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Front Cover: The reef crest indicator species, *Acropora palmata*, on Gaulin's Reef, San Salvador Island. Gaulin's Reef is a classic bank-barrier reef that has shown remarkable resilience following two significant disturbances: El Niño-induced warming of the sea surface in 1998 and Hurricane Floyd in September, 1999 (see Peckol et al., this volume). Photo by Janet Lauroesch.

Back Cover: The oolite shoals of Joulter's Cay, north of Andros Island, Bahamas, site of the pre-meeting field trip. Photo by Ben Greenstein.

PALEOCOMMUNITY RECONSTRUCTION OF A TROPICAL CARBONATE LAGOON, GRAHAM'S HARBOR, SAN SALVADOR, BAHAMAS

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ABSTRACT

Molluscan assemblages (both living and dead) from three distinctive habitats were sampled from Graham's Harbor, a high-energy lagoon in the Bahamas. Transects were identified as Seagrass (dense seagrass bed), Backreef (located behind a barrier reef) and Transition (a sand-seagrass transitional area). We examined seagrass density, species composition, class of mollusc, habitat preference, and trophic role at each transect. We wanted to know 1) if the death assemblages at each transect were distinctive enough to characterize three different communities, 2) whether the death assemblages were reflections of the living communities at those transects, and 3) how representative the living communities were of the death assemblages.

What we found was 1) that the three transects are distinctive, 2) the living and dead assemblages were similar for both the Seagrass and Backreef transects, but not for the Transition transect, and 3) the living assemblage is unique from the death assemblage at all transects, especially in terms of species composition and abundance.

INTRODUCTION

Earth scientists have long been concerned with how representative any given fossil record is to the living community that produced it. Past studies laid the foundation for paleoecological analyses (Efremov, 1940; Warme, 1969; Walker and Bambach, 1971; Lasker, 1976; Peterson, 1976 and 1977). Within the last decade, numerous studies focused on fidelity between living and dead molluscan assemblages (Zuschin et al., 2000; Kidwell and Flessa, 1996; Kidwell and Bosence, 1991; Russell, 1991), time-averaging of the death assemblage (Kowalewski, 1995; Kidwell, 1998; Staff et al., 1986) and other taphonomic processes that influence the formation of fossil assemblages (Parsons et al., 1997; Cox, 1993; Par-

sons and Brett, 1991; Miller and Cummins, 1990; Miller, 1988; Cummins et al., 1986).

The intent of this study was to characterize molluscan assemblages in a tropical carbonate lagoon and examine similarities and differences between the living and dead assemblages. More than 15,000 mollusc shells and 900 living molluscs were collected for this study.

Graham's Harbor is a shallow (<10m deep) marine environment with varying wave and current energy, sediment texture and seagrass cover. Three distinctive habitats in Graham's Harbor were studied, first to characterize the molluscan death assemblages, then to compare them to the living communities at each habitat. Seagrass cover was assessed and used to quantify variations in seagrass density within and among the transects.

Ecological parameters, such as species composition, trophic roles, type of mollusc, and habitat, were used to evaluate community characteristics from three distinct communities: a dense seagrass bed, an area behind a barrier reef, and a seagrass-sand transition. Based on the ecological parameters, we hoped to distinguish three distinctive habitats, characterized by different living and dead molluscan communities.

METHODS

Site Description

Graham's Harbor is a shallow, high-energy tropical lagoon located at the north end of San Salvador Island, Bahamas. The Harbor is roughly two by three kilometers, with a maximum depth of about six meters (Colby and Boardman, 1989). There is a barrier reef bordering the east side of the Harbor, with small cays marking the north and east borders. Over its 6000-year history, Graham's Harbor has developed into a

higher energy lagoon (Colby and Boardman, 1989).

Three 40 m transects were placed in distinct communities within Graham's Harbor (Figure 1). These three sub-environments within Graham's Harbor have uniform water temperatures, salinity and storm frequency. However, there are variations in sediment textures and seagrass densities (Colby and Boardman, 1989). The three transects were identified by dominant substrate features in or near the transects: Seagrass Transect (located in a dense seagrass meadow), Backreef (located *just west and south* of the barrier reef) and the Transition Transect (characterized by seagrass beds and sand flats).
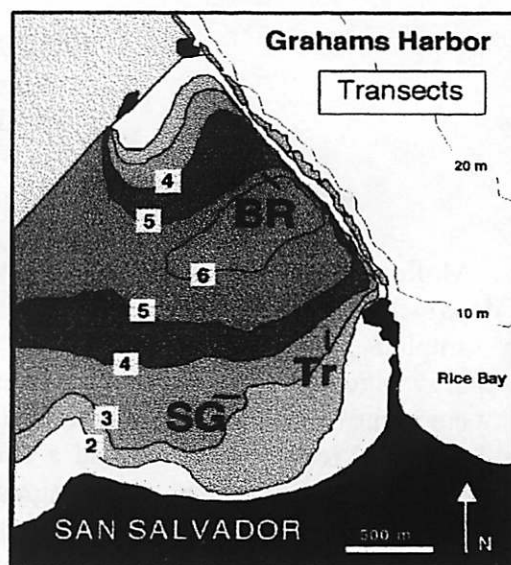

Figure 1. Bathymetric map of Graham's Harbor, San Salvador, Bahamas. Transects are indicated as: SG = Seagrass Transect, BR = Backreef Transect, and Tr = Transition Transect. Contours in meters.

