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# Nutrient Pollution and the Molluscan Death Record: Use of Mollusc Shells to Diagnose Environmental Change

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#### ABSTRACT



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Anthropogenic alteration is a persistent and growing problem in coastal marine ecosystems. Changes may have occurred and gone undetected in coastal systems, and analysis of the molluscan death assemblage provides a useful tool for detecting changes where long-term observational monitoring of living organisms has not been conducted.

During the early 1980s, a series of experiments were conducted along Cross Bank, Florida Bay (inside Everglades National Park) to assess the effects of nutrient pollution by seabirds roosting on implanted marker posts on underlying sea grass beds. Over time, *Halodule wrightii* replaced *Thalassia testudinum* as the dominant sea grass at these altered sites. The present study focuses on the effects of this nutrient pollution on the molluscan death assemblage. Two parallel transects were established, one using altered sites as sampling stations and the other using unaltered, *Thalassia*-dominated localities. A series of surficial push cores were collected along these transects (24 in all) to compare compositionally the assemblages on both transects. Results demonstrate detectable differences in the composition of molluscan death assemblages between altered and unaltered sites. Several molluscs were virtually excluded by the change in sea grass composition, and results suggest that differences in root and blade morphology of the two sea grass species are causal factors. Therefore, the results demonstrate that molluscan death assemblages effectively recorded environmental change through some two decades in the study area and that similar environmental changes may be diagnosed elsewhere in coastal ecosystems on the basis of assemblage composition.

ADDITIONAL INDEX WORDS: Molluscan death assemblages, sea grass, carbonate bank, Florida Bay.

#### INTRODUCTION

In general, historical investigations of biotic change in marine ecosystems have been limited to assessments of living organisms. However, because of the time-intensive nature of this work, habitat monitoring may be infrequent and, even in well-studied settings, observational records are only available for the second half of the last century. A ready source of untapped ecological data, spanning both short- and long-term timescales, is available in the form of molluscan shells deposited in the accumulating sedimentary record. The composition of molluscan death assemblages have been shown to reflect, with high fidelity, the living biotas from which they were derived (e.g., FERGUSON, 2003; KIDWELL, 2001; KO-WALEWSKI et al., 2003; MILLER, 1988; PANDOLFI and MIN-CHIN, 1995; PETERSON, 1976). When a persistent environmental change occurs, compositional changes should take place in the associated biota, and evidence of this transition should in turn be recorded in the death assemblage.

In the emerging field of applied paleoecology (KOWALEW-SKI, 2001), several researchers have used novel approaches to address ecological and environmental questions for which paleoecological techniques are well suited (e.g., ARONSON *et*  al., 2002; BREWSTER-WINGARD and ISHMAN, 1999; BREW-STER-WINGARD, ISHMAN, and HOLMES, 1998; BREWSTER-WINGARD, STONE, and HOLMES, 2001; CRONIN *et al.*, 2001; KOWALEWSKI *et al.*, 2000). In a similar vein, while others have recognized and attributed compositional differences in subfossil assemblages to physical or biological causes (PE-TERSON, 1976; TREWIN and WELSH, 1972), the present investigation is the first empirical attempt to assess the benthic marine molluscan response to a known, temporally constrained environmental change resulting from an instance of anthropogenically induced nutrient pollution.

Previous ecological research conducted on Cross Bank, located at the southeastern margin of Everglades National Park inside Florida Bay, caused a nutrient enrichment in local benthic marine environments (POWELL, KENWORTHY, and FOURQUREAN, 1989). During experiments designed to assess the nocturnal feeding habits of wading birds (POWELL, SOGARD, and HOLMQUIST, 1987), it was observed that seabirds roosting on marker posts affected the productivity and composition of underlying sea grass beds (POWELL, KENWOR-THY, and FOURQUREAN, 1989). Original marker posts were removed after the initial work was completed and a new transect was established along Cross Bank, consisting of polyvinyl chloride posts topped with wooden blocks, to measure the effects of nutrient pollution via excrement from pesciverous

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avian occupants of the marker posts, royal terns (*Sterna maxima*) and double-crested cormorants (*Phalacrocorax auritus*). This enrichment induced replacement of local populations of turtle grass, *Thalassia testudinum*, with the more thinly bladed sea grass, *Halodule wrightii* (POWELL *et al.*, 1991). The effects of this type of anthropogenic alteration of the landscape were recognized during the mid-1980s and, as long as the posts remain intact, birds supply the nutrients necessary to maintain *Halodule* populations below. Areas in Florida Bay where *Halodule* is present tend to have higher levels of dissolved organic phosphorus in sedimentary pore waters (FOURQUREAN, ZIEMAN, and POWELL, 1992). Exclusion of *Thalassia* at nutrient-enriched sites is likely the result of superior competition for light resources by *Halodule* (DAWES and TOMASKO, 1988; FOURQUREAN *et al.*, 1995).

