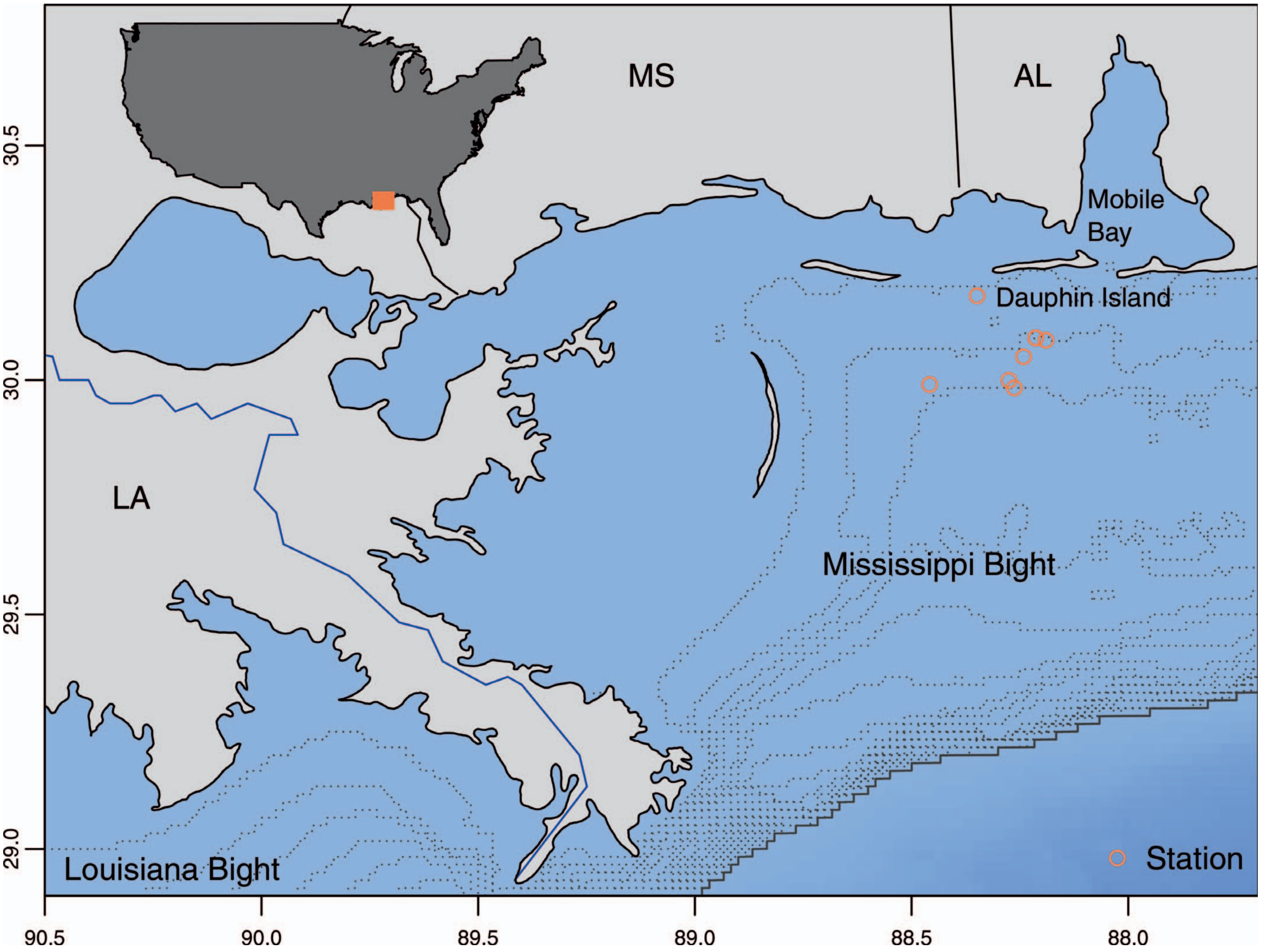

FIG. 2.—Location map. Orange square denotes the location of the study area in the northern Gulf of Mexico (North America). Detailed map includes stations sampled in this study on the continental shelf seaward of the Mississippi-Alabama barrier islands. Ten-meter bathymetric contours (dotted lines) are plotted out to the continental shelf break (solid gray line). The Mississippi River is indicated on the detailed map by the blue line.

MATERIALS AND METHODS

We collected live-dead samples from multiple stations on the continental shelf seaward of Dauphin Island, Alabama in May 2015 and June 2016 (Fig. 2, Table 1). We focused on shelf localities in order to examine the effects of regional, rather than point-sourced, increases in nutrients in relatively well-mixed habitats that have not been subject to extensive seasonal hypoxia. Time averaging of molluscan remains also tends to be greater in shelf versus inshore environments (Flessa and Kowalewski 1994; Kidwell 2013; Tomašových et al. 2014, 2016), which increases the likelihood that dead individuals in our samples predate the onset of anthropogenic eutrophication in the Mississippi Bight (Brunner et al. 2006) (Fig. 1). Most of our samples were collected from water depths of approximately -20 meters, west of the Mobile Bay Channel (Fig. 2, Table 1). Surficial sediments in this area tend to be dominated by fine siliciclastic sand (Doyle and Sparks 1980); at station AL7/AL8, a site where we have collected quantitative grain size data, sediments consist of 75% finer-grained sand, 15% medium-grained sand or coarser size classes, and 10% silt and clay, by weight.

Surficial sediments were collected using a Grey O'Hara style box corer. The box corer took a 0.1 m^2 core and 150 kg of weight was added to the corer in order to penetrate the upper 10 to 30 cm of sediment. Multiple replicate live-dead samples (from 3 to 54) were collected at each station; because of substantial dead shell material, a quarter of each core was typically sieved and processed for later study. Samples were sieved through a 2 mm mesh and all live and dead mollusks larger than 2 mm were retained. Live specimens were sorted while offshore in order to keep track of sample sizes which can be quite limited due to sparse and/or patchy live populations.

Live samples were stored in 95% ethanol during the first year of the project. This is a standard benthic sampling protocol for preserving soft tissues. Ethanol however can result in fine-scale surface alteration of molluscan shells through dissolution (Geiger et al. 2007). This fine-scale alteration can obscure features of the prodissoconch while having no apparent effect on the macroscopic conditions of shell. Consequently, during the second year of the project all live specimens were frozen and later air-dried in a vented hood prior to preparation for scanning electron microscopy.