The Seagrass Transect is located approximately one kilometer from the northern shore of San Salvador. *Thalassia testudinum* and *Syringodium filiforme* grow densely in this area, where the water is approximately 3 m deep. The transect runs parallel to the shoreline.

The Backreef Transect is in 5 – 6 m of water roughly two kilometers from shore. The transect runs NW-SE, paralleling the reef. This transect passes through both seagrass and sand/coral rubble areas.

The third study site, the Transition Transect, is located 500 m west of North Point. Water depth is about three meters; the transect, passing through both sand and seagrass areas, is parallel to the North Point landform.

Data Collection and Analysis

At five meter intervals, sediment samples were collected at each site using a shallow core (25 cm deep x 30 cm diameter). Additionally, a seagrass census was completed in order to report seagrass densities at all sampling sites. Seagrass coefficients were calculated following Miller (1988). Each transect was sampled two times, beginning in September 1990 with the second sampling occurring six months later (total of 16 samples at each transect). Sediment samples were preserved in a 5% formalin solution and stained with Rose Bengal to facilitate sorting of live individuals. Samples were wet-sieved using 0.5 mm mesh sieve, and the first 300 dead molluscan individuals were identified to species whenever possible, following the methods of Staff and Powell (1999). All living individuals were identified to genus and most to species. Taxonomic authorities include Abbott and Dance (1990), Warmke and Abbott (1962) and Morris (1975). For an analysis of the living communities, see Zimmerman et al. (this volume). For bivalves, right and left valves of the same species and size were paired and considered one individual; all unpaired valves were considered as separate individuals. Fragments of any mollusc were counted only if a beak was present on the bivalve shell or the apex was present on the

gastropod shell. Molluscan fragments were included in all statistical analyses.

To analyze relationships between, among and within transects, all identified molluscan species were assigned class of mollusc, life habit preferences (habitat), and trophic role. Information for each was gathered from past literature (Stanley, 1970; Abbott, 1974; Robertson, 1975; also Slone, 1990). Classes of mollusc used for analyses were gastropod, bivalve and scaphopod (referred to as "type of mollusc" hereafter). Life habit was simplified to identify each specimen as either an epifaunal or infaunal species. Five classifications of trophic roles were used: herbivore, filter feeder, carnivore, detritivore and parasite. Chi square tests of similarity ($\alpha = 0.05$) were used to identify relationships between transects for the death assemblages and within transects for living to dead comparisons. Spearman Rank Order Correlation tests ($\alpha = 0.10$) were done sample by sample within each transect to determine if the rank orders of abundances were similar within each 40 m transect. Additionally, Spearman Rank analyses were used to identify transect covariance of species by examining the rank order of the top ten species at each transect for both living and death assemblages.

RESULTS

Paleocommunity Reconstructions

Seagrass Transect.

At the Seagrass transect, 4482 individuals were counted, representing 113 taxa. The average coefficient of seagrass density at the Seagrass transect was 8.6 (Figure 2). Gastropods dominated the transect, in terms of both numbers of individuals and numbers of species (Figure 3). The dominant species was the bivalve *Parastarte triquetra*, follow-
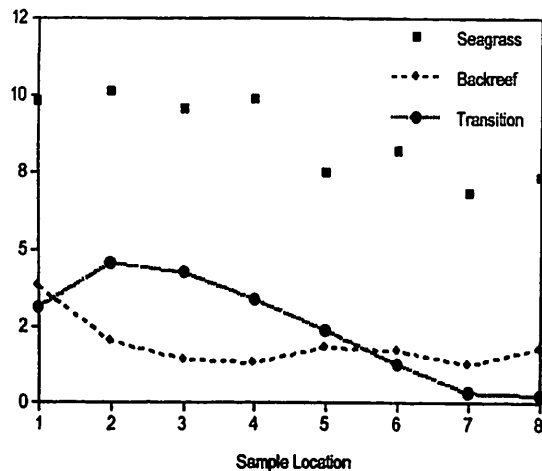
Figure 2. Seagrass coefficients for each of the transects (calculations based on Miller, 1988).
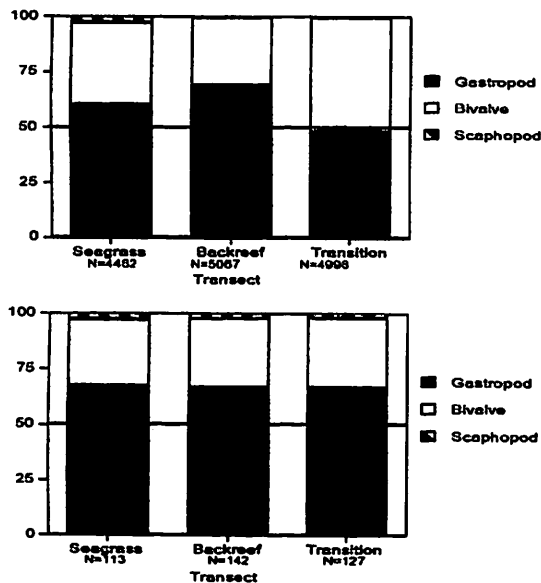

