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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.

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LIVING MOLLUSCAN COMMUNITY DISTRIBUTION AND SPECIES COMPOSITION AS IT RELATES TO SEAGRASS DENSITY IN A TROPICAL CARBONATE LAGOON, GRAHAM'S HARBOUR, SAN SALVADOR, BAHAMAS

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ABSTRACT

The living invertebrate community of molluscs was measured at three distinct environments within Graham's Harbour, San Salvador, in order to characterize the living molluscan community of the lagoon. Three 40-meter transects were conducted in: 1) dense Seagrass, 2) a Backreef area, and 3) in a seagrass-sand Transition zone. Sixteen shallow cores were taken per transect and all living molluscs greater than 0.5 mm were identified. Seagrass densities were also calculated for each transect. In addition to species composition, parameters used to identify relationships of transects include trophic roles and mollusc type, and habitat preference. The living mollusc community of these three transects have distinctly different species compositions and trophic structures.

INTRODUCTION

In the last few decades, paleontologists have focused on Recent assemblages of living and dead marine benthic communities to better understand how the fossil record forms. These actualistic studies have yielded much important information on taphonomic processes from a wide variety of environments (Warme, 1969; Walker, 1971); Peterson, 1976; Cummins et al., 1986 a,b; Cummins, 1994; Fursich and Flessa, 1987; Miller, 1988; Parsons, 1989; Russell, 1991; Staff and Powell, 1999; Zuschin et al., 1999). One fact that has become clear is the rarity of living potentially preservable molluscs, particularly when compared with the abundance of preservable molluscan remains in most lagoon sediments. Long-term ecologic studies have more information on living molluscan community composition, but, studies that are no more than "ecologic snapshots" report a paucity of living molluscs. Consequently, ecologic analyses of living mollusc communities are often ignored or woefully inadequate.

The purpose of this paper is to define the living molluscan community of Grahams Harbour along the northern coast of San Salvador Island, Bahamas. We were particularly interested in determining ecological distinctions (trophic roles, species composition and abundance, habitat type, and infauna/epifauna ratios) among three distinctive environments in this shallow tropical lagoon. By better understanding the "ecology" of the living molluscs in these environments, we hoped to be better able to interpret the long-term record in the death assemblage (see Dehhr et al, this volume).

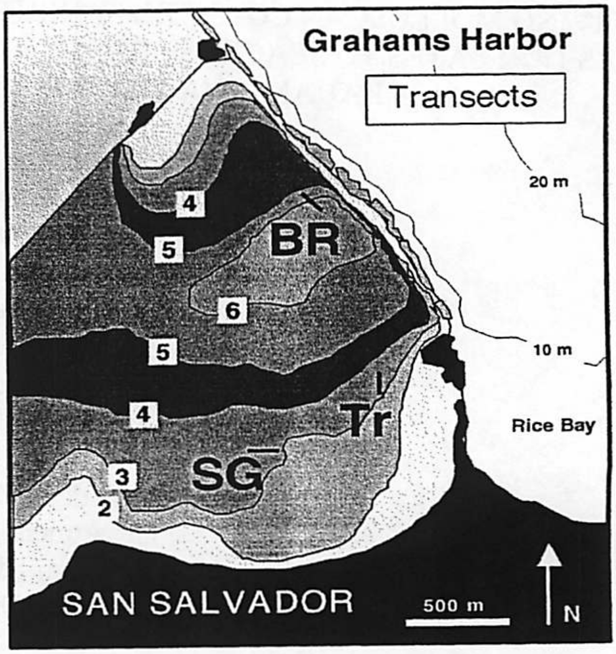

Figure 1. Bathymetric map with locations of study sites within Graham's Harbour: Seagrass Transect (SG), Backreef Transect (BR), and Transition Transect (Tr). Contours in meters.