For our comparison of larval shell size, we focus on the bivalve *Nuculana acuta* because of its abundance in living and death assemblages on the Alabama shelf. In our two years of sampling at station AL7/AL8, *N. acuta* comprised approximately 40% of live specimens (data pooled across

TABLE 1.—*Stations sampled in this study. Data include latitude, longitude, water depth in meters, sampling date, and sampling gear, as well as total number of live and dead Nuculana acuta specimens from each station whose larval shells were examined using a scanning electron microscope.*

Station number	Latitude	Longitude	Water depth (m)	Sample dates	Gear	# Specimens
AL2	30° 05.42′N	88° 12.80′W	19.7	May 2015	Box	384
AL7	30° 05.39′N	88° 12.79′W	19	May 2015	Box	40
AL8	30° 05.39′N	88° 12.83′W	19.8	June 2016	Box	55
AL9	30° 10.80′N	88° 20.97′W	12.6	June 2016	Box	2
AL10	29° 59.47′N	88° 27.50′W	27.5	June 2016	Box	2
AL11	29° 59.00′N	88° 15.77′W	29.3	June 2016	Box	6
AL12	29° 59.99′N	88° 16.53′W	27.6	June 2016	Box	5
AL13	30° 03.01′N	88° 14.50′W	21.4	June 2016	Box	6
AL14	30° 05.12′N	88° 11.43′W	19.7	June 2016	Box	13

all replicate live samples collected at the site) and approximately 13% of dead individuals (data for one of our replicate dead samples). *Nuculana acuta* is a deposit-feeding, infaunal, protobranch bivalve that commonly occurs in organic-rich sands (Mikkelsen and Bieler 2008; Tunnell et al. 2010). *Nuculana acuta* live between 0 and -274 m throughout the Gulf (Turgeon et al. 2009; Tunnell et al. 2010). *Nuculana* are lecithotrophic and have relatively large eggs, short larval durations ($<$ 12 hours), and limited dispersal distances (Ansell et al. 1978; Marine Macrofauna Genus Trait Handbook 2017). *Nuculana* individuals live for approximately 10 years (Moss et al. 2016), and their relatively short generation times and limited dispersal make them well suited for assessing life history adaptation in response to anthropogenic eutrophication.

All live (N = 129), and a subsample of dead (N =384), *N. acuta* specimens were examined using a scanning electron microscope (Evex Mini-SEM SX-3000). Given our protocol for picking live specimens offshore at the time of collection, we were unable to use Rose Bengal stain to definitively identify live individuals. Consequently some dead, but still articulated, specimens may have been included in our live data set. These dead but still articulated specimens may be less well preserved than specimens that were truly alive at the time of sampling thus subsequent filtering of our data according to taphonomic condition (see below) may remove "pseudo-live" as well as poorly preserved dead specimens from our analyses.

The *N. acuta* PI has several distinctive features compared with later growth (Malchus and Sartori 2012): (1) distinctive corrugated surface; (2) prominent ring delimiting the margin; and (3) greater convexity (Fig. 3A). PI diameters were measured along the long-axis of the larval shell, parallel to the hinge. We examined dead specimens with intact umbos that macroscopically preserved surface ornamentation. Among these, considerable fine-scale variation in taphonomic condition was visible with the SEM. Because such variation might affect live-dead comparisons of PI size, each specimen was assigned a taphonomic grade using a four part scale (Fig. 3).

Several potential sources of measurement error need to be considered, especially when analyzing PI data collected by multiple individuals. PI measurements may be sensitive to the orientation of specimens on the SEM stub as well as variation in the working distance set between specimens and the detector. Measurements may also vary for less well preserved specimens that lack distinct PI margins. To assess these potential sources of measurement error, (1) we remeasured the PI diameters of two specimens twelve times each; and (2) we replicated our study using data gathered by different individuals in two successive years. When live-dead comparisons are restricted to data gathered by single individuals, measurement error may add noise but is not expected to result in a bias of live versus dead PI size. Mean PI size measurement error for an individual data collector was 2.6 microns with a standard deviation of 0.6 microns (data collected by Williams).

To assess variation among data collectors, each data collector examined a randomly chosen subsample of 41 live and dead *N. acuta* specimens. We observed systematic differences in PI size between data collectors (Torstenson and Williams) which may reflect differences in their preparation of specimens for the SEM and/or delimitation of PI margins. PI measurements were significantly positively correlated (Spearman Rho = 0.76, $p < 0.001$), with Torstenson's measurements tending to be larger than those of Williams ($t = -7.7$, df = 39; $p < 0.001$) (Fig. 4). We used reduced major axis (model II) regression to model the relationship between the measurements made by Torstenson and Williams and then transformed Williams' data using this model (slope = 1.06, intercept = 13.72; $R^2 = 33.4$) in order to analyze a fuller dataset and make use of a subset of Williams' PI measurements that had associated radiocarbon dates (Fig. 4). Model II regression is recommended when both x and y variables have measurement error (Legendre and Legendre 1998). In the results that follow we present the pooled data for live and dead specimens collected in 2015 and 2016 which include Williams' transformed measurements. We also show that restricting our analyses to data collected by a single individual yields qualitatively similar results.

To assess (1) the magnitude of time-averaging of *N. acuta* death assemblages on the continental shelf seaward of Dauphin Island; (2) long-term variation in *N. acuta* PI size through the Holocene; and (3) the relationship between PI taphonomic grade and shell age, we dated a subset of dead shells using AMS ^{14}C at the Woods Hole Oceanographic Institution NOSAMS facility. One hundred *N. acuta* shells were randomly sampled from all of the dead specimens examined in the SEM. These specimens varied considerably in taphonomic grade; 65% had sufficiently well-preserved prodissoconchs that we could generate a PI size estimate whereas the remaining 35% were not. We used Calib6.0 to convert from radiocarbon ages to calendar years (Stuiver and Reimer 1993), calibrated with a regional marine reservoir correction (ΔR) of 28 years (standard deviation = 16). Our regional marine reservoir correction was a weighted mean ΔR derived from three nearshore mollusk specimens collected along the northwest coast of Florida (Hadden and Cherkinsky 2016), and one coral specimen collected from -20 m in the Flower Garden Banks (Wagner et al. 2016).

All *N. acuta* PI measurements and radiocarbon ages are archived in the Online Supplemental material. Live and dead *N. acuta* specimens analyzed for this study are stored in the Paleobiology Collections in the Department of Earth and Environment at Franklin and Marshall College.