Figure 3. Types of mollusc for the death assemblages of each transect.
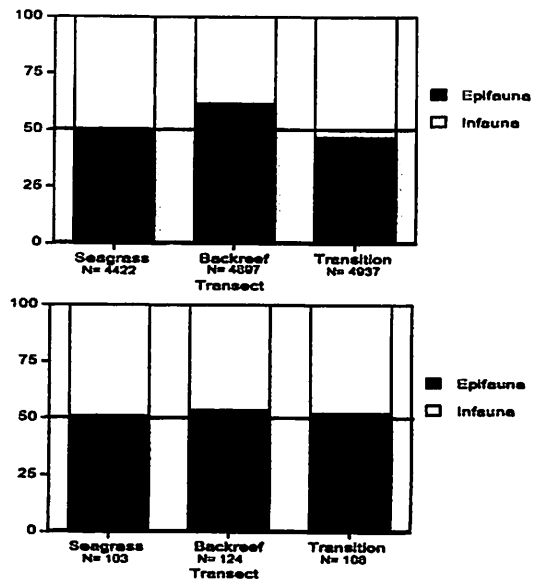

Figure 4. Death assemblage habitats by transect.

dant gastropods included *Tricolia affinis* and *Cerithium lutosum*) or filter feeders (the trophic role of the most abundant species, *Parastarte triquetra*) (Figure 5).

Backreef Transect.

At the Backreef transect, a total of 5067 individuals were identified, with 142 taxa represented. The coefficient of seagrass density averaged 1.9, the lowest density of seagrass at all transects (Figure 2). The most dominant mollusc type by both numbers of individuals and numbers of species was gastropod, approaching 75% of the total individuals (Figure 3). The gastropod *Tricolia affinis* was the most abundant mollusc. Of the top ten taxa in this transect, there was equal representation of gastropod and bivalve species. There were more epifaunal individuals and species, the highest of all transects (Figure 4). The greatest number of individuals was gastropods (40%), and most Backreef molluscan species were predominantly herbivores, filter feeders and carnivores (almost 80% of the species) (Figure 5).

fed closely by the gastropod *Tricolia affinis*, both totaling about 20% of all individuals collected.

There were six gastropod species, three bivalve species and one scaphopod species represented in the top ten. There are about equal numbers of epifaunal and infaunal species and individuals (Figure 4). Most molluscs collected were herbivores (abun-
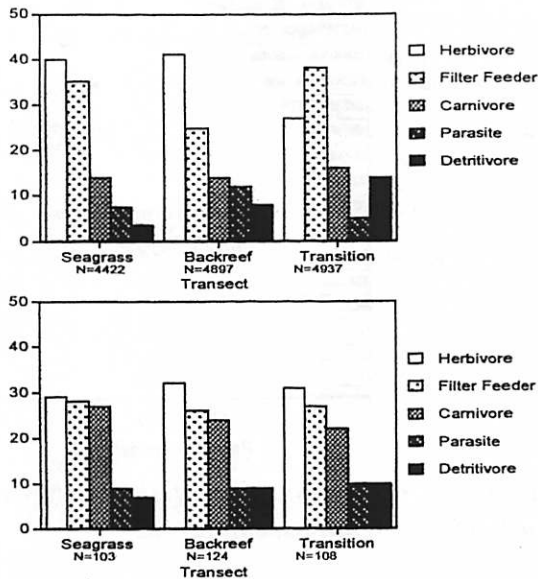
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Figure 5. Trophic roles of death assemblage by transect.

Transition Transect.

Nearly 5000 individuals were identified at the Transition transect (N = 4998), representing 127 taxa. The average coefficient of seagrass density of the Transition transect was 2.4 (Figure 2). Although there were more gastropod species, there were slightly more bivalve individuals than gastropods (see Figure 3). Seven of the top ten species are bivalves. Almost 25% of the individuals were either the gastropod *Tricolia affinis* or the bivalve *Tellina candeana*. There were more epifaunal individuals, yet more infaunal species (Figure 4). The most important trophic role by number of individuals was filter feeder, though herbivore, carnivore and detritivore were important roles represented by the specimens collected. There were more herbivore species, and the combination of herbivore, filter feeder and carnivore species accounted for almost 75% of the species present (Figure 5).

