RELATIONSHIPS BETWEEN LARGE BENTHIC FORAMINIFERA AND THEIR SEAGRASS HABITATS, SAN SALVADOR, BAHAMAS

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Olivia Claire Buchan

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VITA

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THESIS ABSTRACT

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Vegetation beds are important in the ecology and depositional history of platform carbonates. The vegetation itself, frequently dominated by the seagrass *Thalassia*, has a low preservation potential, but plants and benthic algae are substrates for a variety of epibionts, including foraminifera, which have a significant fossil record. This actualistic study examines the potential of large benthic foraminifera to serve as proxies for the presence, taxonomic composition, density, and environmental variables of ancient vegetation beds.

Six sites having a range of vegetation densities, water depths, and water energies were selected. Grass-bed densities were measured by counting individual sea grasses and algae in 50x50-cm grids. One hundred individuals of each of the major vegetation genera were collected from each site, as well as the top 1 cm of sediment. Foraminifera were picked from the collected vegetation and from the 2.0 to 0.5-mm sediment fractions. Live and dead foraminifera were counted from vegetation and sediment samples, and total foraminiferal density was recorded. Dead foraminifera were categorized by taphonomic condition. Cluster analysis was used to group sites according to foraminiferal data and by vegetation type.

Sorites and *Planorbulina* were the dominant live foraminifera found on the favored substrates, *Thalassia* and *Halimeda*. Sediment assemblages from the same sites were dominated by (dead) *Archaias*, *Quinqueloculina/ Triloculina*, and *Valvulina*. Cluster analysis shows that the sediment foraminiferal assemblages do not separate according to vegetation type. The density of tests in the sediment corresponds to vegetation density to some degree, but factors such as nutrient supply may play major roles. Thus, the species composition and density of foraminifera alone do not accurately reflect the taxonomic composition and density of sea-grass beds.

In contrast, taphonomic condition is a consistent indicator of the presence and density of sea-grass beds. Lush stands of *Thalassia* protect delicate tests on the seafloor. Here altered tests are frequently encrusted, whereas breakage and abrasion are more common in higher energy, sand-dominated sparse beds. For these reasons, taphonomic states should be included in carbonate-platform foraminiferal studies.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Foraminifera are single-celled protists that secrete a test to house protoplasm (Fig. 1). The protoplasm that lies outside the test (ectoplasm) contains thread-like, branching, and anastomosing pseudopodia, called rhizopodia, which transport food material, expel waste, and assist in locomotion. Inside the test, the endoplasm contains the nucleus or multiple nuclei of the foraminifer and also can house cells of algal symbionts, which may help foraminifera to survive nutrient-deficient conditions (Hallock, 1982). Foraminiferal diets vary by species but generally include bacteria, diatoms, and sometimes other small protists. Some foraminifera feed on small crustaceans, molluscs, nematodes, and invertebrate larvae (Armstrong and Brasier, 2005). Foraminifera can be benthic or planktonic and have a geologic range of Cambrian through Recent. The size of those benthic species known as “larger” varies according to individual authors (e.g., Ross, 1974; Haynes, 1980; Murray, 1991). In this investigation, those species that regularly reach a maximum dimension over 1 mm are the objects of study.

The tests of foraminifera may be composed of organic matter (tectin); of minerals such as calcite, aragonite, or silica; or of agglutinated particles. Tests can be single chambered or consist of several chambers that can develop into a variety of growth patterns adapted for a specific habitat. Each of the three major living suborders of foraminifera – Textulariina, Miliolina, and Rotaliina – include some species that are

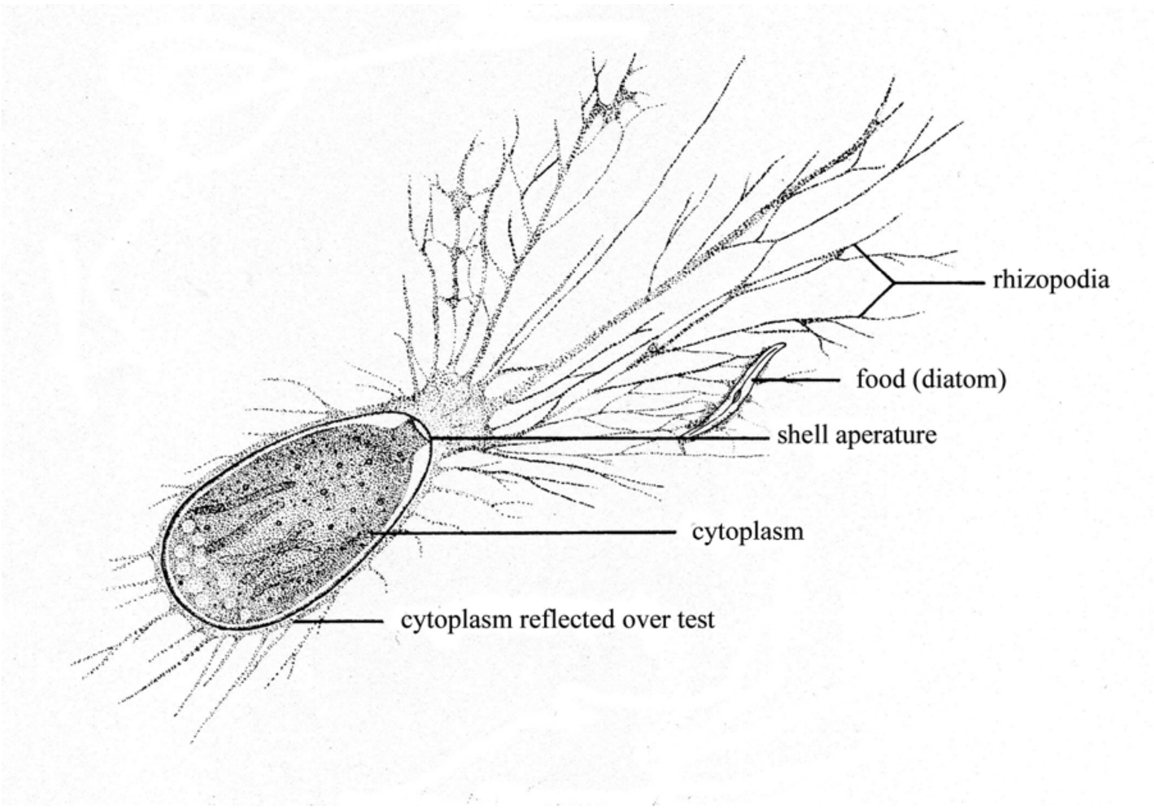


FIGURE 1—The single-chambered foraminifera *Allogromia* (from Beck and Braithwaite, 1968).

considered large benthic foraminifera, and these are important elements for actualistic and paleocommunity studies (Brasier, 1980; Loeblich and Tappan, 1988).