RESULTS

Live-collected individuals comprise 25% (live N = 129) of all *N. actuta* shells (live and dead N = 513) that we examined with the SEM. Prodissoconch measurements were made on 48% (N = 186) of dead-collected shells and 72% (N = 93) of live-collected shells; the PI was not sufficiently well-preserved on the other 234 valves to generate a size

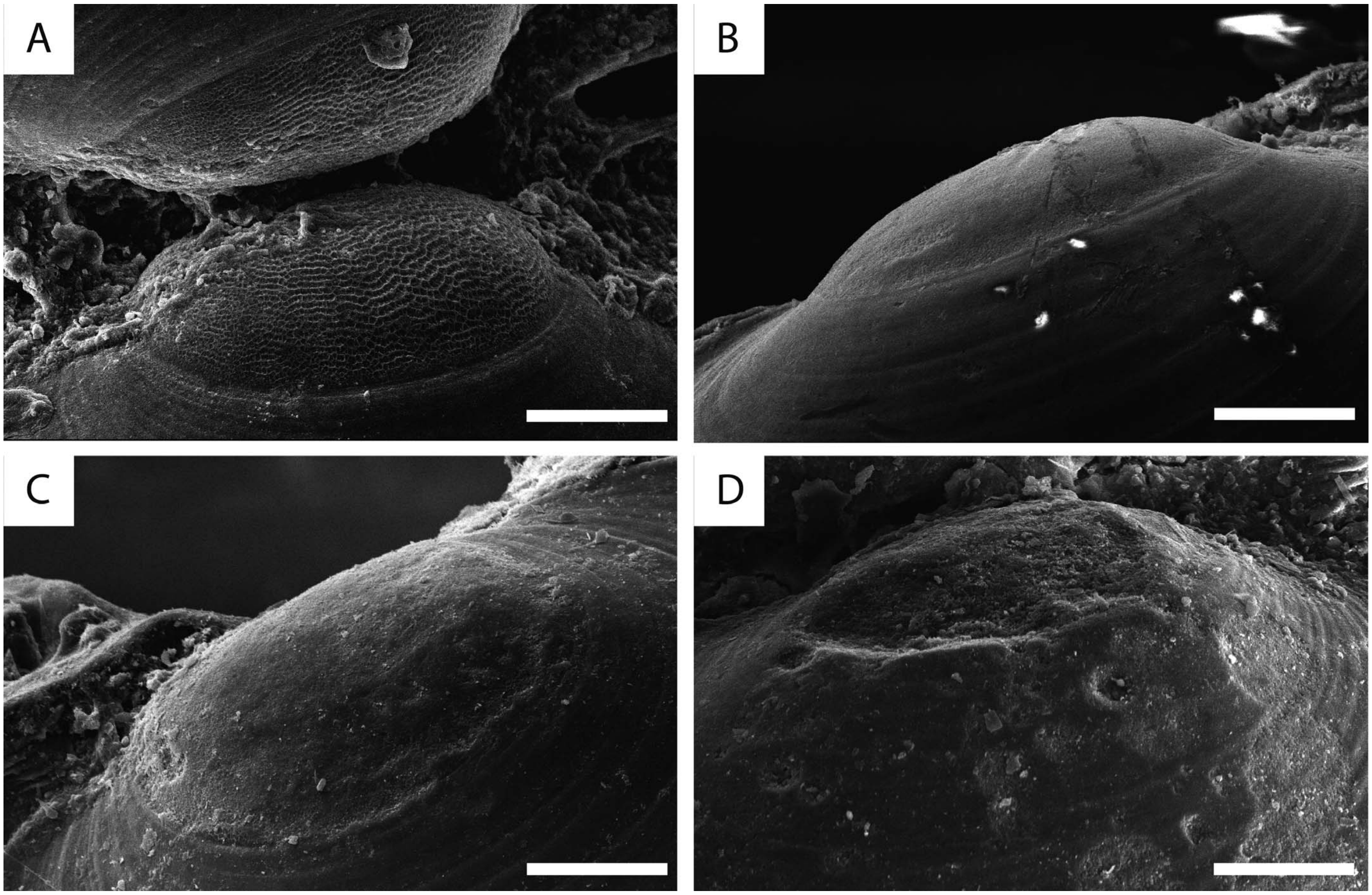

FIG. 3.—Taphonomic grades used to characterize the prodissoconchs (PI) of live and dead *Nuculana acuta* specimens. Figured specimen for Taphonomic Grade 1 exhibits *Nuculana*'s characteristic corrugated PI surface, prominent PI margin, and greater PI convexity relative to growth later in ontogeny. White scale bar = 50 microns. **A**) Taphonomic Grade 1: PI margin completely preserved with negligible damage, PI relief completely preserved, surficial ornamentation of adult shell completely preserved, and portions of the corrugated PI surface preserved. **B**) Taphonomic Grade 2: both PI anterior and posterior margins preserved, PI relief partially preserved, surficial ornamentation on adult shell present but may be worn. **C**) Taphonomic Grade 3: either anterior or posterior margin of PI preserved, PI relief partially preserved or absent, surficial ornamentation on adult shell present but worn. **D**) Taphonomic Grade 4: lacks distinct PI margin, PI relief and surficial ornamentation of adult shell not preserved.

estimate. Live-dead comparison using this full dataset (i.e., shells of all taphonomic grades collected in both years, measured by multiple data collectors) reveals a modest difference in average prodissoconch size, with specimens in the living assemblage having, on average, smaller prodissoconchs than specimens in the associated death assemblage (Fig. 5A, Table 2). The mean prodissoconch size of dead-collected *N. acuta* in the full dataset was 156 microns (standard deviation = 9.9 microns) whereas the mean prodissoconch size of live-collected *N. acuta* was 152.5 microns (standard deviation = 9.8 microns). Because some subsets of our PI dataset are not normally distributed, we report the results of both parametric (Student's t-test) and non-parametric (Mann-Whitney U test) statistical tests of mean and median PI values in living and death assemblages (Table 2).

Similar results are observed when live-dead comparisons are restricted to data collected by a single individual using live specimens collected during the first versus second field season (i.e., Williams data for 2015 live-collected specimens vs. Torstenson data for 2016 live-collected specimens). In both data subsets, live specimens have prodissoconchs that are approximately 2 to 3 microns smaller on average than dead specimens, although the statistical significance of this live-dead difference varies (Table 2).