Rank Order Comparisons of Samples Within Habitats

For these analyses, the null hypothesis is that the rank orders of abundance of the top ten species will be independent from sample to sample within a habitat. Significant results ($p < 0.10$) imply that the comparisons of the rank orders of abundance of the top ten species from sample to sample are correlated. At all transects, within transect comparisons were highly correlated. At the Seagrass transect, 93% of the comparisons were significant. At the Backreef transect, comparisons were significant between 86% of the sample-to-sample analyses. The Transition transect comparisons were all significant, indicating that the rank orders of the top species from sample to sample were very similar.

Paleocommunity Comparisons: Are the Transects Similar?

Chi Square Analyses.

Inter-transect comparisons of three ecological parameters (type of mollusc, habitat preference and trophic role) indicate that there are several significant differences among the death assemblages. Visual inspection of Figure 4 indicates that the percent of species of mollusc type is similar among the three transects, and this is supported statistically. In comparing percents of individuals between transects, the Seagrass Transect is statistically different from the Transition Transect ($X^2 = 6.56$, df = 2, $p = 0.04$). It would also seem that the Backreef Transect differs from the Transition Transect as well; however, due to the fact that percent representation of scaphopods in both transects was less than 0.5%, a Chi Square analysis could not be performed.

In terms of habitat preference, are the transects similar? There is no signifi-

cant difference between the epifauna:infauna ratios of the Seagrass Transect and the Backreef Transect or the Seagrass and Transition transects. The habitat preference ratios by individuals for the Backreef and Transition transects show that there are more epifaunal individuals in the Backreef Transect (X^2 = 4.52, df = 1, p = 0.03). In terms of species, statistical analyses for habitat preference indicate similarities in the death assemblages among all transects.

Figure 5 illustrates the percent abundance of individuals and species classified by trophic role in the death assemblages at each transect. Chi square tests indicate that the role ratios (by individuals) are statistically different between the Seagrass and Transition transects (X^2 = 10.23, df = 4, p = 0.04) and between the Backreef and Transition transects (X^2 = 10.22, df = 4, p = 0.04). There were no significant differences in comparisons of trophic roles by species between any of the transects.

Spearman Rank Correlations.

Spearman rank order tests were used to determine if there is correlation between the rank order of the top ten species among transects. While molluscan species composition at the three transects are similar, we failed to reject our null hypothesis, that the rank order of species from one transect is independent of the top ten of another transect. Another way of saying this, knowing the rank order of the top ten species of any transect does not help predict the rank orders of the other two transects. In fact, Spearman rank correlation tests indicate a weak inverse correlation between the Seagrass and Backreef transects
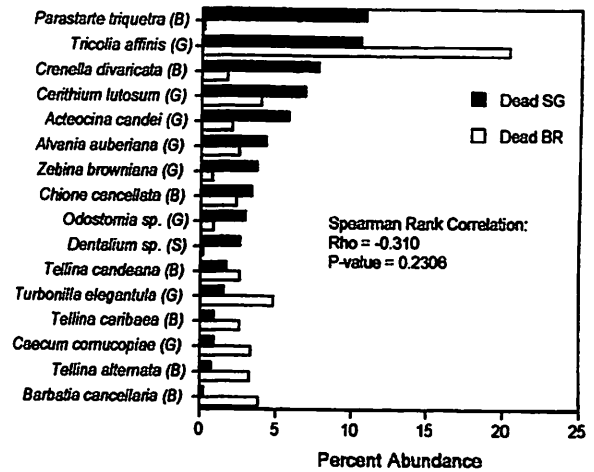

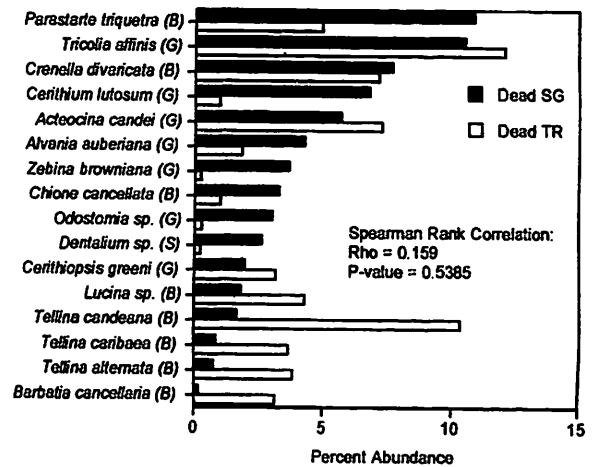Figure 6. Top ten species of the Seagrass and Backreef death assemblages.