Value of Foraminifera

Foraminifera are excellent biostratigraphic indicators because many individual species have short geologic ranges and widespread distributions (Scoffin, 1987). Furthermore, they are compact, resistant to breakage, easily preserved, common in marine sediments, and easily detectable in cores. Although the preservation potential of grass beds is very poor, foraminifera are easily preserved in the fossil record. Therefore, assemblages of foraminifera that lived on plants and algae may be used to reconstruct paleocommunities.

Modern benthic foraminifera are found in surface sediments in many parts of the world's oceans. Large benthic foraminifera are especially abundant in lagoonal, reef, and shallow neritic settings where their principal habitat is on the sea floor. Many foraminifera also prefer to attach to phytal substrates such as seagrasses or algae (Brasier, 1980). Temperature is the most important factor governing the distribution of benthic foraminifera (Scoffin, 1987). Depth is also important because sunlight must reach the endosymbionts, which photosynthesize, providing energy for the foraminifera (Hallock, 1985).

Study Area

The island of San Salvador, Bahamas, located 640 km southeast of Miami, Florida, is a modern example of a carbonate platform (Fig. 2). The tropical, clear,

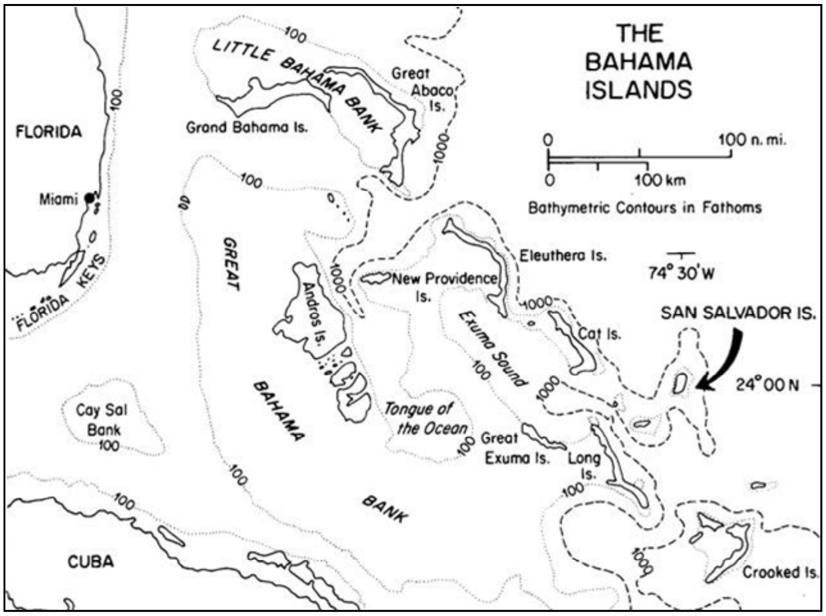


FIGURE 2—Map of the Bahama Islands. Arrow points to location of San Salvador (from Curran, 1984).

shallow waters provide excellent environments for many seagrass beds and coral reefs, which offer ideal habitats for large benthic foraminifera.

Anthropogenic nutrification pollution, common off the Florida coast, may destroy grass beds and lead to algal blooms, which block the sunlight necessary for photosynthesis (Collins et al., 2004). However, the remote, natural setting of San Salvador allows for an accurate, in-depth study of the relationships between large benthic foraminifera and their grass-bed habitats.

GRASS BEDS AND ASSOCIATED LARGE BENTHIC FORAMINIFERA

Grass-bed Communities

Grass beds are a combination of marine grasses, such as *Thalassia* (turtle grass) and *Syringodium* (manatee grass), and benthic macroalgae, such as *Halimeda* and *Penicillus.* Grass beds are important in the ecology and depositional history of platform carbonates (Brasier, 1973, 1975a). Just as many land grasses help prevent erosion and stabilize sand dunes on the coast, marine grasses and benthic algae help to stabilize backreef sediment throughout the Caribbean and elsewhere. The seagrasses and macroalgae of the grass beds have extensive root and rhizoid systems, repectively, which prevent erosion of shallow lagoonal sediments, while the grass blades and thalli (stalks) of algae reduce current speeds and allow suspended sediments to settle on the sea floor. The surface of the vegetation often has a biofilm consisting of algae, bacteria, diatoms, and other microbes (Brasier, 1975a). Larger epibionts such as polychaetes, gastropods, and foraminifera also live and feed on this biofilm. Some of the attached organisms on the grass blades, along with benthic calcareous algae and a variety of associated organisms, are producers of biogenic $CaCO_{3,}$ making the grass-bed community (Fig. 3) a major contributor to the formation of carbonate platforms (Brasier, 1975a). Also, the vegetation increases the amount of organic matter in the sediment. The vegetation thus provides food sources directly and indirectly and aids in the production of calcium carbonate (Braiser, 1973).