The median age of dead *N. acuta* collected offshore Dauphin Island is 592.5 years before present (YBP), with an interquartile range from 174 to 1040 YBP (Fig. 6); all post-bomb ("> Modern") specimens were arbitrarily assigned an age of 25 YBP in calculating this median value. More than 75% of our dated *N. acuta* shells predate the mid-twentieth century rise of chemical fertilizers. Prodissoconch measurements are available for 65 of the 100 radiocarbon-dated dead *N. acuta* specimens. For these dated specimens, there is no secular linear trend in PI size over the past 3100 years (Fig. 7; linear regression model, $p = 0.69$). Furthermore, there is no evidence for a non-linear reduction in PI size over time (Spearman Rho = -0.12, $p = 0.35$). The average PI size for *N. acuta* that lived after the onset and/or intensification of anthropogenic eutrophication in the 1950s (i.e., all live specimens and dead shells with post-bomb radiocarbon age estimates) however was significantly smaller than that of older specimens ($p = 0.001$ for both Student's t-test and Mann-Whitney U test of mean and median PI size values, respectively). The observed live-dead difference in *N. acuta* prodissoconch size thus reflects a relatively recent (e.g., decadal scale) shift in the life histories of populations on the Alabama shelf (Fig. 7), coincident with the onset and/or intensification of anthropogenic eutrophication.

The shells that we measured vary in taphonomic grade. In the full live-dead dataset, 8% of shells were scored as taphonomic grade 1, 20% as grade 2, 27% as grade 3, and 45% as grade 4. Taphonomic variation could affect live-dead comparisons by generating apparent live-dead differences in PI size where none existed; for example, if, prodissoconch preservation

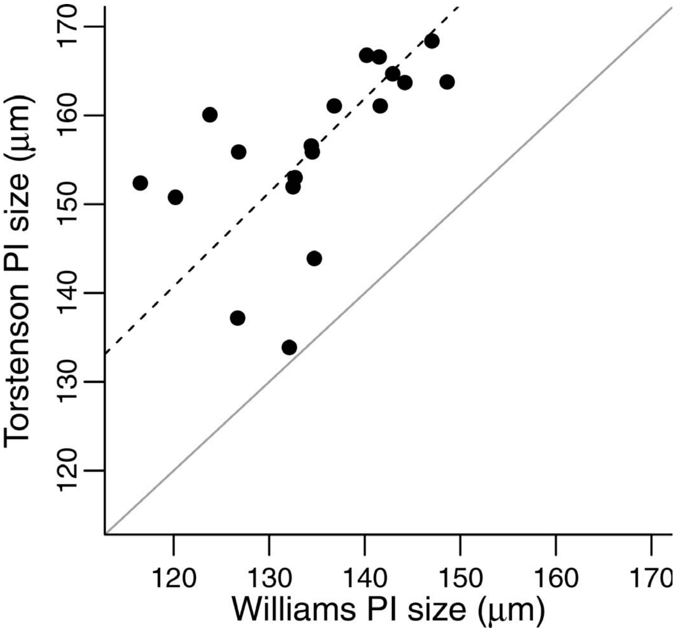

FIG. 4.—Systematic differences exist between measurements of PI size made by different data collectors (Williams and Torstenson). PI size data collected by different individuals are significantly positively correlated, though measurements of smaller prodissoconchs tend to be more variable. The dashed black line denotes the reduced major axis regression model used to transform Williams' PI data; the solid gray line is the 1:1 line. Note that this subsample of live and dead *N. acuta* shells includes specimens of all taphonomic grades.

tends to decline with postmortem age and poor preservation results in the systematic under- or overestimation of prodissoconch size. Alternatively, taphonomic variation could mask real live-dead differences, if measurement error tends to increase as the quality of shell preservation decreases. To determine if the quality of preservation declines with increasing shell age, we compared the median ages of shells of each taphonomic grade. The median ages of less well-preserved shells (taphonomic grades 3 and 4) tend to be greater than those of shells that are in better condition (taphonomic grades 1 and 2) (Fig. 8A). The median ages of shells categorized as taphonomic grades 3 and 4 were 681 and 655 YBP respectively, whereas the median ages of shells categorized as taphonomic grades 1 and 2 were 182 YBP and 236 YBP. Yet, all four taphonomic grades exhibit substantial variation in shell age (Fig. 8A), and Mann-Whitney tests indicate that the median ages of shells of each taphonomic grade are statistically indistinguishable with the exception of grades 2 versus 4 ($p = 0.03$). These data provide little support for a systematic relationship between taphonomic grade of the prodissoconch and shell postmortem age (i.e., a "taphonomic clock").

If the margins of the prodissoconch are not as well preserved, PI size could be underestimated. We assessed this potential bias by comparing the PI sizes of shells of different taphonomic grades and found little difference in PI size as a function of preservation (Fig. 8B). The median PI sizes of less well-preserved dead shells (taphonomic grades 3 and 4) were not significantly smaller than those of more well-preserved shells (taphonomic grades 1 and 2) (Fig. 8B). All four taphonomic grades exhibit substantial, and overlapping variation in P1 size, and Mann-Whitney tests indicate that the median PI sizes of shells in each taphonomic grade are statistically indistinguishable with the exception of taphonomic grades 2 versus 3 ($p = 0.01$). No evidence is found in this dataset for systematic variation in PI size with taphonomic grade.

To evaluate the robustness of the live-dead comparisons of PI size to potential taphonomic biases, we restricted our statistical comparisons to