METHODS

Research Area

Graham's Harbour, located at the northeastern end of San Salvador Island, Bahamas (Figure 1), is a shallow carbonate lagoon with patches of seagrass meadows and sand flats. The harbor is approximately two by three kilometers, with depths to six meters (Colby and Boardman, 1989). The lagoon is bordered on the east and north by a combination of barrier reefs and small cays, and to the south by San Salvador Island. Graham's Harbor has been an evolving carbonate lagoon for the past 6,000 years (Colby and Boardman, 1989). Our research was conducted at three different environments within the lagoon chosen for substrate variability (Figure 1). The three specific environments were 1) a dense seagrass bed (SG), 2) a backreef area (BR), and 3) a seagrass-sand transition zone (Tr) (Figure 1). The Seagrass environment was dominated by dense *Thalassia testudinum* and *Syringodium filiforme*. The Backreef area was characterized by patches of seagrass located on the lagoonal side of the barrier reef in Graham's Harbour. The Transition transect was a seagrass-sand transition zone 300 m west of the "Cut" at North Point. The "Cut" is a shallow channel that connects Graham's Harbour and the Atlantic Ocean, concentrating a vigorous inflow/outflow of water in a small area of Graham's Harbour.

Forty meter transects were established in each of the three habitats. At each transect, eight shallow cores were collected at five meter intervals twice during a six month interval (resulting in 16 core samples per transect). The entire volume of each sediment core (~500cm^3) was processed for living specimens following the methods of Staff and Powell (1999)

Ecological Measurements

Seagrass Density

Along each transect, seagrass blades were counted in ten 100 cm^2 quadrats at each sediment core location (16 cores/transect), Blade counts were used to calculate blade surface area of *Thalassia testudinum* and *Syringodium filiforme* using the method described by Miller (1988). Species blade surface area for each quadrant was calculated using a modification of Miller's (1988) coefficient. For our study, the seagrass coefficient was calculated as:

$$SGC = T * 0.0025 + S * 0.0007$$

where T and S are the densities per square meter of *Thalassia* and *Syringodium*, respectively, and SGC is m^2 of blade area per m^2 of seafloor area. This provided us with a measure of seagrass density (m^2 blade area/m^2 bottom area) for each core sample at each transect.

Molluscan Analyses

In the evaluation of the mollusc community, the following measurements were made:

1. Species composition: Each living organisms > 0.5 mm in size was identified to the most detailed level possible (species). References for identification of living molluscs include Abbott (1974), Abbott and Dance (1990), Warmke and Abbott (1962), and Morris (1975);
2. Size: The size (long dimension) of each organism was measured and categorized into size subclasses of 0.5 mm between 0.5 and 4 mm and subclasses of 2 mm for sizes larger than 4 mm. A size frequency distribution was calculated for the living community by combining all individuals into one "super" dataset to determine which size classes dominated the living community;
3. Mollusc type: Bivalve, gastropod, or scaphopod;
4. Habitat preference: infaunal or epifaunal;
5. Trophic role: The primary trophic role (herbivore, detritivore, filter feeder, carnivore, parasite) of each organism was categorized using the feeding guild classification of Stanley (1970), Abbott (1974), Robertson (1975), and Slone (1990).

Statistical Analyses

We conducted Spearman rank tests to determine the correspondence of rank orders of abundance of the living molluscan assemblages among transects. Spearman rank tests ($p > 0.1$) of the ten most abundant species of each transect were used to assess the similarity of the species compositions of the three transects. The nature of the correlation is signified by the rho value, with a negative value implying an inverse relationship.

Chi square tests (significance level of 0.05) of each trophic role, habitat type, and molluscan type were conducted to evaluate the distinctiveness of trophic roles, habitat type and molluscan type between transects. The analyses were done for *percent living individuals* and *percent living species* represented for each ecological comparison.

RESULTS

Seagrass Density

The Seagrass transect (average SGC = 8.62) had a much greater seagrass density than the Backreef (average SGC = 1.86) and Transition (average SGC = 2.41) transects (Figure 2). We predicted that seagrass coverage would be a factor of species composition,

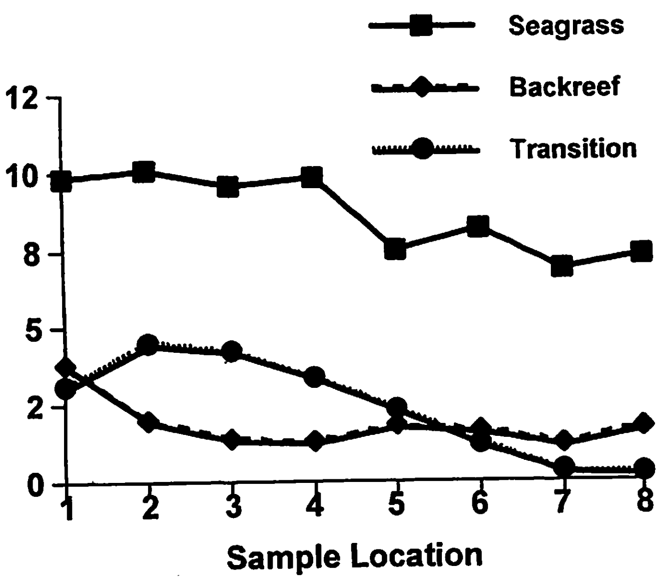

Figure 2. Seagrass density for all transects (following the method of Miller, 1988).

mollusc type, trophic composition, and habitat type.