Molluscs are among the most promising members of the benthos for historical investigations of marine coastal ecology because they are (1) highly abundant; (2) possess robust skeletons; and (3) have well-understood ecological tolerances. Although groups such as benthic foraminifera have also been shown to be highly effective indicators of salinity (BREWSTER-WINGARD, ISHMAN, and HOLMES, 1998; HAYWARD et al., 2004), molluscs are known to be correlated with substrate type and benthic vegetation (HECK, 1979; JACKSON, 1973; MILLER, 1988). Environmental factors such as dissolution of calcite, transportation, and breakage via predation may influence the fidelity of a subfossil record for historical analysis. For the purposes of the present investigation, these issues are mitigated because Florida Bay is a low-energy, protected carbonate setting and sea grass beds have been shown experimentally to be centers of trapping and binding of sediment, minimizing taphonomic loss, and providing refuge from predation (Almasi et al., 1987; JACKSON, 1973; PETERSON, 1982; PRAGER and HALLEY, 1999; SCOFFIN, 1970). Molluscan death assemblages have been shown to provide faithful indicators of the benthic environments from which they were derived, recording transitions in the relative abundances of taxa on decadal timescales (e.g., FERGUSON, 2003; KIDWELL, 2001). However, because of time averaging, the long-term preservation of transitions on this fine a scale may be compromised (CARROLL et al., 2003; KIDWELL and BOSENCE, 1991; KOWALEWSKI et al., 2000; MELDAHL, FLESSA, and CUTLER, 1997). Therefore, the goal of this investigation is to assess the usefulness of the molluscan death assemblages at the nutrient-enriched sites in Florida Bay as indicators of historical transitions in sea grass community composition associated with pollution.

### STUDY AREA

This investigation is set along the shallow ( $\sim$ 30-cm water depth) crest of Cross Bank, inside the Everglades National Park, in south-central Florida Bay (Figure 1). An investigation of the response of sea grass communities to nutrient enrichment (FOURQUREAN *et al.*, 1995) showed that less than a decade after placement of the bird posts, the standing crop of *Thalassia* at experimental, nutrient-enriched sites had nearly been eliminated, while *Halodule* had attained a standing crop density equal to that of *Thalassia* at its highest ob-



Figure 1. Map of the Cross Bank study area. Cross Bank is a carbonate bank measuring 3000 + m in length and up to 200 m in width. Experimental sites consist of *Halodule* "halos", orientated toward the northwest, that are exaggerated spatially in this figure (actually measure 2 m by 4 m). Control and experimental transect localities are paired at 200-m lateral intervals running from southeast to northwest along the bank crest. The background vegetation state of Cross Bank is moderate *Thalassia* coverage with occasional barren mud zones where sea grass has been removed by storm activities.

served background level (Figure 2). After 3 years of enrichment, *Halodule* became more abundant than *Thalassia*, measured in grams of dry weight per square meter, and has maintained that dominance at localities where nutrient addition continues (*i.e.*, where bird excrement addition persists). Sampling for the current investigation was conducted in October 2004. Therefore, the expectation is that conditions favorable to altered molluscan fauna may have persisted for as many as 18 years (1986–2004). Previous work in shallow marine carbonate settings has shown that changes in the composition of molluscan communities occurring over similar intervals have been successfully recorded in the sedimentary record (FERGUSON, 2003).

During the work of POWELL, KENWORTHY, and FOURQUR-EAN, (1989), a 3000-m transect with bird posts at 100-m intervals was developed along the crest of Cross Bank. For the purposes of the present investigation, a 1200-m experimental transect, with stations at 200-m intervals (six stations total per transect), was established using the sites of POWELL, KENWORTHY, and FOURQUREAN (1989), along with a corresponding parallel "control" transect, with stations situated 50 m N-NW of the control sites (Figure 1). This experimental design was used to assess the nature of molluscan death assemblages at the Halodule-dominated experimental sites in POWELL, KENWORTHY, and FOURQUREAN (1989) in comparison to the unaltered, Thalassia-dominated sites. However, there is a 400-m gap between control and experimental stations 5 and 6 because of an anomalous spit (likely the result of a storm blowout [WANLESS, 1981]) protruding from Cross Bank where station 6 would have otherwise been.



Figure 2. Mean standing crop of *Thalassia testudinum* and *Halodule* wrightii. Mean values come from five experimental and control sites along Cross Bank and are displayed against a time series. Values are reported in grams dry weight of sea grass biomass per square meter and illustrate a pattern of turnover of these two sea grass species at experimental sites and stasis of *Thalassia* populations at control localities. *Halodule* achieved equal biomass to *Thalassia* at experimental sites within 4 y of initial nutrient loading and became dominant thereafter, while *Halodule* was only rarely reported at control localities. Error bars about the mean represent calculated standard error. Figure modified from Fourqurean et al. (1995).