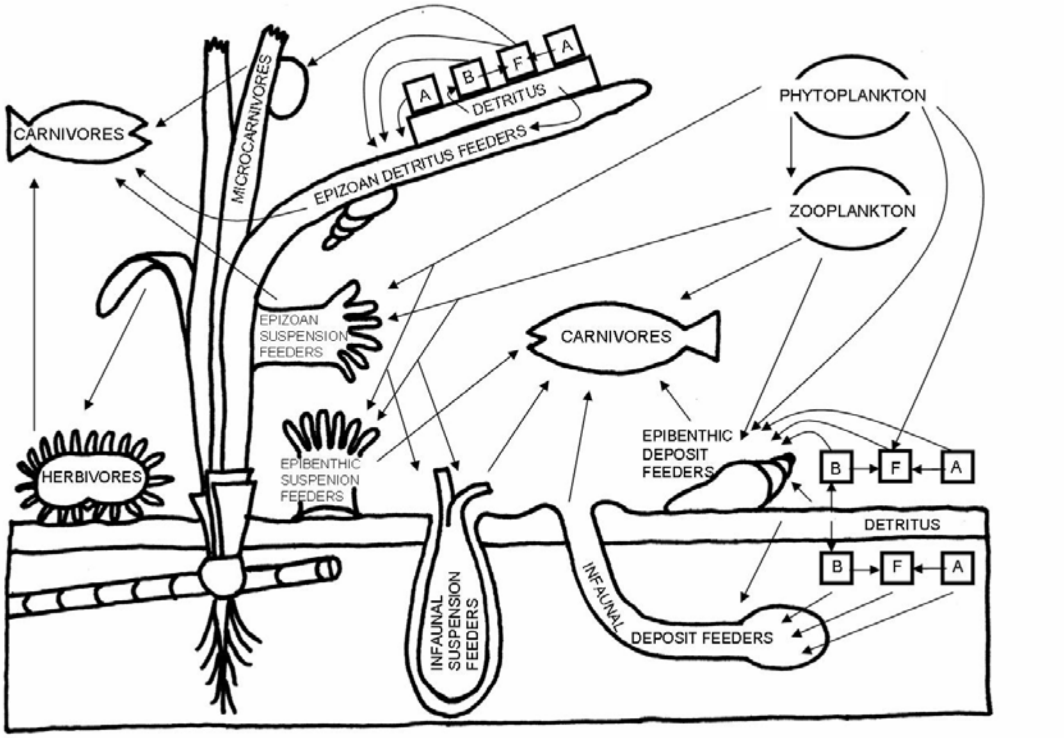


FIGURE 3—Trophic relationships among groups in a seagrass community. A = algae, B = bacteria, F = foraminifera (modified from Brasier, 1975a).

Seagrass beds are most prolific at 2 to 15 m of water depth and can tolerate a wide range of salinities: from 32‰ to 55‰ (Scoffin, 1987). High-density grass beds are generally dominated by finer-grained sediment, whereas low-density grass beds are frequently dominated by coarser-grained sediments (Scoffin, 1987).

Several factors can influence the grass-bed community: interspecific competition and availability of resources, stress and life-history characteristics, and disturbance and succession (Rose, 1997). Rose (1997) states that, in most seagrass communities, seagrasses may directly compete for space with other seagrasses and algae or they may compete for available resources in changing environments. Seagrasses also are affected by their tolerance to stress. The seagrasses that are tolerant during changing environmental conditions may out-compete those grasses that are less tolerant. This can force some grasses to change their life-history strategies and adapt to a new growth style when competition increases. Finally, seagrass communities can be affected by disturbances involving a loss of biomass. When all or part of a seagrass meadow is destroyed (e.g., by herbivory, propeller scars, or storms), the bare areas may be recolonized by new species of grasses that were formerly not present due to competition with other grasses. The succession of seagrasses that recolonize may be controlled by nutrient requirements and water quality or tolerance to frequent disturbances.

Seagrass communities are also dependent on levels of CO_2 in the atmosphere. An increase in CO_2 leads to an increase in production of seagrasses. However, this also will allow an increase in epiphytic algae, which can cause more shading. In addition to an increase in production of seagrass, higher CO_2 levels can result in an overall global temperature rise, and this may allow expansion of the seagrass community into higher latitudes (Brouns, 1994).

Evolution of Grass Beds

Today’s Caribbean seagrass communities are dominated by *Thalassia testudinum* and *Syringodium filiforme*. Such shallow, sheltered, tropical to subtropical marine grasses have a poor fossil record, especially in the Caribbean. Seagrass in general is believed to have existed since the Late Cretaceous. However, the silicified fossil remains of the grasses themselves are meager, and those that do exist are not always identified as marine grass with certainty (Domning, 2001). The reproductive parts are not generally well preserved, so it becomes difficult to distinguish seagrasses from other monocotyledons. In addition, the pollen lacks exine, a substance that, when present, increases the preservation potential of the pollen grain (Brasier, 1975a). The only reported occurrence of fossil seagrass in the Caribbean region is in the Middle to Late Eocene Avon Park Formation of northern Florida (Domning, 2001).

Overall, distributions of Recent seagrasses are similar to the faunal realms of lagoonal, large benthic foraminifera. The presence of seagrass around the world as early as the Eocene is also indirectly supported by fossil foraminiferal evidence (Brasier, 1975a; Eva, 1980). Foraminifera that attach to seagrass and other vegetation commonly have a discoidal shape with a specialized attachment surface. Fossil foraminifera with test morphologies similar to living species found attached to grass blades flourished at the same time as seagrasses. Also, the fossil record of Sirenians (aquatic herbivores) coincides with the invasion of seagrass in the Caribbean (Domning, 2001).

Published investigations of the evolutionary history of seagrass illustrate that grass-bed foraminifera can be used as proxies for the vegetation itself. Figure 4 shows the geologic ranges of seagrass taxa and associated large benthic foraminifera discussed in this thesis. The systematic relationships of large benthic foraminifera that are associated with grass beds and discussed in this study are shown in Table 1.