Species Composition and Rank Order Comparisons

Sixty-four species were observed among all transects. Forty-two species were identified in the Seagrass transect, and forty-one species were found at both the Backreef and Transition transects. There were 23 species common to all transects and 27 species were found at only one of the three transects (Figure 3).

The most abundant species in all the transects combined were: *Caecum cornucopiae, Acmaea pustulata, and Aclis floridana* comprising approximately 26 percent of all individuals identified.

Within the Seagrass transect, *Acmaea pustulata, Chione cancellata,* and *Cerithium sp.* were the most numerous, comprising 34 percent of all the individuals collected. In the Backreef transect, *Aclis floridana, Tricolia affinis,* and *Caecum cornucopiae* compose approximately 40 percent of the individuals collected. Eight of the top 10 species were gastropods. In the Transition transect, 38 percent of the living molluscs were *Caecum cornucopia, Acteocina candei, Tellina caribaea,* and *Aclis floridana*. Six of the top ten species were gastropods.

Spearman rank comparisons are shown in Figure 4. The following rank order of abundance comparisons were independent and have a non-significant *inverse* relationship: Seagrass and Backreef (rho = -0.47, p = 0.15) and Backreef and Transition (rho = -0.38, p = 0.25). Only the Seagrass and Transition comparison was significantly correlated (rho = -0.59, p = 0.07). Thus there is an inverse relationship between the rank orders of living abundance at these two sites.

Trophic Relationships

In the Seagrass and Backreef transects, herbivorous individuals dominated; whereas carnivorous individuals were the most prevalent in the Transition transect. Based on an evaluation (Chi Square) of the trophic roles using numbers of individuals, all three transects have different trophic structures [Seagrass and Backreef (df = 4, X^2 = 16.680, p = 0.0022), Seagrass and Transition (df = 4, X^2 = 16.027, p = 0.0030), and Backreef and Transition (df = 4, X^2 = 21.533, p = 0.0002)]. However, based on the same evaluation using species, the transects have similar trophic structures. Figure 5 illustrates these comparisons.

Habitat Relationships

Epifaunal individuals dominated all environments; however, infaunal species were more abundant than epifaunal species (Figure 6). Evaluations of epifaunal to infaunal abundance of individuals and spein indicate that all transects are similar (p > 0.05).