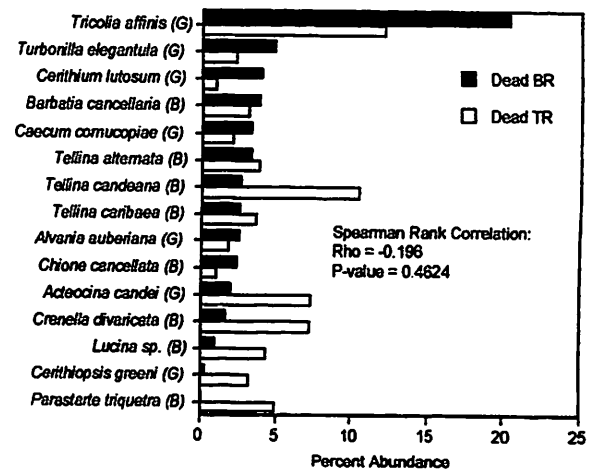Figure 7. Top ten species of the Seagrass and Transition death assemblages.

Figure 8. Top ten species of the Backreef and Transition death assemblages.

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	Trophic Role (Ind)	Trophic Role (Spp)	Class (Ind)	Class (Spp)	Habitat Preference (Ind)	Habitat Preference (Spp)	Rank Order Top 10
Seagrass: Backreef (Dead)	similar	similar	similar	similar	similar	similar	**independent**
Seagrass: Transition (Dead)	**different**	similar	**different**	similar	similar	similar	**independent**
Backreef: Transition (Dead)	**different**	similar	**different?**	similar	**different**	similar	**independent**

Table 1. Between transect comparisons of dead molluscan assemblages for individuals (Ind) and species (Spp).

as well as between the Backreef and Transition transects. Spearman rank test rho and *p*-values are given on Figures 6, 7, and 8.

Summary of Death Assemblage Comparisons.

A synopsis of death assemblage comparisons is shown in Table 1, above. Results of Chi Square tests are reported as "similar" if *p* > 0.05 and "different" if comparisons yielded *p* ≤ 0.05. Spearman Rank Order comparisons are recorded as "independent" if *p* > 0.10 and "correlated" if *p* ≤ 0.10.

Comparisons of Living and Dead Assemblages

Seagrass Transect.

The living assemblage is very similar to the death assemblage in the Seagrass Transect. With the exception of a statistically significant difference in the percentage of species classified by trophic role (X^2 = 25.58, df = 4, *p* < 0.0001), there were no differences in comparisons of specimens classified by type of mollusc or habitat preference (Figures 9 and 10, respectively). Figure 11 illustrates the comparisons of trophic roles,

the rank orders of which were similar at all transects.

The species composition of the live and dead assemblages is different. The most abundant dead species (*Parastarte triquetra*) is absent from the living assemblage, and *Acmaea pustulata*, the most abundant living species, is not in the top ten species of the death assemblage. The rank order of abundance of the top ten dead individuals is different from the rank order of the top ten living individuals (Spearman Rank test: Rho = -0.43, *p* = 0.11). There appears to be an inverse correlation between the living and dead assemblage top ten species (Figure 12).

While the rank orders of the species may be independent, there is species composition fidelity between the rank order of the living and dead species. Within the living assemblage, there were 42 species represented. Of those 42, 41 of them (or 97.6%) appear in the death assemblage. We suspect that synonymous nomenclature could account for the one species in question. The 41 species held in common between the two assemblages only account for 36.3% of the death assemblage species. The death assemblage has nearly three times as many species represented as the living assemblage. This was expected due to the time-averaging death assemblage; Kidwell and Flessa (1996) found similar results in
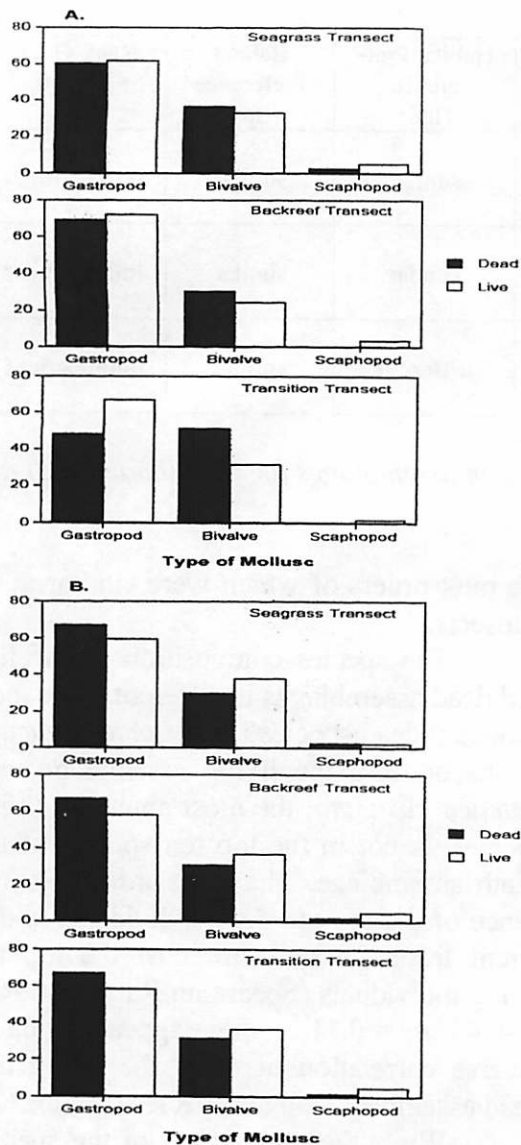
Figure 9. Live:dead comparisons of mollusc type A) by individuals and B) by species for each transect.