Brasier (1975a) discusses the geographic distributions and geologic ranges of seagrasses and associated foraminifera. He states that seagrasses are distributed in three broad provinces: (1) *Zostera* has a temperate water, bipolar distribution; (2) *Cymodocea* is mostly tropical but is absent from the Caribbean and tropical west Africa and (3) *Thalassia* is mostly tropical, is present in the Caribbean, and is absent from the Mediterranean. *Zostera* ranges from the Late Cretaceous to Recent and is not associated with any specific foraminifer except occasionally *Planorbulina* (Eocene to Recent). Soritids foraminifera are commonly absent from the *Zostera* communities because of the temperate climates these grasses prefer. *Cymodocea* ranges from the Lower Eocene to Recent. *Peneroplis planatus* is known to live on *Cymodocea* today and has a similar distribution to this grass throughout the Mediterranean. The soritid *Orbitolites* (Lower to Middle Eocene) also is associated with early occurrences of *Cymodocea*. Both *Peneroplis planatus* and *Orbitolites* were widespread in the Tethyan region, but are not presently known from the Caribbean, so this seagrass probably did not exist in the Caribbean during the Eocene. After *Orbitolites* became extinct in the Eocene, its living relatives *Marginopora* and *Sorites* (both Miocene to Recent) flourished. Records of *Thalassia* show that this grass invaded the Caribbean in Early Miocene and is closely linked with the foraminifer *Sorites*. Seagrass flourished in the Caribbean during the Early

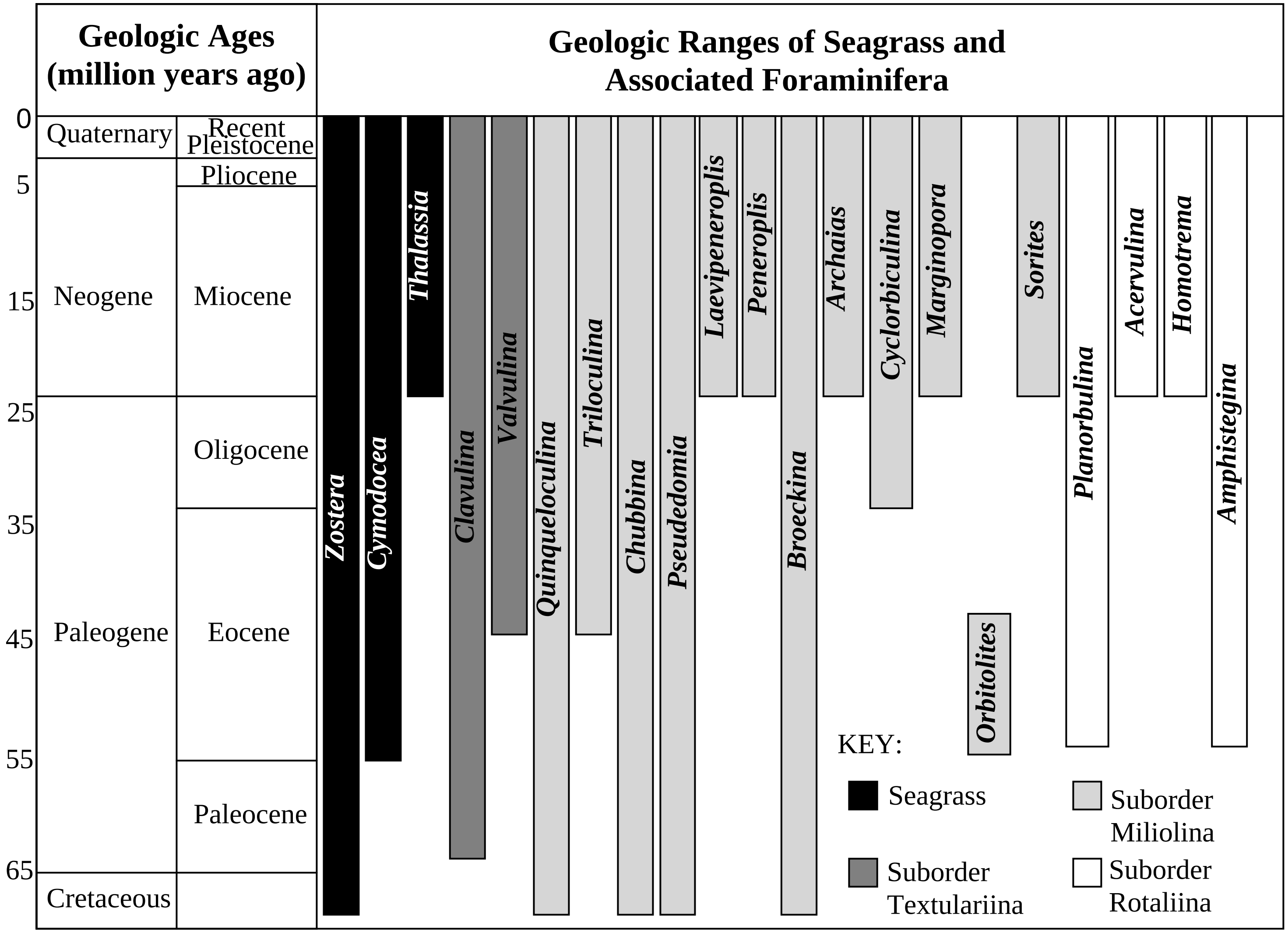


FIGURE 4—Geologic ranges (approximate) of genera of common seagrass and associated foraminifera (Brasier, 1975a; Loeblich and Tappan, 1988).

TABLE 1—Systematic relationships of large benthic foraminifera discussed in this study.