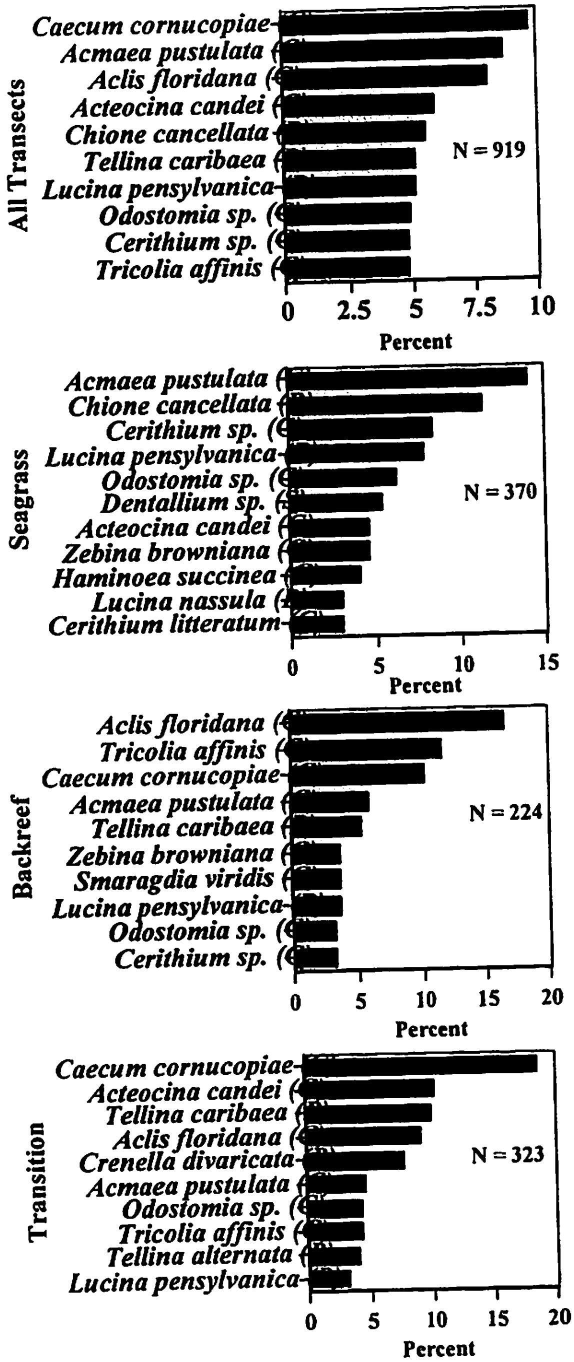

Figure 3. Percent relative abundance of the ten most abundance species along each transect, and from combined transects.

Mollusc Types

Gastropod individuals and gastropod species were the most abundant mollusc type in all transects (Figure 7). Chi square analyses ($p > 0.05$) indicate that all three transects have a similar mollusc type whether using percent individuals or percent species.

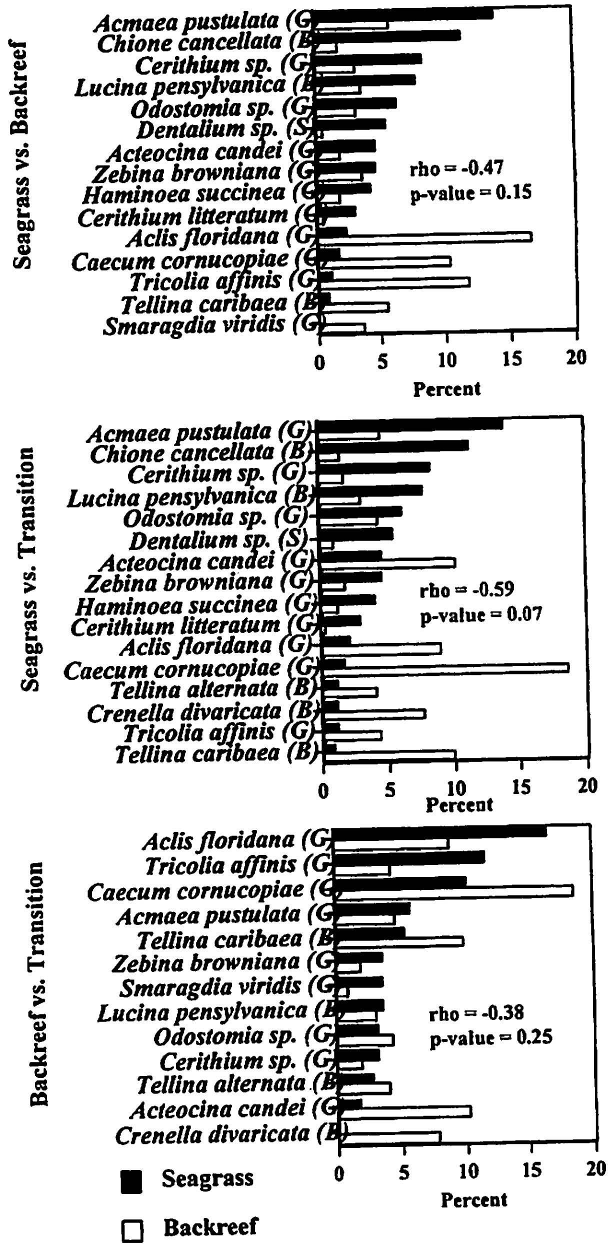

Figure 4. Spearman rank correlations between all transects. Negative rho values indicate an inverse correlation.