Figure 10. Live:dead comparisons of habitat preference A) by individuals and B) by species for each transect.

coastal subtidal habitat studies.

Backreef Transect.

There are no statistically significant differences in dead and live assemblages with regard to bivalve:gastropod ratios and epifauna:infauna ratios (Figures 9 and 10). Comparisons of trophic roles (by individuals) between the live and dead
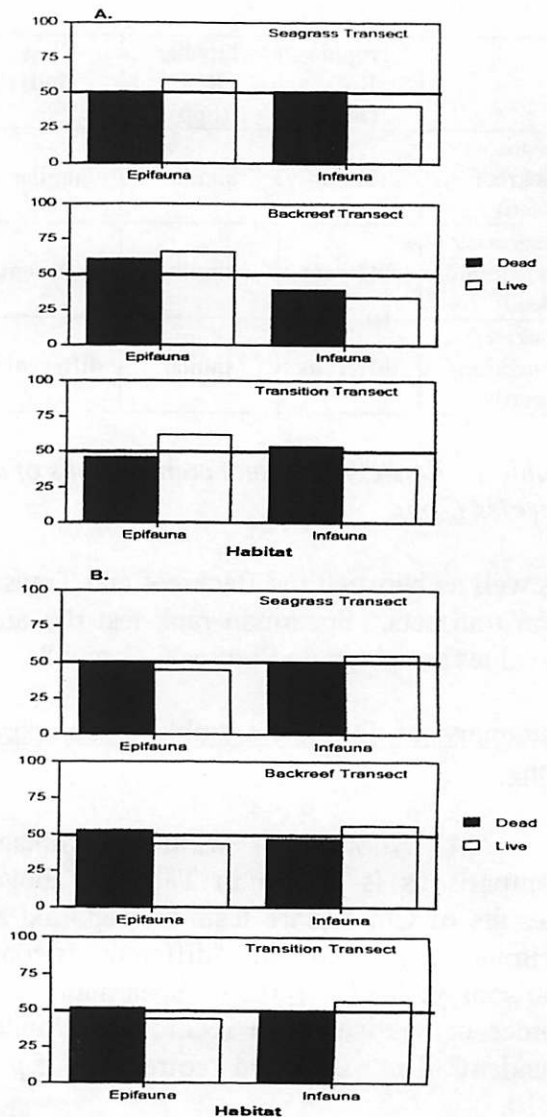
assemblages show similarities in ratios (Figure 11). However, the species percentage of trophic roles of the live assemblage differed significantly from the percentage of species in the death assemblage ($X^2 = 12.51$, df = 4, $p = 0.01$). The rank order of abundance of the top ten dead individuals is different from the rank order of the top ten living individuals. We failed to reject the null hypothesis (Spearman Rank test: Rho = -0.30, $p = 0.24$). There is a weak inverse correlation

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between the living and dead assemblage top ten species (Figure 13).

Forty of the 41 species of the living assemblage (97.6%) show up in the death assemblage. Those 40 species only account for 28.2% of the death assemblage species.
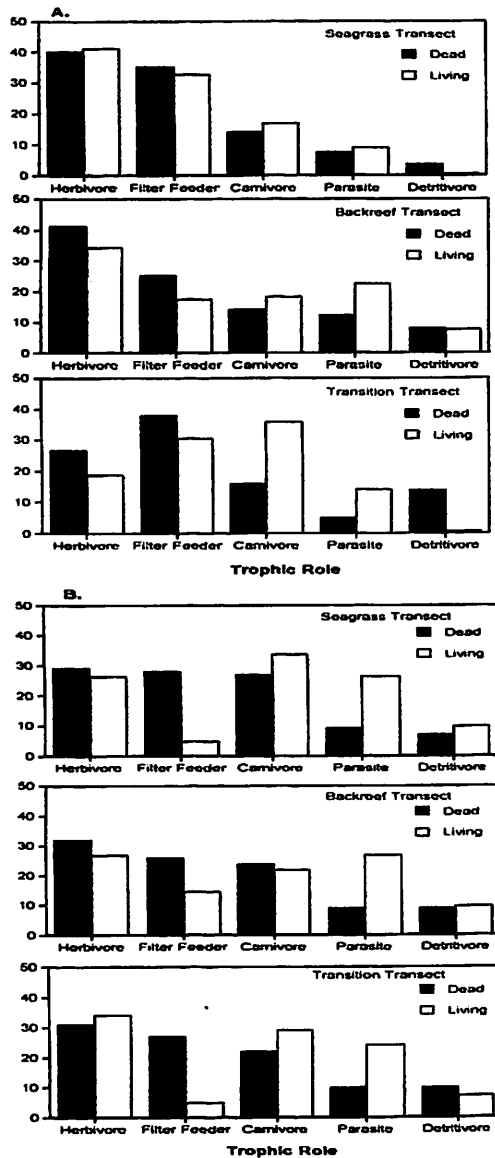