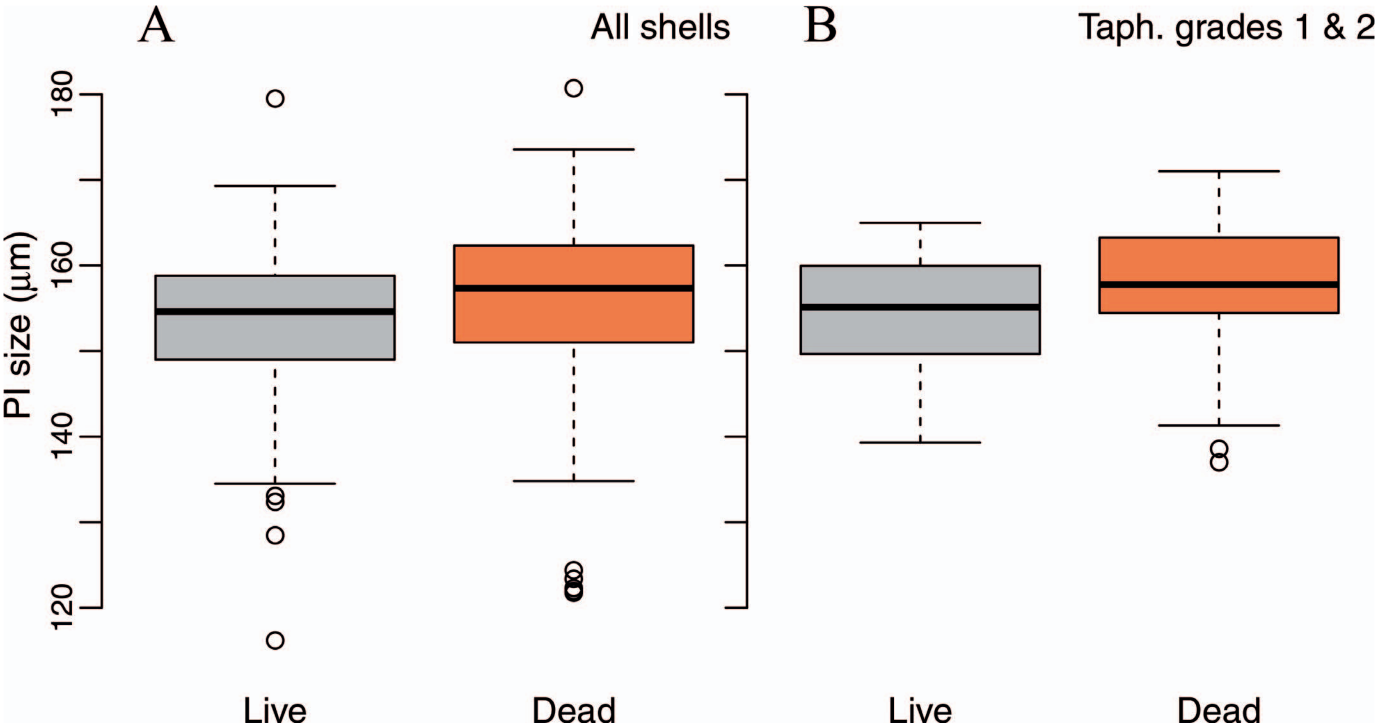

FIG. 5.—Comparison of *Nuculana acuta* prodissoconch (PI) size in living and death assemblages in coastal Alabama. **A**) All live-dead PI data (full dataset), including specimens of all taphonomic grades. **B**) Live-dead PI data restricted to only better preserved specimens (Taphonomic Grades 1 and 2). *Nuculana acuta* mean PI size is significantly smaller in the living assemblage relative to the historical death assemblage by approximately 3.5 microns.

TABLE 2.—*Variation in Nuculana acuta mean prodissoconch (PI) size in living and death assemblages in coastal Alabama. All PI measurements are in microns. The "Full" dataset includes measurements made by Torstenson and Williams using specimens collected in both years of the study. "Williams" and "Torstenson" summarize subsets of the data collected by individual data collectors. The live specimens examined by Torstenson were collected in the second year of the study and were not exposed to ethanol. "Taph. Grade" refers to the range of taphonomic grades of shells included in that comparison. Student's t-test and Mann-Whitney U test results are for the live-dead comparison of mean and median PI sizes for that data subset. ΔPI denotes live minus dead mean PI values for that data subset.*

		Live					Dead					Live-Dead	T-test			Mann-Whitney U test
Dataset	Taph. grade	Mean	SD	Median	Interquartile range	N	Mean	SD	Median	Interquartile range	N	ΔPI	t	df	*p*	*p*
Full	All	152.5	9.8	154.6	149.0–158.8	93	156	9.9	157.4	151.1–162.3	186	-3.5	-2.79	186	0.006	0.002
	1 & 2	154.4	6.5	155.1	149.7–159.9	31	158.4	7.3	157.8	154.4–163.2	87	-4	-2.85	59	0.006	0.007
Williams	All	156.2	5	156.2	153.6–160.0	34	159.3	9.1	160.1	154.5–165.3	98	-3.1	-2.46	105	0.015	0.006
Torstenson	All	150.4	11.1	151.5	143.4–157.8	59	152.3	9.4	153.9	148.5–158.6	88	-1.9	-1.07	110	0.285	0.221
	1 & 2	151.4	6.2	150.1	149.0–155.4	17	154.6	6.4	155.3	150.8–158.6	37	-3.2	-1.77	32	0.086	0.078

well-preserved live and dead specimens (taphonomic grades 1 and 2). As in the analyses of the full dataset, mean prodissoconch size in the well-preserved live sample was significantly smaller than in the well-preserved dead sample ($t = -2.85$, df = 59; $p = 0.006$; Fig. 5B). In this subset of our data, the mean live prodissoconch size was 4 microns smaller than that of the associated death assemblage. Similarly, no secular trend in PI size is present in this restricted dataset over the past 3100 years (linear regression model, $p = 0.57$).

Because contact with ethanol can result in the dissolution of molluscan larval shells (Geiger et al. 2007), we reran our analyses on a dataset restricted to: live-dead specimens of taphonomic grades 1 and 2 that were not exposed to ethanol and were all measured by a single data collector (Torstenson). Although this t-test was not statistically significant ($t = -1.77$, df = 32; $p = 0.09$), the live-dead difference in mean PI size (3.2 microns) was comparable to other partitions of the data (Table 2).

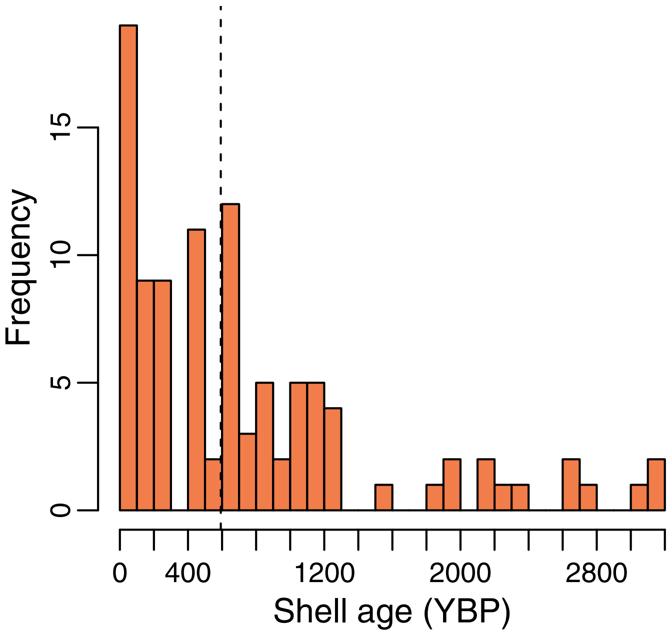

FIG. 6.—Age frequency distribution of *Nuculana acuta* dead shells (N = 100) collected from surficial sediments on the inner shelf seaward of the Mississippi-Alabama barrier islands. The median age of dead *N. acuta* is 592.5 YBP (dashed line), with an interquartile range from 174 to 1040 YBP; modern (i.e., post-bomb) specimens were arbitrarily assigned an age of 25 years before present (YBP).