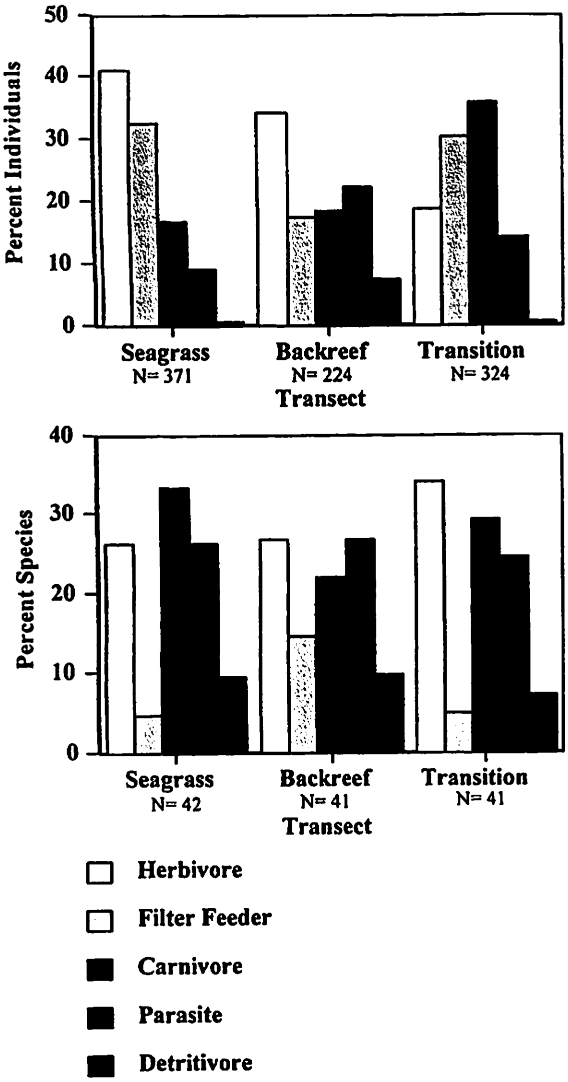

Figure 5. Trophic roles of individuals (top) and species (bottom) from each transect.

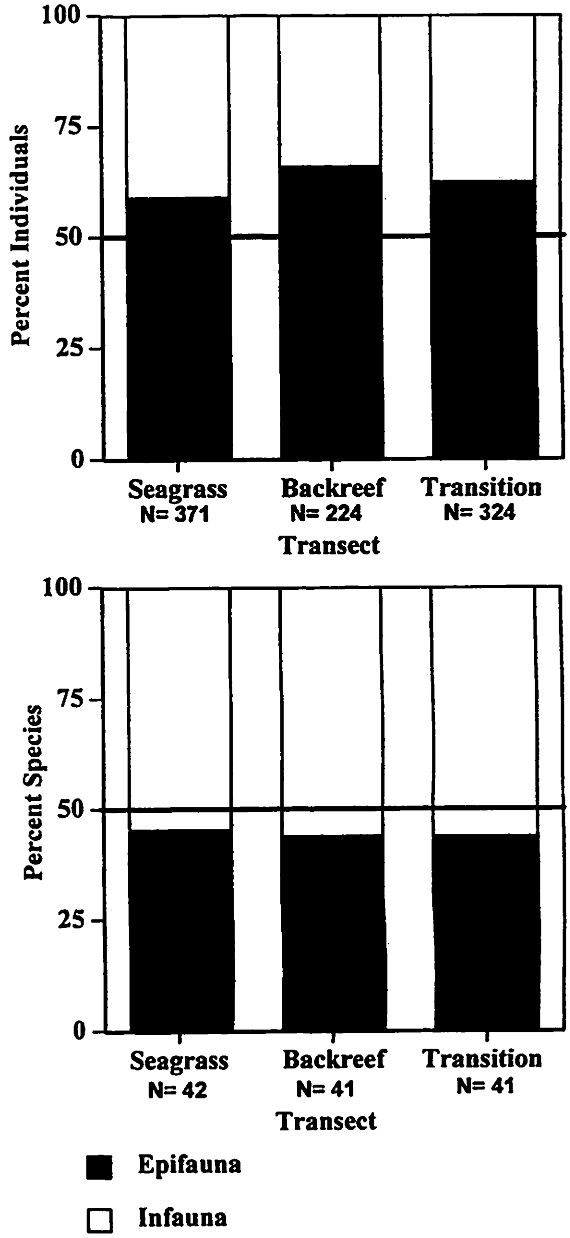

Figure 6. Percent abundance of epifaunal and infaunal individuals (top) and species (bottom).