- Kingdom Protista
  - Phylum Sarcodina
    - Class Rhizopoda
      - Order Foraminiferida Eichwald, 1830
        - Suborder Textulariina Delage and Hérouard, 1896
          - Superfamily Textulariacea Ehrenberg, 1838
            - Family Valvulinidae Berthelin, 1880
              - Subfamily Valvulininae Berthelin, 1880
                - Genus ***Clavulina*** d'Orbigny, 1826
                - Genus ***Valvulina*** d'Orbigny, 1826
        - Suborder Miliolina Delage and Hérouard, 1896
          - Superfamily Miliolacea Ehrenberg, 1839
            - Family Hauerinidae Schwager, 1876
              - Subfamily Hauerininae Schwager, 1876
                - Genus ***Quinqueloculina*** d'Orbigny, 1826
              - Subfamily Miliolinellinae Vella, 1957
                - Genus ***Triloculina*** d'Orbigny, 1826
          - Superfamily Alveolinacea Ehrenberg, 1839
            - Family Rhapydionindae Keijzer, 1945
              - Subfamily Rhapydionininae Keijzer, 1945
                - Genus ***Chubbina*** Robinson, 1968
          - Superfamily Soritacea Ehrenberg, 1839
            - Family Peneroplidae Schultze, 1854
                - Genus ***Laevipeneroplis*** Šulc, 1936
                - Genus ***Peneroplis*** de Montfort, 1808
            - Family Meandropsinidae Henson, 1948
                - Genus ***Broeckina*** Munier-Chalmas, 1882
            - Family Soritidae Ehrenberg, 1839
              - Subfamily Archaiasinae Cushman, 1927
                - Genus ***Archaias*** de Montfort, 1808
                - Genus ***Cyclorbiculina*** A. Silvestri, 1937
              - Subfamily Soritinae Ehrenberg, 1839
                - Genus ***Marginopora*** Quoy and Gaimard, 1830
                - Genus ***Orbitolites*** Lamarck, 1801
                - Genus ***Sorites*** Ehrenberg, 1839
        - Suborder Rotaliina Delage and Hérouard, 1896
          - Superfamily Planorbulinacea Schwager, 1877
            - Family Planorbulinidae Schwager, 1877
              - Subfamily Planorbulininae Schwager, 1877
                - Genus ***Planorbulina*** d'Orbigny, 1826
          - Superfamily Acervulinacea Schultze, 1854
            - Family Acervulinidae Schultze, 1854
                - Genus ***Acervulina*** Schultze, 1854
            - Family Homotrematidae Cushman, 1927
                - Genus ***Homotrema*** Hickson, 1911
          - Superfamily Asterigerinacea d'Orbigny, 1839
            - Family Amphisteginidae Cushman, 1927
                - Genus ***Amphistegina*** d'Orbigny, 1826

Miocene when *Thalassia* and several soritids known to be epiphytes on seagrass migrated into the area (Brasier, 1975b).

Eva (1980) suggests that seagrass first appeared in the Caribbean in the Late Cretaceous. Evidence for this is based on foraminifera with similar morphologies to the soritids discussed above. Specifically, Eva (1980) states that the foraminifera *Chubbina* and *Pseudedomia* have strikingly similar discoidal forms to later phytal foraminifera and that they existed in the Caribbean during the Late Cretaceous. Although *Orbitolites* is only known from the Mediterranean, the foraminifer *Cyclorbiculina jamaicensis* has a similar morphology and is known from the Caribbean in Pre-Miocene time (Eva, 1980).

Symbiosis and the Significance of Large Size in Foraminifera

Hallock (1985) explains the reasons for the larger size of some foraminifera. Water energy, depth, salinity, food availability, and pH are a few of the factors that can influence a foraminiferal population's chances for survival. Not only do environmental factors influence the survival rate, but size of the foraminifer also can determine whether an individual can survive until reproduction. Juvenile foraminifera under 0.5 mm are at the greatest risk for predation. Known predators that may selectively prey on foraminifera include nematodes, polychaetes, gastropods, and crustaceans (Lipps, 1983). Young foraminifera are extremely vulnerable to predation because their thin tests and protruding protoplasm leave them relatively unprotected (Hallock, 1985).

In order to survive and reproduce, many foraminifera delay maturation and grow to a larger size because the size of the parent is directly proportional to the number of young produced. Changing environmental conditions as well as small juvenile size can reduce the chances of survival of foraminiferal offspring. Therefore, a foraminifer that delays maturation and grows to a larger size can produce more offspring, increasing the chances of survival against predation and under changing conditions.

In addition, the high temperatures of tropical waters can increase the metabolism of many foraminifera. Since many tropical foraminifera live in nutrient-depleted waters around coral reefs, foraminifera obtain algal symbionts to recycle nutrients and gain additional energy. The additional energy allows the foraminifera to continue to grow and reach a larger size to maximize the number of offspring (Hallock, 1985; Langer, 1993).

Foraminifera permanently attached to plants also must compete with the lifespan of the substrate (Langer, 1993). If the phytal substrate has a shorter life span than the attached foraminifer, the foraminifer must grow rapidly to a large size to produce as many offspring as possible before the plant dies. Thus, large size can be achieved either by delayed or rapid maturation.

The photosynthetic endosymbionts (photosymbionts) found in many large benthic foraminifera living in grass beds supply the foraminifer with nutrients, increase calcification rates, and provide the foraminifer with a way to remove waste from the cell (Hallock, 1985; Richardson et al., 2001). In return, the foraminifer can supply the photosymbiont with nutrients that may be scarce in some marine waters (Hallock, 1985; Richardson et al., 2001). Richardson et al. (2001) showed that the selection of certain endosymbionts by soritid foraminifera occurred in conjunction with the development of seagrass as a substrate preference.

Richardson et al. (2001) discussed the various types of symbionts and their evolution in the soritid foraminifera over time. There are three basic types of photosynthetic endosymbionts: rhodophyte, chlorophyte, and dinophyte. All members of Superfamily Soritacea contain one of these photosymbionts. The foraminifera in this Superfamily show a succession through geologic time from rhodophyte photosymbionts (e.g., *Peneroplis*) to chlorophyte photosymbionts and from chlorophyte photosymbionts to dinophyte photosymbionts (e.g., *Sorites*). Richardson et al. (2001) suggested that the dinophyte photosymbionts decrease feeding rates and produce photosynthates that are used more efficiently. As a result, some foraminifera made a change from motile to attached.