In summary, we document a modest reduction in *N. acuta* prodissoconch size in present-day populations on the Alabama shelf relative to a historical baseline provided by associated death assemblages (Fig. 5, Table 2). The magnitude of this live-dead difference in prodissoconch size (approximately 2 to 4 micron reduction) is consistent across various data treatments, with statistical significance varying somewhat, in part, due to variations in sample size (Table 2).

DISCUSSION

Humans currently play a global role in nitrogen and phosphorous cycles (Vitousek et al. 1997a; Seitzinger et al. 2005; Canfield et al. 2010). Human activities, including fertilizer production, landscape modification, and the combustion of fossil fuels, have doubled the rate of nitrogen fixation on land, such that unreactive atmospheric nitrogen is converted to biologically available forms of nitrogen at an unprecedented rate (Vitousek et al. 1997b;

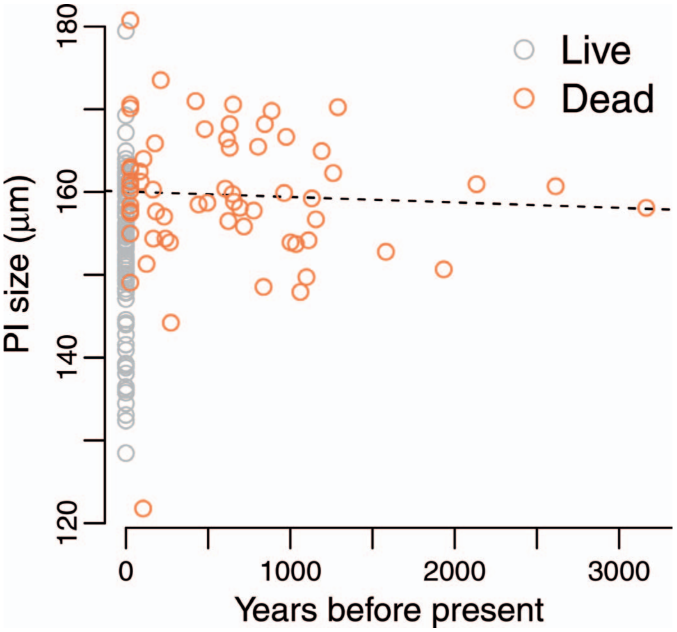

FIG. 7.—*Nuculana acuta* PI size over time. There is no secular trend in PI size over the past 3100 years for dated shells in the death assemblage (dashed line, linear regression; $p = 0.69$). The observed live-dead difference reflects a recent shift in the life histories of *N. acuta* populations on the Alabama shelf.

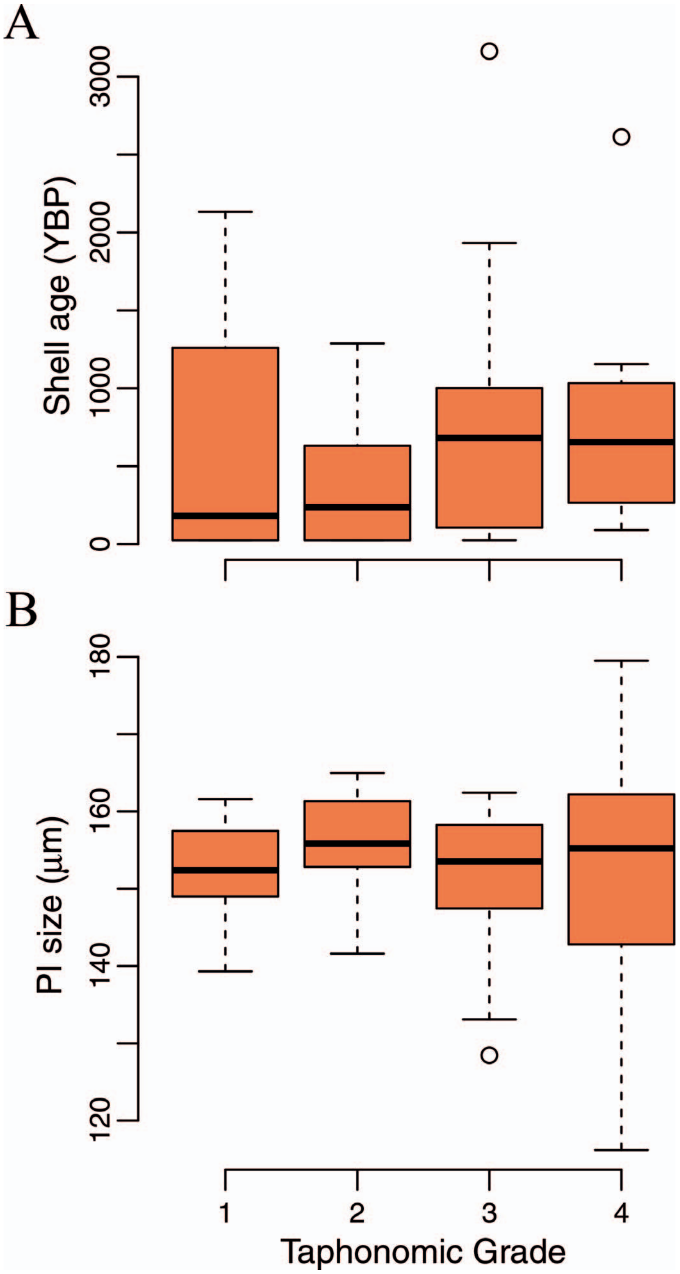

FIG. 8.—Variation in *Nuculana acuta* shell age and PI size with respect to taphonomic grade. **A**) The median ages of less well-preserved *N. acuta* shells (grades 3 and 4) tend to be greater than those of shells that are in better condition (grades 1 and 2). Yet all taphonomic grades exhibit substantial variation in shell age and the median ages of shells of each taphonomic grade are statistically indistinguishable with the exception of grades 2 versus 4. **B**) All four taphonomic grades exhibit substantial, and overlapping variation in P1 size, and Mann-Whitney u-tests indicate that the median PI sizes of *N. acuta* shells in each taphonomic grade are statistically indistinguishable with the exception of taphonomic grades 2 versus 3.

Gruber and Galloway 2008). The use of nitrogen fertilizers has also increased markedly; between 1960 and 2000 fertilizer application increased by approximately 800% (Canfield et al. 2010). The use of phosphorus as an agricultural fertilizer has doubled phosphorus inputs to the environment over background levels due to weathering processes (Seitzinger et al. 2005).