## METHODS

## Sampling

Sampling for this investigation was designed to assess the state of molluscan death assemblages deposited at experimental, *Halodule*-dominated sites of POWELL, KENWORTHY, and FOURQUREAN (1989) over some two decades *vs.* control samples from a *Thalassia*-dominated environment that should more faithfully represent background conditions along Cross Bank. In all cases, a replicate pair of shallow push cores with diameters of 5.1 cm and a length of 15–25 cm were taken at each station, for a total of 12 per transect (24 in all). The molluscan response to environmental change is likely de-

posited in this upper decimeter of the sedimentary veneer on the basis of estimated sedimentation rates ranging between ~1 cm/y derived from Pb<sub>210</sub> dating (HOLMES *et al.*, 2001) and 0.3–3 mm/y derived from C<sub>14</sub> (STRASSER and SAMANKASSOU, 2003) in this part of Florida Bay. Therefore, this sampling protocol is designed to obtain a sample of molluscan material that can be used to assess two decades of accumulated differences in surficial composition between death assemblages collected along the control and experimental transects.

## Sample Treatment

Push-core samples, with an average volume of about 1.6 L of sediment, were wet-sieved to retrieve coarse material (>150  $\mu$ m). This coarse fraction was dry-sieved through 2-mm mesh to extract all but the smallest shell material visible to the naked eye and it is from this >2-mm-size fraction that the data considered here were collected. All samples were uniformly sieved and picked so as to reduce the chance of bias in removing the smallest size class of taxa, such as those of the genera *Bittiolum*, *Rissoina*, and *Schwartziella*.

Specimens were identified using standard malacological references (*e.g.*, ABBOTT, 1974; REDFERN, 2001) and the author's previous experience working with tropical West Atlantic molluscs. The numbers of individual species were tallied for each sample and bivalve counts were halved to account for two retrievable skeletal parts per individual (GILINSKY and BENNINGTON, 1994). This is a more conservative approach to assessment of abundance than counting left and right valves individually but is appropriate for counting shell material from bivalves that do not display taphonomic differentiation between valves and that are not subject to a high degree of postmortem transport.

To be counted as a specimen, a shell had to (1) possess an umbo, for bivalves, and either an apex or aperture, depending on the species, for gastropods; (2) possess greater than threefourths of its original shell or valve; and (3) be preserved well enough to identify. The objective of this strict counting is to control for potential worker bias in identification and minimize artificial differences between control and experimental samples.

Shell counts make up the data matrices used during this investigation and, for multivariate analyses, abundancebased data were limited to the top 20 specimens common to both experimental and control series. The top 20 species were determined by the rank order of the sum of abundance totals from control and experimental groups and represent 89% of total specimens considered. Patterns illustrated here are robust at both higher and lower levels of inclusion; below the top 20 threshold are taxa with a total abundance of less than 50 specimens aggregated from all 24 push-core samples. Abundance values for the top 20 molluscan taxa were transformed to a percentage of total within-sample specimen abundance for multivariate comparisons of samples (i.e., Q-mode analysis), and this initial percentage transformation was followed by a transformation to a percentage of the maximum abundance of each species found among all samples for comparisons of species distribution (R-mode analysis). Use of percentage data here is justified because overall per-sample Table 1. Mean specimen abundance and species richness from control and experimental samples along Cross Bank. Specimen abundance and species richness ( $\pm$  standard error) are both higher along the control transect, but only the difference in species richness is statistically significant. Therefore, while abundance is comparable, species richness is negatively affected by the transition to Halodule via nutrient enrichment.

	Control	Experimental	<i>p</i> -value
Richness	$37.58 \pm 1.62$	$\begin{array}{r} 29.83 \pm 1.70 \\ 283.75 \pm 55.48 \end{array}$	$0.003^{*}$
Abundance	$383.75 \pm 59.18$		0.231

On the basis of independent samples t test, \* indicates significance at p < 0.01, two-tailed test.

abundance varies despite holding sediment volume roughly constant, and this likely reflects postmortem processes. This second, "percent-maximum" transformation has been shown previously to be effective in R-mode analyses for comparing the abundance distributions of taxa with widely varying total abundances (e.g., MILLER, 1988). Similarity matrices were derived from these transformed data using the Bray-Curtis similarity coefficient (BRAY and CURTIS, 1957). Nonmetric multidimensional scaling (MDS) and cluster analysis (unweighted pair-group method) were both used for comparisons of samples (Q-mode), and cluster analysis was used for comparisons of species (R-mode). The PRIMER 5 for Windows software package (PRIMER-E, Ltd.; Plymouth, United Kingdom) was used for all multivariate analyses and SPSS 11.0 for Windows (SPSS, Inc.; Chicago, IL) was used for correlation procedures, such as Spearman Rank, and comparison of means using independent samples t tests for normally distributed variables and the Mann-Whitney U test for nonparametric data.