Size Frequency Distribution

The majority of all individuals identified (86%) were between 0.5 mm and 4 mm in size (Figure 8). In the Seagrass transect 69% of the individuals were small (< 4 mm), in the Backreef site, 82% were small, and in the Transition site, 89% were small. The larger molluscs only contribute 14% of the individuals.

DISCUSSION

Species Composition

Based on Spearman rank order of abundance of the species and individuals, each transect has a distinct assemblage of

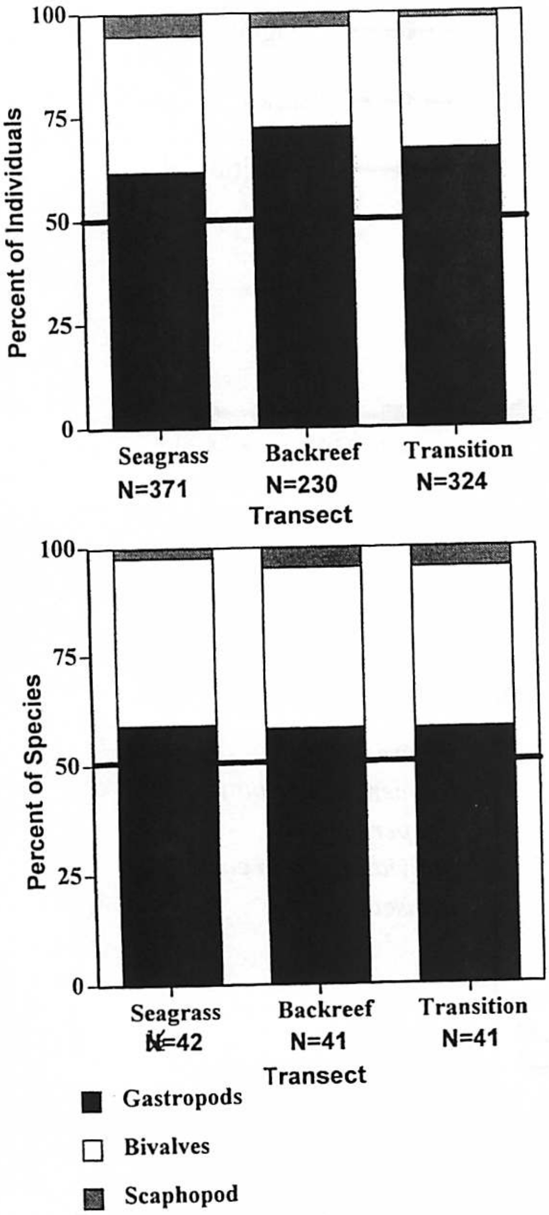

Figure 7. Ratios for percent individuals (top) and species (bottom) for gastropods, bivalves and scaphopods.

molluscs, i.e. the transects are different from each other.

Our original hypothesis, that the seagrass transect would have more gastropod species than any other transect, proved to be incorrect. Gastropods were the most abundant molluscan taxon in all the environments sampled in Graham's Harbour (Figure 3). We are not sure why this is so, but the backreef environment might offer a wider range of diverse habitat, including patches of dense seagrass punctuated with sandy areas. The Seagrass transect doesn't have much exposed sand, thus potentially excluding many infaunal gastropods.

Grahams Harbour is a dynamic biological system that we are only now beginning to characterize.

Trophic Relationships

The evaluation of feeding habits is an important aspect of comparing living and ancient communities. Some have argued that, due to the destructive "taphonomic mill" all individuals face at death, the relative proportion of trophic groups is more readily preserved in the fossil record (Scott, 1978; Staff and Powell, 1999) than is numerical abundance.

The trophic compositions of the three transects are significantly different from each other (Figure 5). The large number of herbivorous organisms in the Seagrass transect is expected due to the greater density of seagrass. However, we did not expect to find the prevalence of herbivores in the Backreef transect.