Increased delivery of nitrogen and phosphorous to coastal ecosystems due to human activities has spurred rates of primary production (Smith 2006). Life history theory predicts that this bottom-up effect will relax life history tradeoffs and enhance juvenile survival at higher trophic levels. Consequently, individuals that produce more numerous, smaller eggs are expected to have greater fitness which should lead to a reduction in mean egg size over time in consumer populations. Whether this is observed may depend on the strength and duration of selection, the standing phenotypic variation in the population, and the strength of associated abiotic physical stresses, in particular hypoxia. We tested the hypothesis that anthropogenic eutrophication has led to the reduction of egg size over time by comparing the larval shells of the marine bivalve, *Nuculana acuta*, in living and death assemblages from the northern Gulf of Mexico. Consistent with our hypothesis, we found that the *N. acuta* living on the inner shelf seaward of the Mississippi-Alabama barrier islands had smaller larval shells than those in associated death assemblages.

A variety of post-mortem processes could potentially affect our live-dead comparison of PI size, however the live-dead difference observed in the full dataset was maintained in all of the sensitivity tests. Storing live-collected specimens in ethanol, for example, can result in microscale dissolution which could inflate live-dead differences through the underestimation of larval shell size in specimens with less distinct PI margins. This bias should be detectable in the taphonomic condition of live specimens, and when specimens preserved in ethanol, and/or more poorly preserved live and dead specimens, are excluded from the analysis, the live-dead difference in mean PI size remains. Similarly, the systematic differences observed among data collectors in PI size estimates could yield apparent live-dead disagreement if different individuals measured live versus dead specimens. This was not the case in our study and we were able to account for this potential bias by limiting analyses to individual data collectors. We found that the magnitude of the live-dead difference in mean PI size was comparable across these data partitions although the statistical significance varied (Table 2), presumably due to differences in sample size and variance in size estimates. Studies involving multiple investigators should include training protocols that reduce measurement error among individuals (e.g., Rothfus 2004) and/or use statistical methods that allow measurement error to be explicitly accounted for in the analysis (e.g., Jacobson et al. 2010). Because PI size estimates can systematically vary among data collectors, we recommend: (1) each data collector measure an overlapping subset of specimens such that differences among individuals can be quantified and, where necessary, used to transform size measurements; and (2) each data collector measure both live and dead specimens such that analyses holding individual data collectors constant are possible.

The diameter of the earliest phase of larval shell growth in marine bivalves (PI) is positively correlated with egg size (Malchus and Sartori 2012). Interspecific variation in marine invertebrate egg size can inversely correlate with temperature and food availability (Lutz and Jablonski 1978; Moran 2004; Marshall and Burgess 2015); whether these environmental factors explain intraspecific life history variation is not as well known (though see Lutz and Jablonski 1978). Factors that affect the generation time of organisms, such as fishing and disease, can also contribute to egg size variation (Powell et al. 2011 and references therein). The observed live-dead difference in *N. acuta* PI size on the Alabama shelf could result from changes in primary production, temperature, or some combination thereof, over time, and may also be affected by top-down changes in predation pressure resulting from commercial fishing and/or hypoxia. Increased phytoplankton production due to anthropogenic eutrophication could explain the observed live-dead difference, but so might increases in nutrients or temperature regionally over longer (centennial to millennial) time scales. We distinguished among these hypothesized drivers of *N. acuta* life history variation by temporally calibrating the PI measurements.

Analyses of a subset of measured specimens with associated radiocarbon dates indicate that the observed live-dead difference in PI size (approximately 3 microns) does not reflect a long-term reduction in egg size over the past 3100 years but instead marks a relatively recent life history shift. Sea surface temperatures in the northern Gulf of Mexico have increased by approximately 2° Celsius since the Little Ice Age (~ 250 YBP) (Richey et al. 2007; Poore et al. 2009) which could have resulted in a reduction in mean egg size, yet there is no support for a linear relationship between *N. acuta* PI size and shell age over this more recent interval of time ($p > 0.05$ for a linear regression model using only specimens younger than 250 YBP). The effects of temperature on life-history traits can be non-linear (e.g., Lappalainen et al. 2008), yet there is also no evidence for a non-linear decrease in PI size over the past 250 years (Spearman Rho = –0.19, $p = 0.36$). The rate of change in mean sea surface temperature has increased over time; between 1985–2009 in the southeastern Gulf of Mexico and Caribbean, for example, average sea surface temperature increased by 0.29° C decade^{-1} (Chollett et al. 2012). As such, recent increases in food availability due to anthropogenic eutrophication (Brunner et al. 2006; Rabalais et al. 2007), perhaps in combination with increasing sea surface temperatures, may explain the observed live-dead difference in *N. acuta* life history. Whether this live-dead difference in *N. acuta* life history reflects adaptation or plasticity cannot be determined from the data that are currently available. Rapid evolution in egg size has however been documented previously in other systems (Heath et al. 2003). Furthermore, plasticity can also lead to adaptation provided it produces a mean phenotype that promotes persistence under new environmental conditions yet is somewhat distant from the optimal value favored by selection (Ghalambor et al. 2007).

Core-top foraminifera assemblages indicate the presence of eutrophic conditions in the Mississippi Bight as early as the 1950s (Brunner et al. 2006 and references therein). Yet to date, anthropogenic eutrophication in the Mississippi Bight tends to be localized and more temporally variable than locations in the Louisiana Bight (Brunner et al. 2006; Rabalais et al. 2007). Using Kidwell's (2007, 2009) semi-quantitative scale for classifying the severity of anthropogenic eutrophication (AE), our study area seaward of the Mississippi-Alabama barrier islands would likely be classified as AE1; demonstrable evidence exists for the occurrence of anthropogenic eutrophication (AE1) (Brunner et al. 2006), and both live and dead samples contain benthic species such as *N. acuta* that are commonly associated with eutrophic and hypoxic environments. Yet in contrast with the Louisiana Bight, greater uncertainty remains about whether this stress will be present at a specific location and/or in a given year (Rabalais et al. 1985; Brunner et al. 2006). Given the cultural and environmental history of eutrophication in coastal Alabama, the observed live-dead difference in *N. acuta* PI size may be modest in comparison with sites elsewhere in the Gulf that have experienced more sustained histories of nutrient enrichment.