## RESULTS

#### Specimens

A total of 24 push-core samples from sites along Cross Bank yielded 8011 specimens, representing 74 species. Mean richness among push-core samples from control sites was 38 taxa (from 4605 specimens), whereas mean richness at experimental sites was 30 species (from 3406 specimens). Mean richness observed between control and experimental sites shows a significant difference, whereas differences in mean abundance are insignificant (Table 1).

## Assemblage Results

Assessment of samples from nutrient-enriched experimental sites illustrates a molluscan death assemblage that is altered relative to assemblages collected at control sites, as demonstrated with MDS (Figure 3). Control and experimental samples plot separately from one another, indicating a clear compositional difference between the two transects.

Both of the replicate samples from control station 4 were compositional outliers relative to other control samples and bear a strong similarity to samples from the experimental transect. The substrate at station 4C was, indeed, covered by the naturally dominant sea grass, *T. testudinum*, but the near absence of a key diagnostic species, the high-spired gastropod



Figure 3. Ordination of molluscan death assemblages. Multidimensional scaling (MDS) analysis of push-core samples illustrates differences in assemblage composition of experimental vs. control samples in ordination space. Results show two distinct groups of samples, almost entirely dependent on whether a sample came from a control (C) or experimental (X) site, with the exception of the push-core samples from control station 4. Stress values are calculated on the basis of the extent to which an arrangement of samples is representative of the calculated distance among samples. Calculated two-dimensional stress of this MDS analysis is 0.12 (lower stress indicates a "better fit"), which is below the threshold of 0.20 generally accepted as indicative of whether an arrangement of ordinated data is representative of variation among samples (Clarke and Warwick, 2001), and this conclusion is corroborated by similar patterns displayed in Q-mode cluster analysis.

*Cerithium muscarum*, caused control station 4 to be more similar compositionally to experimental stations (see below).

Further dissecting the faunal patterns, a two-way cluster analysis was constructed using both R-mode and Q-mode dendrograms, from the same top 20 data set as MDS analysis, populated with symbols representing the percentage of maximum abundance attained for each species throughout the study area corresponding to a station (Figure 4). In this analysis, replicate samples for each station were combined. Three groups of species are expressed in the R-mode cluster analysis, from top to bottom in the dendrogram:

- Species that occur readily in the control, *Thalassia*-dominated, environments, represented most reliably by *Cerithium muscarum*, but also including *Carditamera floridana* and *Pitar fulminatus*.
- Species that are generally present at both control and experimental sites but demonstrate slight habitat preferences as illustrated by percentage maximum abundance values arrayed in two-way cluster analysis. This second grouping includes important species such as *Brachidontes exustus* and *Bittiolum varium*, which occur at higher abundance at nutrient-enriched, *Halodule*-dominated experimental sites, and *Chione cancellata* and *Modulus modulus*,



Figure 4. Two-way cluster analysis. Q- and R-mode clusters arrayed with data points representing percentage of maximum abundance for each species. Sample replicates from each station were combined for the Q-mode cluster analysis. Two Q-mode clusters are recognized with samples (replicates combined) grouped according to whether a sample came from an experimental (X) or control (C) site, with the exception of control station 4, which incorporates species indicative of both transects, with Cerithium being the strongest differentiating taxon. Three R-mode clusters are defined on the basis of the occurrence of taxa within Thalassiadominated environments, Halodule-dominated environments, or both; this is illustrated by abundance values arrayed on the figure. Maximum abundance, within a sample, for each species is provided in parentheses next to the species name and is useful for determining which species are most important for comparisons of assemblage composition among samples. Species in the Thalassia-only cluster, with Cerithium muscarum being the most important, are present near their maximum abundance throughout the control transect but are not found above 20% of their maximum abundance (if at all) at experimental transect sites.

which are more likely to occur in higher abundance at control sites.

• Species that are present more ubiquitously at *Halodule*dominated experimental sites and more sparsely at control sites. This third group is best represented by the micrograzing gastropod, *Schwartziella bryerea*, and the swimming and actively burrowing bivalves, *Limaria pellucida* and *Tellina alternata*. The abundance distributions of micrograzing gastropods (*Schwartziella*, *Rissoina*, *Eulithidium*, and *Bittiolum*) at experimental stations suggest that exclusion of *Cerithium* is not related to its grazing feeding habits (Table 2).