In addition to selecting the most efficient endosymbiont, foraminifera must compete for space on their selected substrate. Permanantly attached foraminifera also must race against time and reproduce before their host substrate dies. Phytal substrates are common among many larger benthic foraminifera. However, the life span of the foraminifer is limited by the life span of the phytal substrate. The macroalga *Penicillus* has a life span of 30 to 63 days, while *Halimeda* can live from 4 to 6 months. *Thalassia*, an abundant seagrass substrate in the Caribbean, has a life span of around 40 days. Therefore, evolution has forced some foraminifera to abandon earlier ontogenic stages in order to reach a large adult size more rapidly (Hallock, 1985; Richardson et al., 2001). This allows the foraminifera to grow larger and compete for space and then complete reproduction before the phytal substrate dies. For example, *Sorites* and other members of the crown group lose their earlier growth stages phylogenetically and achieve the annular growth stage, which aids in the competition for space on substrates such as seagrass blades.

Epiphytic Foraminiferal Morphotypes

There are four basic morphotypes of epiphytic foraminifera. Permanently attached foraminifera (e.g., *Planorbulina*, *Acervulina*, and *Homotrema*) secrete a substance that acts like a glue to bond the foraminifera to the surface. They tend to grow in an orbitoidal pattern and have a flat attachment surface (Langer, 1993). Although these foraminifera types grow rapidly to compete for space, their cytoplasms does not host symbionts (Reiss and Hottinger, 1984). Permanently attached foraminifera are suspension feeders because they do not have the freedom to graze along the surface. They extend their pseudopods from their aperatures to collect food, and some types have even been found to use sponge spicules to extend their reach (Lipps, 1983; Reiss and Hottinger, 1984). Permanantly attached foraminifera are categorized as Morphotype A and have an average life span of 1 year. Although *Sorites orbiculus* is not permanently attached, and lacks a distinct attachment surface, it also has been placed in this category because of similar test shape and growth pattern (Langer, 1993).

Morphotype B consists of temporarily attached foraminifera. These species (e.g., *Rosalina*) have a flat attachment surface and trochospiral shape, but are predominately mobile. They are able to attach to a substrate and then detach to search for food or to reproduce. These foraminifera have a short lifespan of 2 to 5 months, and colonies have been found in a variety of microhabitats on vegetation and in sediment samples, both infaunally and epifaunally. Distribution of these foraminifera seems to be controlled by food availability rather than substrate. They can unattach from a substrate when environmental conditions change and force the foraminifer to search for food elsewhere.

Morphotype C foraminifera are suspension feeding and mobile (e.g., *Elphidium*). They constantly move in search of food and lack any attachment surface. They can extend pseudopods out of many supplementary apertures that cover the test. The pseudopods form a network that suspends the test as particles of food are collected. These foraminifera have a life span of 3 to 4 months and have been found living on vegetation and in the sediment.

Langer's last category, Morphotype D, consists of permanently mobile, grazing foraminifera. These foraminifera also lack an attachment surface and are constantly moving. All species in this category move in an upright position by extending pseudopods in the direction of travel. Species in this group do not seem to have a preference for substrate: they have been found both on vegetation and in sediment microhabitats. Instead of substrate type, other environmental factors (temperature, light, oxygen, nutrient levels, etc.) control their distribution. Their mobility allows them to search for food sources in a variety of places. This group includes the largest number of epiphytic species (Langer, 1993) and contains many large benthic foraminifera, including *Archaias*, *Cyclorbiculina*, *Peneroplis*, *Quinqueloculina*, and *Triloculina*.

Previous Distributional Studies of Grass-Bed Foraminifera

Bock (1967) performed one of the first studies that focused on grass as a substrate as opposed to the sea floor. He studied foraminiferal distributions in Big Pine Key, Florida, collecting samples from an array of sites with various depths and plant densities. He noted that the primary phytal habitat of foraminifera was on the blades of *Thalassia testudinum,* and that there was a difference in the *Thalassia* fauna and the sediment fauna.

He concluded that the substrate controls the distribution of foraminiferal fauna to a degree. Bock (1969) studied *Thalassia* blades as a means of dispersal for shallow water benthic foraminifera. Currents transport foraminifera that are attached to broken or dead pieces of *Thalassia*, allowing the foraminiferal population to become cosmopolitan.

Wright (1964) and Wright and Hay (1971) studied the foraminiferal distributions along a transect from Rodriguez Key to Molasses Reef. Results showed that vegetation was the primary habitat of living foraminifera and that the largest numbers of foraminifera in the sediment (death assemblage) are found shoreward of the densely vegetated areas.

Grant et al. (1973) studied the habitats of foraminifera in Coupon Bight. They concluded that *Thalassia*, *Dasycladus*, *Penicillus*, and *Halimeda* were all important phytal substrates. They also reported that most living individuals were found on phytal surfaces and that species found living on plants were represented by empty tests in the sediment assemblages.

Steinker (1973) and Steinker and Steinker (1976) researched shallow-water foraminifera on Jewfish Cay, Bahamas. They studied marine vegetation and surrounding sediments to determine if certain foraminifera prefer particular environments. In addition, they mapped the distributions of certain foraminiferal assemblages around the island. Counting of total foraminiferal populations indicated that live foraminifera accounted for less than 10% of the total. The presence of live foraminifera seemed to correlate with the presence of organic material, which can serve as food for some species. *Thalassia* and other calcareous algae were the preferred phytal habitats for foraminifera living on vegetation.

Brasier (1975b) sampled from sediment and phytal substrates and noted four major habitats: marsh, creek, lagoon, and channel. Results showed that changes in salinity, temperature, grain size, vegetation, and predation affected the distribution of various species throughout each habitat. The foraminifera found in the sediment samples and were controlled largely by the vegetation in the area. Different hosts provided various substrates for foraminifera and ultimately determined the sedimentary biofacies that formed in each habitat. Phytal faunas included foraminifera on plants, rocks, shells, and corals. These faunas were controlled by the host’s structure, sediment content, and physical conditions of the habitat.