Figure 11. Live:dead comparisons of trophic roles A) by individuals and B) by species for each transect.
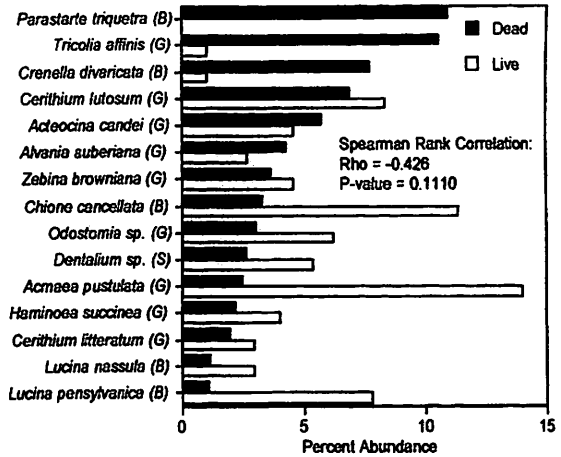

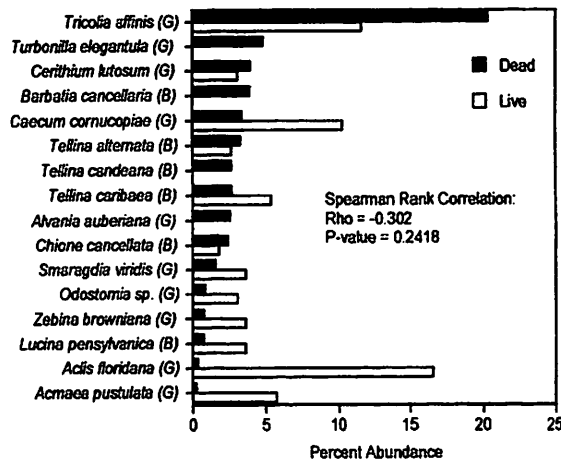Figure 12. Top ten dead and live molluscan species of the Seagrass Transect.

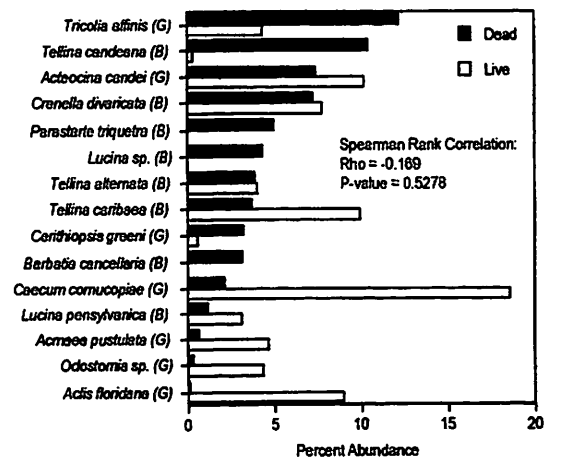Figure 13. Top ten dead and live molluscan species of the Backreef Transect.

Figure 14. Top ten dead and live molluscan species of the Transition Transect.

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Transition Transect.

The Transition Transect proved to be the most interesting transect in terms of live-dead uniqueness. This was the only transect with a significant difference in type of mollusc ($X^2 = 9.47$, $p = 0.01$), since the bivalves were more dominant than gastropods in the death assemblage (Figure 10). There were significant differences between habitat percentages (by individuals: $X^2 = 5.15$, df = 1, $p = 0.02$) and between trophic roles (by individuals: $X^2 = 25.32$, df = 4, $p < 0.0001$; by species: $X^2 = 22.51$, df = 4, $p = 0.0002$). Figures 10 and 11 show this information graphically.

Results of a Spearman Rank Correlation test between the rank order of the top ten dead individuals and the top ten living individuals support the independence of the dead and live assemblage (Rho = -0.17, $p = 0.58$). There seems to be a weak inverse correlation between the two rank orders (Figure 14).