Rather, dramatically low abundance of *Cerithium* at experimental sites (often present, but always <20% of it maximum studywide abundance), while its far smaller guildmates seem unaffected, indicates that grazing gastropods Table 2. Life habits of common bivalves and gastropods from push-core samples collected on Cross Bank. Bivalves: Ep, epifaunal; Si, semiinfaunal; Ne, nestling; Is, infaunal siphonate; Ia, infaunal asiphonate; Su, suspension feeding; Sd, surface deposit feeding; Sed, sedentary; Mo, actively mobile; Im, immobile; Sw, swimming; By, byssate; Un, unattached. Gastropods: Hrb, herbivorous; Pc, carnivorous predator; Ps, parasitic; Pb, browsing predator. All gastropod codes relate to feeding because all species discussed here are epifaunal. Length is maximum dimension reported from common references. References: (1) Abbott, 1974; (2) Redfern, 2001; (3) Todd, 2001a; (4) Todd, 2001b; and (5) Mikkelsen et al., 2004. Pinctada longisquamosa (\*) had, until recently, been assigned to the genus Pteria; see Mikklesen et al., 2004 for a review of the most recent taxonomy. Life habit codes modified from Neogene Marine Biota of Tropical America project (NMITA: http://eusmilia.geology.uiowa.edu/).

Species	Substrate	Diet	Mobility	Attach- ment	Length (mm)	n Refer- ence
Bivalves						
Arcopsis adamsi Brachidontes	Ep	Su	Sed	By	13	2,3
exustus Carditamera	Ep/Si/Ne	Su	Sed/Mo	By	19	1,3
floridana	Ia	Su	Sed/Mo	Bv	38	1.3
Chione cancellata	Si/Is	Su	Mo	Un	44	1,3
vanhyningi Laevicardium	Is/Ne	$\operatorname{Sd}$	Sed	Un	16.5	2,3
mortoni	Is	Su	Mo	Un	27	2.3
Limaria pellucida	Ep	Su	Mo/Sw	Un/By	26	2,3
Pinctada						
longisquamosa*	Ep	Su	Im	By	63	2,3,5
Pitar fulminatus	Is	Su	Mo	Un	22.5	2,3
Tellina alternata	Is	$\operatorname{Sd}$	Mo	Un	58	2,3
Transennella						
stimpsoni	Is	Su	Mo	Un	9	2,3
Species		Die	et L	ength (m	m) I	Reference
Gastropods						
Bittiolum varium		Hı	rb	6.5		$^{2,4}$
Cerithium muscarum		Hı	rb	22		$^{2,4}$
Costoanachis avara		Pc		22		1,4
Crepidula sp.		Su	L	13		1,4
Eulithidium affine	Hı	rb	9		$^{2,4}$	
Modulus modulus	Hı	rb	11		$^{2,4}$	
Prunum apicinum		Pb	)	13.5		$^{2,4}$
Rissoina sp.		Hı	rb	7		2,4
Schwartziella bryerea		Hı	rb	6		2,4

above a certain size threshold cannot inhabit Halodule blades. In addition to abundance, there are differences in mean size between Cerithium specimens pooled from control and experimental sites. The maximum dimension of Cerithium was measured (apex to siphonal canal), and the mean size of specimens collected from control sites is more than a millimeter larger than mean size  $(\pm$  standard error) from experimental sites: 6.96  $\pm$  0.49 mm vs. 5.95  $\pm$  1.14 mm with significance of p = 0.022, derived from a Mann-Whitney U test. Cerithium specimens collected at experimental localities rarely attained a size  $\geq 10 \text{ mm}$  (6.25% of experimental specimens), which appears to be a threshold for those living on Halodule, whereas specimens of this size were comparatively abundant at control localities (16% of control specimens). It is important to note that the sample size of Cerithium specimens was low, as a result of its reduced abundance, at experimental sites (n = 32 specimens) relative to the sample size from control sites (n = 194 specimens) and is reflected in the higher standard error reported for the experimental population.

Overall, therefore, three trends emerge from consideration of the biotic patterns: (1) *Cerithium muscarum* is highly abundant in the death assemblage at control group sites but is never present at >20% of its maximum abundance at experimental sites; (2) *Brachidontes exustus* is highly abundant throughout the study area, but is consistently more abundant in the death assemblage at experimental sites than at control localities; and (3) Small grazing gastropods, such as *Bittiolum varium* and *Eulithidium affine*, show the opposite pattern to *Cerithium* in that they were consistently more abundant in experimental than control locales.

As in MDS, sample site 4C groups outside of control samples in cluster analysis, and it can be seen here that this relationship is based primarily on the low abundance of *C. muscarum* and the relatively higher abundance of *B. exustus* (Figure 4). Interestingly, however, station 4C also clusters outside of the experimental group, suggesting that it is compositionally unique relative to other samples.