Another observation is that the trophic role that dominates a specific transect by abundance of individuals does not necessarily dominate in the same transect according to the abundance of species. In other words, the analysis based on numbers of individuals is different than the analysis based on species. We see this in all of the transects (Figure 5). Of particular note is that carnivore species dominate in the Seagrass transect rather than herbivore species, i. e., the herbivores are more abundant in the

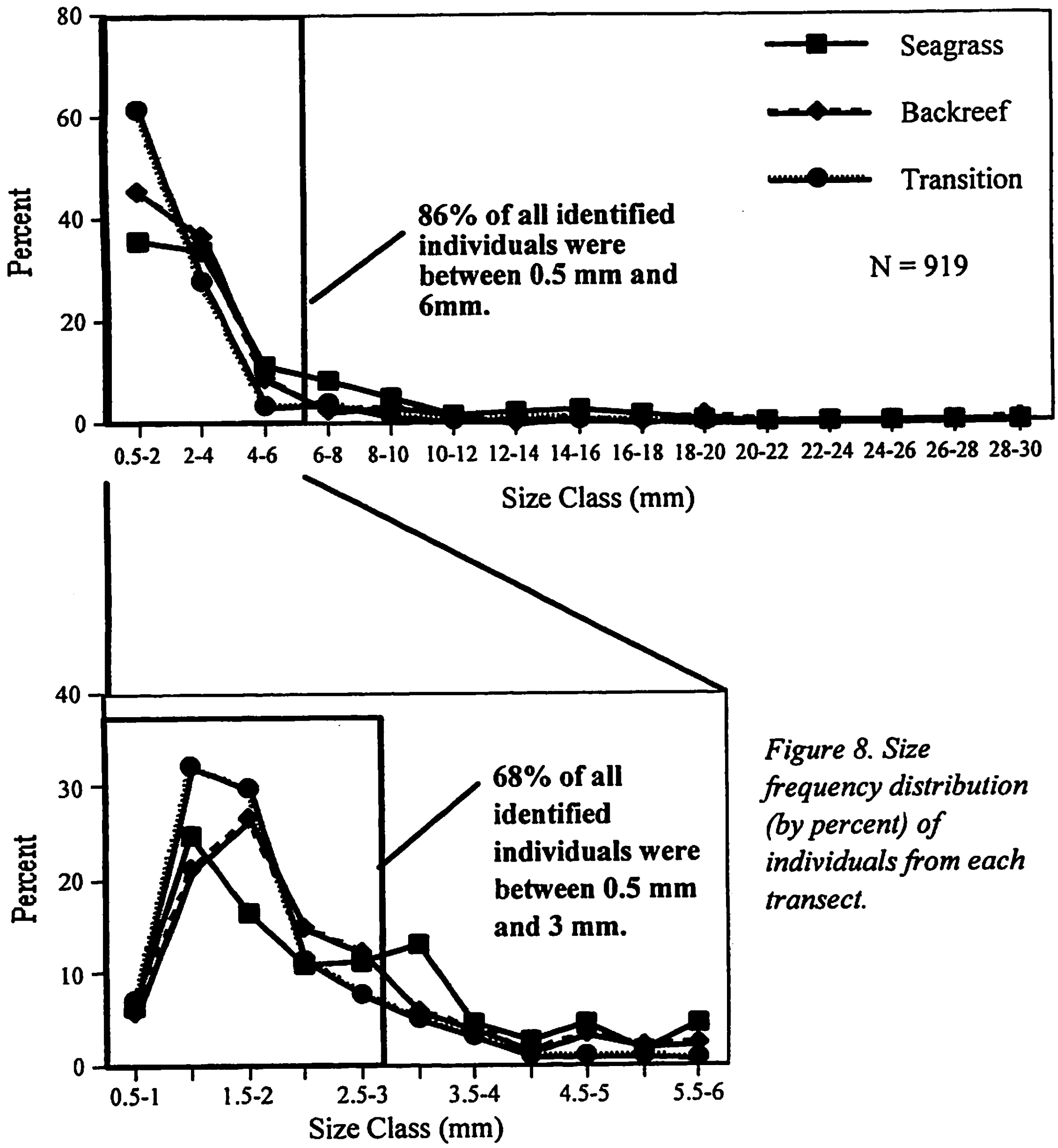

Figure 8. Size frequency distribution (by percent) of individuals from each transect.

seagrass beds, but the carnivores are more diverse.

Why the difference in results when using percent individuals and percent num-ber species? Which analysis better describes the community? The number of molluscan living individuals can widely fluctuate from location to location and from season to season. The numbers are not stable due to natural mortality. Our sampling grossly underestimates the number of living individuals that actually set between sampling times (Cummins et al., 1986). Using percent species as the index of measurement is more conservative. While the number of individuals of a species may widely fluctuate, the presence or absence of a common species is not likely to change as readily as the number of individuals.