There were 41 species represented in the living assemblage, 39 of which (95.1%) were found in the death assemblage. Within the death assemblage, those 39 shared species account for 32.0% of the total death assemblage species.

Summary of Live:Dead Comparisons.

Table 2 is a summary of the live:dead comparisons within each transect. Results of Chi Square tests are reported as "similar" if $p > 0.05$ and "different" if comparisons yielded $p \leq 0.05$. Spearman Rank Order comparisons are recorded as "independent" if $p > 0.10$ and "correlated" if $p \leq 0.10$.

DISCUSSION

For each transect, within-habitat comparisons of dead molluscs indicate that the rank order of species abundance from sample to sample are quite similar. This indicates to us that each of the three transects is relatively homogeneous within each environment. However, with regard to species rank orders of abundance, comparisons among the transects show that the rank orders of dead mollusc species are quite distinctive. Certainly, this is what we had hoped to find – three distinct communities, at least in terms of species abundance and rank order.

Within each transect, the rank orders of the top ten death assemblage species by abundance were independent of the top ten living assemblage species' rank orders of abundance. Most of the species in the living assemblages (95 – 98%) appeared in the respective death assemblage at each transect. However, the most abundant species in the Graham's Harbor living assemblage was not even present in the top ten of the Graham's Harbor death assemblage. If this were the only criterion for community comparisons, we could conclude that the living

	Trophic Role (Ind)	Trophic Role (Spp)	Class (Ind)	Class (Spp)	Habitat Preference (Ind)	Habitat Preference (Spp)	Rank Order Top 10
Seagrass Dead:Live	similar	**different**	similar	similar	similar	similar	**independent**
Backreef Dead:Live	similar	**different**	similar	similar	similar	similar	**independent**
Transition Dead:Live	**different**	**different**	**different**	**different**	**different**	similar	**independent**

Table 2. Within transect comparisons of living and dead molluscan assemblages for individuals (Ind) and species (Spp).

assemblage cannot be used as a predictor of paleocommunity and vice versa. However, the death assemblage is most likely time-averaged, while our living community is only an "ecological snapshot." The molluscan fossils recovered at each transect reflect many years (upwards of hundreds; see Colby and Boardman, 1989) of accumulation. Time averaging of such death assemblages is supported by a wealth of studies (Kidwell, 1998; Kidwell and Flessa, 1996; Warme, 1969; Russell, 1991; Kidwell and Bosence, 1991; Staff et al., 1986; Walker and Bambach, 1971; Peterson, 1976 and 1977).

There are some distinctive features of the individual transects. Within the Seagrass transect, gastropods dominated both the live and dead assemblages. Miller (1988) found similar results of mollusc type within dense seagrass communities in Tague Bay, St. Croix. Because the bivalve *Parastarte triquetra* and the gastropod *Tricolia affinis* account for 20% of the death assemblage, filter feeders and herbivores, respectively, dominated trophic role classifications. In such a detritus-rich environment, we were surprised that the detritivorous molluscs were relatively unimportant.

The Backreef transect had the highest percentage of gastropods and epifauna of all transects, both in the living and dead assemblages. Since the seagrass coefficient was lowest of all transects, it seems counterintuitive that the epifaunal gastropod *Tricolia affinis* was the most important dead species, accounting for 20% of the individuals in the Backreef transect. Similarly, the most abundant living species was *Aclis floridana*, a parasitic gastropod.

The Transition transect is the most difficult to characterize, due to the fact that the living and dead assemblages differ with regard to *all* the ecological parameters examined in this study. What could account for these differences? It is possible that

since this is a transitional community, ranging from dense seagrass to sand flat, the effects of minor within-habitat transport could influence the assemblages. However, using techniques described by Cummins et al. (1986), there was a low percentage of species covariance among samples, indicating little within-habitat transport. Based on past research in similar environments, this is not an unusual result (see Cummins et al., 1986; Miller and Cummins, 1990; Kidwell and Flessa, 1996).

CONCLUSIONS

We are able to conclude that each of the three habitats is distinctive in terms of the molluscan death assemblages. Comparisons of living and dead assemblages at each of the habitats were variable. In terms of the ecological parameters studied, the living and dead assemblages at both the Seagrass and Backreef transects were similar; however, the Transition Transect had distinct living and dead molluscan communities. In general, the living molluscan communities are not very representative of the paleocommunities at any of the three habitats, especially in regards to species composition and abundance.

Analyses of additional data from this study will further benefit the understanding of the Graham's Harbor habitats. Future work will include lateral sample comparisons along the length of the transects, with special consideration given to seagrass density. Since seagrass density is quite variable and a necessary habitat for certain benthic molluscan species, it seems that we are overlooking potentially significant information about small-scale community variability within habitats. Similarly, continued sampling of the living communities could increase the fidelity of live:dead species com-

position comparisons at each of the transects.

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