#### DISCUSSION

The results of this study illustrate the molluscan response to change in sea grass community composition, and demonstrate that such a response is recorded in the accumulating molluscan death assemblage. The faunal differences described above are the basis for sample differentiation in the multivariate analyses and demonstrate that assemblages deposited at nutrient-enriched experimental sites are different from those at control sites. The explanation for this difference likely relates to the structural characteristics of blades of *H*. wrightii relative to T. testudinum. In this case, nutrient enrichment itself can largely be discounted as a controlling mechanism on the basis of recent research that has established bivalves, mussels and oysters in particular, as potential tools for pollution remediation. Representatives of these groups have been shown to remove heavy metal pollution and excess nutrient content from estuarine systems in both temperate and tropical settings (GIFFORD et al., 2005). This seems intuitive when one considers that nutrient increases would cause blooms in the microorganisms and algae that grazing and filter-feeding molluscs consume and, therefore, would provide a favorable habitat so long as extreme eutrophication did not develop.

Halodule and Thalassia possess distinct morphologies and sediment controlling abilities in shallow marine environments. An assessment of the average blade surface area of *Thalassia* and *Halodule* was undertaken by MILLER (1988), who found that, in his study area in St. Croix, U.S. Virgin Islands, *Thalassia* averaged 0.25 cm<sup>2</sup> of blade surface area, whereas *Halodule* averaged 0.02 cm<sup>2</sup>. Although the absolute values of blade size are likely to vary considerably among different settings, the numbers from St. Croix reflect what is certainly appreciable, a consistent difference in relative surface area of the two kinds of blades. *Thalassia* blades are more robust relative to the wispy blades of *Halodule* and are capable of supporting larger invertebrate grazers. A second difference relates to relative densities of root structure. *T. testudinum*, the slow-growing, long-lived climax sea grass in this region (DEN HARTOG, 1971), possesses a dense root-rhizome layer capable of binding sediment to a depth of 10-20 cm below the sediment-water interface. Large-scale bioturbation is not possible in dense *Thalassia* beds and sediment is stabilized during all but the most intense storm events (KALBFLEISCH and JONES, 1998). By contrast, *H. wrightii*, a fast-growing opportunist (FOURQUREAN et al., 1995), possesses only a slight root system that is not suited to stabilizing sediment and as a result, experimental sites in the present study possessed a soft substrate that was easily disturbed and penetrated.

In light of these differences, it is apparent that larger, mobile molluscs preferring large, strong blade structures or stable sediment would be less likely to inhabit a Halodule-dominated environment than those that are adaptable to small blades and active substrates. The characteristics of the molluscs discussed here, and described in Table 2, are useful in assessing the reasons for the differential molluscan response to changes in sea grass community composition. Of interest are the feeding strategies of gastropods and the life habits of certain bivalves. Six herbivorous gastropods of different sizes occur in the top-20 species from Cross Bank: C. muscarum, M. modulus, B. varium, Rissoina sp., S. bryerea, and E. affine. Cerithium is the largest of this group and, as noted earlier, is the only highly abundant member of this guild that shows a strong decrease in abundance at experimental sites relative to controls (Figure 4). The dramatic difference in Cerithium abundance, coupled with the observation that a significantly higher proportion of Cerithium from experimental sites falls below the 10-mm size threshold, supports the argument that blade size is a likely control on the distribution of large grazing gastropods. On the basis of these results, it appears that Halodule blades cannot support the mass of a full grown Cerithium and might not provide adequate blade surface area for foot attachment. Future work on this topic will include a comparison of size and mass among Cerithium and Modulus, the two most abundant large grazing gastropods in the region.

The infaunal bivalves, *Carditamera floridana* and *Pitar fulminatus*, which are generally found in *Thalassia* beds at low abundances (Figure 5), are asiphonate, byssate and siphonate, nonbyssate, respectively (Table 2). Other byssate bivalves *Brachidontes exustus*, *Arcopsis adamsi*, and *Pinctada longisquamosa* (previously identified as *Pinctada radiata* by TURNEY and PERKINS [1972] and later reported as *Pteria longisquamosa* by BREWSTER-WINGARD, STONE, and HOLMES [2001]; see MIKKELSEN *et al.* [2004] for the current taxonomic placement), either epifaunal and attached or of variable life habit, seem to be numerically unaffected by the switch to *Halodule*. Bivalves with an infaunal life habit may be ill equipped for the increased sediment mobility that is associated with the far less developed root-rhizome network of *Halodule* relative to the dense network possessed by *Thalassia*.