Habitat Preference and Molluscan Type

Overall, the ratios of epifauna to infauna were very similar whether using percent individuals or species (Figure 6), and gastropods dominate at each transect whether using percent species or individuals (Figure 7).

It was expected that seagrass environments would support a more fertile niche for epiphytes, promote the formation of detritus, and protect smaller organisms from predators (Wood et al. 1969). With this in mind, we hypothesized that we would find a greater number of herbivorous gastropods and epifaunal individuals in the Seagrass transect relative to that found in the Backreef and Transition transects.

However, our observations do not support such a simple model. We found in the Seagrass transect sites that herbivores were dominant (Figure 5), but gastropods were not as prevalent in the Seagrass environment as they were in the Backreef or Transition environments (Figure 7). Although epifaunal individuals were numerically dominant in the Seagrass transect, they individuals also dominated the Backreef and Transition transects (Figure 6).

The dominant habitat preference in all transects using percent individuals is epifaunal. while infaunal species dominate the transects. Thus infaunal taxa are more diverse, whereas epifaunal taxa are more abundant. For the reasons discussed in the section dealing with trophic analyses, the time-averaged habitat preferences using species is less affected by wide seasonal fluctuations in the number of individuals. Using species is a more conservative measurement and may more accurately reflect the long-term habitat preference in the living community.

Size Frequency Distribution

Many actualistic studies of benthic communities use a mesh size of 4 mm (e.g. Miller, 1988). In our studies 86 percent of the living individuals were less than 4 mm in size (Figure 8). By not using a smaller sieve size, a significant proportion of the living community will remain unobserved. This sampling bias should be included in interpretations of mollusc (and lagoon) communities.

CONCLUSIONS

The three habitats in Grahams Harbour support distinctive molluscan communities.

The time averaged molluscan death assemblage provides a more accurate representation of long-term molluscan community characteristics in Grahams Harbour than does a short-term study of the living community. The combined use of the death assemblage and the living community in assessing the impact of local- and global- change on community structure has great potential. Ecologists, who frequently ignore the long-term record in the sediments, and geologists, who frequently ignore the short-term record in the living community, would do well to combine the analyses of the living and the dead in their assessments of global change in marine communities.

Living Community Characterization

Seagrass Transect.

The seagrass transect had the highest seagrass index and was dominated by *Acmaea pustulata* and *Chione cancellata*. Herbivory was the dominant trophic type using percent individuals. As for habitat and species type, epifauna and gastropods made up the majority of individuals analyzed.

Backreef Transect.

Seagrass density at this transect was similar to the Transition transect and much less than the Seagrass environment. *Aclis floridana* was numerically dominant species found, and herbivory was the dominant trophic type using percent individuals. The dominant species habitat was epifaunal, and the major species type was gastropods.

Transition Transect.

This transect had a seagrass density similar that of the Backreef environment. The dominant species were *Caecum cornucopiae* and *Acteocina candei*. The most abundant trophic role by using percent individuals was carnivores, followed by filter feeders. The major habitat type was epifauna, and the major species type was gastropods.

Distinctions

Analysis of species composition and trophic composition are different when viewed using the number of individuals rather than number of species among transects. Why are the transects different in these ways? The high variability between species and trophic composition among transects may be due to different environmental conditions. The Seagrass transect has more seagrass which may create significantly slower currents and alter the sedimentological structure. The Backreef transect was located in close proximity to a barrier reef and in relatively deeper water than the other two transects. Finally, the Transition transect was in a seagrass-sand transition zone and was also exposed to a different current energy pattern due to the "Cut" connecting Graham's Harbour with Rice Bay. These environmental differences seem to have a profound effect on the living community species composition.

Similarities

We expected to see some differences in the habitat preference and mollusc type among transects. However, we observed habitat preference and mollusc type to be similar among transects . We also found that the trophic roles were similar when comparing percent species among transects Overall, the three living molluscan communities of each environment within Graham's Harbour are distinctive with respect to species composition and trophic roles, probably due to the different environmental and physical conditions. Varying seagrass densities, along with different current exposure and sedimentological structure create very distinct living communities of molluscs. Graham's Harbour is a more complex environment than we ever imagined!

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