Martin (1975) studied the effects of dredging-induced turbid waters on the distribution and ecology of foraminifera from John Pennekamp Coral Reef State Park in Key Largo, Florida. The author found that the primary phytal habitats for foraminifera were blades of *Thalassia*, with smaller populations occurring on the macroalgae *Penicillus* and *Cladophoropsis*. The different phytal habitats in this study were characterized by levels of wave and current action in the areas. Martin (1975) concluded that wave and current action can affect the diversity and species richness of foraminiferal populations, but that dredging-induced turbidity had little effect on the populations.

Buzas et al. (1977) sampled sediments from two homogenous *Thalassia* beds in Jamaica. Environmental variables and species densities were measured monthly over a year in an attempt to relate distributional patterns and abundances of foraminifera to environmental variables. Results showed that no significant statistical relationship was found between fluctuating environmental variables and foraminiferal densities.

Therefore, it was concluded that foraminiferal densities and distributions are controlled by biotic variables such as competition for food and space.

Waszczak and others (Waszcak, 1978; Waszczak and Steinker, 1987a, b) sampled marine grass, algae, and sediment from the Big Pine Key area to determine if the epiphytal assemblages were reliable indicators of the environment in which they lived. Although the assemblages on various plants at a single station were similar, the assemblages varied from station to station. Vegetation and sediment assemblages at individual stations were dissimilar.

Steinker and Clem (1984) conducted a study of foraminiferal distributions in Bermuda. Live foraminifera were rare in nearshore sediments, but were more abundant on the marine vegetation. Preferred vegetation substrates included *Thalassia*, *Halimeda*, and *Penicillus*. *Sorites* and *Planorbulina* were found attached to *Thalassia* blade surfaces, while foraminifera such as *Archaias* and *Peneroplis* were found in detritus that accumulated on blades and on other vegetation. The authors found that foraminiferal densities are linked to detrital covering on the vegetation. Quieter environments had more detrital covering and higher foraminiferal densities, while high energy environments had less detrital covering and a lower foraminiferal density. The vegetation and sediment assemblages became less similar as the energy of the environment increased; i.e., fossil assemblages may not resemble the once living fauna, especially in higher energy environments. This shows that the distribution of species can be regulated not only by variety of vegetation but also by environmental variables.

Hallock et al. (1986) studied *Archaias* population biology in Largo Sound, FL. In this study, a rubble sample, a mixed algae and seagrass sample, and a predominantly seagrass sample were taken monthly for one year. All *Archaias* from each sample were counted, live or dead determinations were made, and taphonomic condition of each test was noted. Results showed that the highest foraminiferal densities were found in mixed algae and sea-grass beds with lush epiphytic growth.

Culver (1993) noted that grazers on algae and detritus may reduce foraminiferal densities, as can some gastropods that apparently selectively prey on certain foraminiferal species. Phytal substrates offer a variety of microhabitats for epiphytes such as foraminifera (Langer, 1993). Langer (1993) conducted research on epiphytic foraminifera, their substrates, and motility types. In his study area, the preferred substrate was *Posidonia oceanica,* a grass that forms meadows in the Mediterranean Sea. He noted the presence on this grass of diatoms, fungi, and bacteria, all of which are major food sources for foraminifera. Similar colonies of microbial epiphytes also have been found on *Thalassia testudinum,* the predominant grass in the Caribbean (Heijs, 1985).

Hallock and Peebles (1993) studied the habitats of six different foraminiferal species in the Florida Keys. Chlorophyte symbiont-bearing foraminifera were collected, and their habitat was described. These authors concluded that chlorophyte symbiont-bearing foraminifera may require richer food sources than dinoflagellate or diatom symbiont-bearing foraminifera because, out of all symbiont types, chlorophyte symbionts bring the least amount of nutrients. Thus, the type of symbiont the foraminifer contains can determine its habitat and nutritional needs.

Fujita and Hallock (1999) examined different plant species as substrates, but only at a single site. These authors collected several samples of vegetation (e.g., *Thalassia*, *Halimeda*, and *Penicillus*) and characterized the relationships between epiphytic algae and foraminifera living on each species. Results showed that *Archaias* preferred vegetation with abundant epiphytic algae, while *Sorites* and *Planorbulina* preferred flat blades of *Thalassia* without epiphytic algae. They found that anthropogenic nutrification of Florida coastal waters promotes epiphytic algae growth, which may smother some foraminifera (e.g., *Sorites*). However, abundances of *Archaias* also may decrease because excess organic matter can accumulate and deplete the oxygen supply in the sediments.

Previous Studies on San Salvador Island

Few other foraminiferal studies have been conducted in and around San Salvador, Bahamas, and those conducted focused on nearshore marine environments. Peebles and Lewis (1988, 1991) conducted a taphonomic analysis of nearshore foraminifera. Samples were collected from backreef, patch-reef, and *Thalassia* bed environments. The authors conducted laboratory experiments on the foraminiferal tests to determine characteristic features of abrasion and dissolution. A tumbling-barrel experiment was done to evaluate abrasion features. *Cyclorbiculina* and *Archaias* were the most resistant to abrasion, while *Discorbis* and *Borelis* were least resistant. Abrasion features include scratches, pits, and some polishing, often accompanied by missing chambers. Dissolution, however, is characterized by coarsened textures and an increase in surface relief as etching progresses. *Amphistegina* and *Discorbis* were most resistant to dissolution, while *Borelis* and *Quinqueloculina* were least resistant. Results showed that, while size seems to be the controlling factor on abrasion, test composition and structure controls the test's susceptibility to dissolution.

Haynes (1991) studied death assemblages of foraminifera off Dump Reef. Sediment samples were collected along five transects through different environments, and the foraminifera were identified in each sample. Results showed that the assemblages were shaped by their habitat and available substrate.

Beck (1991) did a similar study at Cut Cay. This author found similar results to Haynes (1991) noting also that the distribution of the tests is related to grain size. Larger, fragmented foraminifera are found in higher energy environments, while the vegetated areas trap finer sediments and small foraminiferal tests.