In summary, two trends are demonstrated: (1) *Cerithium muscarum*, the largest gastropod collected among the top-20 specimens, decreases dramatically in abundance with transition of the sea grass community to *Halodule* coverage, whereas other smaller herbivorous gastropods were not affected in the same way; and (2) bivalves, in general, were not dramatically affected by the loss of *Thalassia* as was *Cerithium*. However, some of the more abundant infaunal forms appear to have been ill-suited to *Halodule*-dominated settings, while epifaunal bivalves were largely unaffected.

#### **Detection of Faunal Change**

The results of this study suggest that assessments of molluscan death assemblages can be used as indicators of transitions among sea grass species in the historical record. That said, the signal of faunal change, in this case, is evidenced mainly by faunal subtraction, primarily the loss of C. muscarum, rather than development of new faunal combinations or the incorporation of ecological immigrants. Comparison of rank-order species abundance compiled from push-core samples along control and experimental transects illustrates the high degree of taxonomic similarity between Thalassia and Halodule habitats (Table 3). Among the top-20 most abundant species, notable shifts in rank abundance are recognized for C. muscarum, P. fulminatus, C. floridana, Crepidula sp., E. affine, L. pellucida, and S. bryerea. A Spearman rank coefficient value of  $0.714 \ (p < 0.001 \ \text{two-tailed test})$  was calculated by comparing the differences in rank between members of two faunal lists pooled for assemblages from both the experimental and control transects. This value demonstrates a moderately strong positive correlation (on a scale of 0 to 1, where 1 would indicate identical ranks and 0 would be no similarity), which indicates that assemblages display a high degree of similarity despite the important individual differences in abundance highlighted by earlier analyses. This result speaks to the nature of change at experimental sites over the duration of nutrient enrichment: differences in the death assemblage are derived from local modifications of the regional molluscan community via exclusion from habitat rather than wholesale reorganization of community structure.

TURNEY and PERKINS (1972) defined several environmental regions in and around Florida Bay, each with a unique faunal assemblage. Cross Bank is situated on the boundary between two of these regions, the Interior Bay and the Atlantic region (tidal influence from Tavernier Creek supplies open marine conditions). The array of fauna recorded here in subfossil form shows that some of the Atlantic region species of TURNEY and PERKINS (Tegula fasciata, Astralium phoebium, Carditamera floridana) occur in low abundances, but are generally found only at control localities. The Interior Bay, a broad, shallow Thalassia-dominated zone of interspersed banks and "lakes" (deeper areas [1-2 m] between banks where only a thin veneer of sediment overlies bedrock), houses species that include Cerithium muscarum, Brachidontes exustus, and Bittiolum varium; of which only Cerithium is negatively affected in the present study by the transition to Halodule at experimental sites. Atlantic region molluscs are restricted to areas that experience normal marine salinities (TURNEY and PERKINS, 1972), but they may also be more suited to Thalassia-dominated habitats, as they are not generally found in assemblages from experimental sites. Although the loss of Atlantic region taxa is not useful for deTable 3. Rank abundances of mollusc taxa from aggregate experimental vs. control samples. Species, aggregated from control and experimental transects, are ranked in order by percentage abundance within these specimen pools. Any change to a species rank order between control and experimental settings is illustrated by the rank change column. Important changes in rank, such as the decline in Cerithium abundance at experimental sites, are apparent in both percentage abundance and change in rank. Spearman rank correlation coefficient shows a moderately strong positive correlation between lists, which illustrates a high degree of similarity between faunas despite the decline of Cerithium muscarum at experimental sites. This analysis illustrates that only a few of the common species from Cross Bank were appreciably affected by the transition to a Halodule-based habitat.

Control			Experimental		Change
%				%	ın Rank From
Abundance	e Species	Rank	Species	Abundance	Control
19.90	Brachidontes exustus	1	Brachidontes exustus	28.50	0
11.98	Cerithium muscarum	2	Bittiolum varium	12.87	+1
7.81	Bittiolum varium	3	Schwartziella bryerea	6.93	+6
7.77	Pinctada longisauamosa	4	Pinctada longisquamosa	6.37	0
5.68	Modulus molulus	5	Modulus modulus	4.77	0
4.96	Chione cancellata	6	Eulithidium affine	4.54	+5
4.02	Pitar fulminatus	7	Rissoina sp.	3.55	+3
3.35	Laevicardium mortoni	8	Chione cancellata	3.46	-2
3.28	Schwartziella bryerea	9	Laevicardium mortoni	3.35	-1
3.25	Rissoina sp.	10	Cerithium muscarum	2.65	-8
2.36	Eulithidium affine	11	Crepidula sp.	2.65	+9
2.12	Cumingia vanhyningi	12	Limaria pellucida	1.87	+6
1.84	Prunum apicinum	13	Prunum apicinum	1.66	0
1.56	Arcopsis adamsi	14	Transennella stimpsoni	1.53	+2
1.56	Carditamera floridana	15	Pitar fulminatus	1.51	-8
1.54	Transennella stimpsoni	16	Cumingia vanhvningi	1.30	-4
1.18	Costoanachis	17	Arcopsis adamsi	1.24	-3
0.85	Limaria pellucida	18	Tellina alternata	1.24	+1
0.85	Tellina alternata	19	Costoanachis avara	1.03	-2
0.66	Crepidula sp.	20	Carditamera floridana	0.18	-5