We expect that the magnitude of live-dead reduction in PI size varies as a function of the magnitude of anthropogenic eutrophication. This hypothesis can be tested by comparing regions such as the Louisiana Bight and Mississippi Bight, with the expectation of greater live-dead disagreement in *N. acuta* PI size in the Louisiana Bight. Such a comparison would also allow us to distinguish the effects of natural versus anthropogenic eutrophication. The Mississippi River's delivery of nutrients has supported tremendous primary production in the marine ecosystems of the northern Gulf of Mexico for millennia (Osterman et al. 2008); evident in part by the network of offshore oil and gas wells that mine the region's hydrocarbon-rich sedimentary deposits. Farming and other human activities have enhanced the delivery of nitrogen and phosphorous to Gulf ecosystems, further spurring primary production (Turner and Rabalais 2003; Rabalais et al. 2007). Geographic differences in phytoplankton production that existed prior to these human activities may be reflected in geographic clines in larval shell size in death assemblages from across the northern Gulf. Comparisons of death assemblages (dead-dead analysis) may provide a pre-anthropogenic baseline, whereas geographic variation in live-dead agreement may serve as an indicator of recent life history shifts in response to anthropogenic eutrophication. Coupled dead-dead and live-dead comparisons in the northern Gulf may provide a framework for distinguishing the effects of natural versus anthropogenic eutrophication on marine life histories.

It is possible however that in expanding spatial scope, we find that live-dead discordance in PI size does not vary markedly despite geographic variation in anthropogenic eutrophication. *Nuculana acuta* prefer meso- and eutrophic environments (Baustian and Rabalais 2009; Briggs et al. 2015, 2017) and thus may have not experienced the onset of anthropogenic eutrophication in the northern Gulf as a significant ecological disturbance (Kidwell 2007). If so, PI size in this species may turn out to be a conservative indicator of the impacts of anthropogenic eutrophication relative to community-level live-dead metrics such as taxonomic fidelity and the percentage of organic-loving species (Kidwell 2007, 2009; Leshno et al. 2015; Negri et al. 2015). Species with more limited tolerance for eutrophication, and/or benthos in coastal regions that have historically received more limited terrigenous input (e.g., west Florida shelf), may be more likely than *N. acuta* to exhibit live-dead discordance in life history characteristics in response to recent nutrient enrichment. Predicted life history responses to enhanced food supply may also be mediated by differences in developmental mode. *Nuculana acuta* are lecithotrophic species with relatively short larval durations (Ansell et al. 1978; Marine Macrofauna Genus Trait Handbook 2017). Consequently, relatively limited dispersal among *N. acuta* populations may result in more pronounced clines in PI size along eutrophication gradients than are observed in planktotrophic species with longer larval durations and greater dispersal potential. Although evidence for local adaptation of life history traits such as egg size to nutrient enrichment may be weaker in planktotrophic versus lecithotrophic species, previous work on planktotrophic species has shown that PI size varies inversely with broad-scale changes in regional primary production (Moran 2004). Future studies comparing the effects of eutrophication on PI size across species that differ in developmental mode, and consequently population connectivity, would be beneficial.

Although anthropogenic eutrophication and associated reductions in dissolved oxygen concentrations could lead to life history adaptation in aquatic food webs by increasing food availability to basal consumers and by reducing predation pressure, these trophic effects may be swamped by abiotic physical stresses if hypoxia is pronounced (Alexander et al. 2017). Hypoxia can lead to population decline and extirpation as organisms physiologically grapple with maintaining function under oxygen stress (Diaz and Rosenberg 1995; Wu 2002). In settings of strong eutrophication, the effects of recent eutrophication may manifest as live-dead shifts in community composition and/or inter- and intraspecific differences in body size, with generally smaller individuals occurring in living assemblages (Diaz and Rosenberg 1995; Payne et al. 2011).

CONCLUSIONS

Given a trade-off between the size and number of eggs that an individual can produce, life history theory predicts that increased food availability will lead to a reduction in mean egg size over time. Previous studies have shown that the egg sizes of suspension-feeding marine mollusks can evolve in response to regional shifts in primary production over geologic time. Using a live-dead approach, we assessed whether anthropogenic changes in the delivery of nutrients to coastal ecosystems in the northern Gulf of Mexico resulted in reductions in the size of marine bivalve larval shells (a proxy for egg size) over historical time scales. We found that the mean PI size of our live sample of *Nuculana acuta* in coastal Alabama was approximately 3 microns smaller than that of the associated death assemblage and that this difference was robust to potential taphonomic biases. This small reduction in PI size is consistent with the modest history of anthropogenic eutrophication on the continental shelf seaward of the Mississippi-Alabama barrier islands. This live-dead discordance reflects a recent shift in *N. acuta* life history, not a longer-term trend over the past 3100 years, and is consistent with life history adaptation to anthropogenic nutrient enrichment. The effects of anthropogenic nutrient enrichment on *N. acuta* life history may be compounded by other biotic and abiotic factors including predatory release due to hypoxia and/or commercial fishing, and increasing sea surface temperatures. Live-dead larval shell data for coastal Alabama provide a baseline for comparison with other regions in the northern Gulf of Mexico that have more sustained histories of anthropogenic eutrophication. Live-dead comparisons of molluscan life history complement existing community-level metrics for assessing the biotic impacts of anthropogenic eutrophication on coastal ecosystems. More broadly, live-dead analyses of molluscan larval traits provide a unique system for investigating life history adaptation in a field context.

ACKNOWLEDGMENTS

For assistance in the field we thank Anik Regan, Luke Grimmelbein, Jared Brush, Kevin Cerna, Danielle Moloney, and Sophia Gigliotti, and the staff of the Dauphin Island Sea Lab, in particular Grant Lockridge, Cy Clemo, Kara Gadeken, and Kelly Dorgan. For assistance in the lab we are grateful to many Franklin and Marshall College students who helped sort live-dead samples. For assistance with radiocarbon dates we thank the staff of the Woods Hole Oceanographic Institution NOSAMS facility, in particular Ann McNichol for her guidance. For input and discussion at various stages of the study, we thank Rowan Lockwood, Susan Kidwell, Tom Rothfus, Craig McClain, Tom Olszewski, Rebecca Terry, and Seth Finnegan. We appreciate the thoughtful reviews of our manuscript provided by Greg Dietl, an anonymous reviewer, and the Palaios Associate Editor, Adam Tomašových. This work was supported by Franklin and Marshall College, the Keck Geology Consortium, the National Science Foundation (NSF-REU1358987), and ExxonMobil Corporation.

SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive:
http://www.sepm.org/pages.aspx?pageid=332.

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Received 18 April 2017; accepted 29 September 2017.