tecting the *Thalassia–Halodule* transition in Florida Bay because of the low abundance of these species, it suggests that in regimes with more stable salinity, these species could prove useful for diagnosing environmental change.

By itself, a comparison of the percentage abundance of *C.* muscarum to *B. exustus* seems to be a useful means of assessing whether a substrate is *Thalassia* or *Halodule* covered (Figure 5). *Brachidontes* is highly adaptable to a wide array of environmental conditions, often thrives in stressed environments, and is capable of inhabiting virtually any substrate (BREWSTER-WINGARD, ISHMAN, and HOLMES, 1998; BREWSTER-WINGARD, STONE, and HOLMES, 2001). These



Figure 5. Comparison of the percentage abundance *Cerithium vs. Brachidontes.* The relationship in abundance of these two species is indicative of the molluscan response to the *Thalassia–Halodule* transition. *Cerithium* has a consistently higher abundance at control sites than at experimental sites. *Brachidontes* is more abundant on a percentage basis at experimental sites. Because the abundance of *Cerithium* drives major differences between assemblages from control and experimental sites, the relationship between these two highly abundant taxa should be a useful indicator of the type of sea grass coverage below the uppermost sedimentary horizon and at other localities. Error bars represent 95% confidence and were calculated using a program written by Raup (1991) for use with percentage values.

characteristics make *Brachidontes* a useful taxon for comparison with *Cerithium* as it behaves rather differently with respect to substrate sensitivity in the study, and it exhibits moderate abundance increases at experimental sites relative to controls in this investigation.

### Long-Term Ecological History

Results of these surficial analyses suggest that a record of change may be preserved in the broader sedimentary column and, if true, would demonstrate the diagnostic power of molluscan death assemblages for discerning ecological and environmental changes through extended intervals of time. Reported sedimentation rates and observed differences in Cerithium abundance between samples from the upper sedimentary veneer at control and experimental sites suggest that if a stratigraphic record of change associated with the Thalassia-Halodule transition at experimental sites is to be found, it will be located in the uppermost two decimeters. One limitation will be the role of time averaging, which is one important difference between control and experimental sites, related to sea grass root-rhizome morphology. This has been discussed here in terms of the effects on less actively burrowing infaunal bivalves relative to more active or epifaunal varieties. However, elevated bioturbation is also expected at Halodule-dominated sites because of low root density relative to Thalassia, which has a dense root-rhizome, and is capable of binding sediment and excluding many bioturbating organisms (SUCHANEK, 1983). The effect on the stratigraphic sedimentary record might be a more gradual and blurred record of change at experimental sites, which is supported by anecdotal observations that the sediment was much less stable and more actively eroded at altered sites. An additional dimension of this study will be the analysis of piston-core samples already collected from the upper meter of sediment on Cross Bank, subsampled at 2-cm intervals, to assess the preservation potential and stratigraphic resolution of changes in assemblage composition. Taphonomy and time-averaging permitting, this will allow detailed construction of long-term ecological and environmental histories of near-shore environments during the Holocene from molluscan death assemblages.

## CONCLUSION

Molluscan death assemblages at experimental, nutrientenriched sites along Cross Bank reflect alteration in the living molluscan community caused by transition between dominant sea grass species and ultimately driven by human activities. These changes are apparent through comparison of molluscan skeletal composition with unaltered environments on Cross Bank and should be apparent in other settings where the wide-bladed Thalassia is replaced by Halodule because of nutrient loading. Cerithium muscarum, the species most strongly affected, appears to be the best indicator for this type of transition in south Florida, the most likely mechanism being the difference in blade size and strength differences between Thalassia and Halodule rather than nutrients directly. Furthermore, initial work in deeper piston cores sampled at a fine vertical scale indicates a decrease toward the surface in the percentage abundance of C. muscarum at experimental sites and suggests that the stratigraphic transition to the Cerithium-depleted biota can be recognized in the sedimentary record. Therefore, despite potential for interference by bioturbation, the results of this study add to the growing body of evidence indicating that molluscan death assemblages have great promise for diagnosing recent environmental transitions on coastal seafloors.

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