Geissler et al. (2000) studied transportation of foraminiferal tests in Rice Bay, again a single area of study. McCormick and Lewis (2004) studied lagoonal foraminifera in Grahams Harbor. However, grass-bed densities were approximated and vegetation samples were not examined for the foraminiferal assemblage.

Finally, Lewis (2004) studied foraminifera in fossil reefs around the island from nearshore to shelf edge. He compared fossil foraminiferal assemblages to Recent assemblages to develop a means to distinguish between different types of reefs and distance from shore. He used taphonomic data along with foraminiferal assemblages in addition to sedimentary characteristics.

OBJECTIVES

Previous research on grass-bed foraminifera has established that sea-floor vegetation provides an important habitat, offering a source of nutrients for living foraminifera and, in some cases, protection. Studies have shown that plants are the dominant substrates for living assemblages (biocoenoses) and that the surrounding sediment contains mostly empty tests of dead foraminifera: assemblages are death assemblages (thanatocenoses). Different species prefer different vegetation types as determined by their mode of attachment, locomotion, feeding strategies, and type of symbionts.

However, previous workers have not attempted to quantify the density of vegetation beds and to compare this with the density of live or dead foraminifera in the sediment. Many previous studies of platform-carbonate benthic foraminifera distinguish between live and dead tests, but very few consider the taphonomic conditions of dead individuals (but see Hohenegger and Yordanova, 2001). Instead, most taphonomic research on foraminifera has focused on taphofacies models (e.g., Martin and Liddell, 1988, 1991) and on laboratory experiments (Peebles and Lewis, 1991; Kotler et al., 1992). Thus, the purpose of this study is to investigate the relationships between large (> 1 mm) benthic foraminifera living on vegetation and those found (live and dead) in the sediment in order to evaluate the extent to which foraminiferal assemblages and densities can serve as proxies for taxonomic make up and density of sea-grass beds. This study was completed by meeting the following objectives:

(1) Determination of and comparison between the foraminiferal assemblages on the vegetation and the foraminiferal assemblages in the sediment;

(2) Evaluation of the taphonomic condition of individual foraminifera to determine the level of post-mortem alteration of the dead foraminifera; and

(3) Comparison of foraminiferal assemblages and taphonomic condition of the tests in the sediment with the grass bed types and density at each location.

Because of the applied nature of these objectives, only the larger foraminifera rather than the full range of sizes, were selected for study. Large benthics are easier to identify and distinguish between live and dead, and taphonomic states are easier to identify, as are the presence of symbionts. In addition, small benthics may only exist in microhabitats due to competition with the large benthics for space and food sources.

METHODOLOGY

Field Methodology

Collection of data was completed during two trips to San Salvador which took place November 15-22, 2003, and June 5-15, 2004. Six sites representing a range of vegetation densities, water depths, and water-energy conditions were selected for study: three in Graham's Harbor at the north end of San Salvador (Dump Reef, Gaulins, and Cut Cay) and three in the Snow Bay area at the south end of San Salvador (Snow Bay 1, Snow Bay 2, and South). All measurements were made during the second trip to San Salvador in June, 2004. Distances from shore were approximated using aerial maps. Water depth and temperatures were measured using dive computers attached to the SCUBA equipment. Relative water energy was approximated at each site. Salinity was measured using a handheld Thomas optical refractometer, and pH was measured using an Oakton pH Testr 2. At each site, four to six stations located at 10-m intervals along transects were studied in detail using SCUBA. Vegetation densities were recorded at each station by counting individual algal thalli and sea-grass blades in a 50x50-cm grid. The top 1 cm of sediment was collected from each station until a sample size of 100 cm^3 was reached. One hundred blades of each of the major genera of sea grasses (*Thalassia* and *Syringodium)* and 100 individuals of the dominant macroalgae *(Halimeda, Penicillus*, *Udotea*, *Rhipocephallus*, and *Batophora*) were collected from each site in order to establish substrate preference. Scissors were used to cut the plant at the surface of the sediment, and vegetation samples were placed in labeled plastic bags according to genus and site. All samples were preserved by covering them with a solution of 10% formalin buffered with sodium borate (Borax) to a pH of 8.0. Laboratory preparations were completed daily at the Gerace Research Center, and samples were transported to Auburn University for analysis.

Laboratory Methodology

In the laboratory at Auburn University, 20 *Thalassia* blades and 20 *Halimeda* thalli from each site were examined with a binocular microscope in order to count the number of live and dead foraminifera per plant and determine the species of each foraminifer if possible. *Cornuspiramia*, a permanently attached, branching foraminifer, was the only large benthic foraminifer present that was not counted. The nature of the test made it difficult to determine where one individual ends and a new one begins. A cursory examination of other vegetation taxa revealed very few attached foraminifera. In addition, the filamentous nature of the other algae made examination difficult because it was hard to determine which foraminifera were actually attached to the algae, and which had been suspended in the water and settled in the filaments of the vegetation. Loose foraminifera that collected in the bottom of the plastic bags were examined as well because they had been attached to the vegetation at the time of collection.

Sediment samples from three stations along each transect were halved and wet sieved using -2, -1, 0 and 1 ϕ size sieves. Large shells and most other organic matter were removed with the -2 ϕ sieve, and all grains smaller than 1 ϕ (0.5 mm) were set aside and archived for possible future use. Sediment samples from the -1, 0, and 1 ϕ fractions were air dried, dry sieved, and weighed to determine original weight. The -1 and 0 ϕ size fractions, containing foraminifera larger than 1 mm, and the 1 ϕ (0.5 to 1.0 mm) fraction were examined for juveniles of large benthics. Large benthic foraminifera are defined in this study as those commonly larger than 1mm in dimension. Approximately 300 to 400 foraminifera were picked from each size fraction, live versus dead determinations were made based on the presence or absence of colored protoplasm when wet, and each individual was identified to species if possible.

Each specimen was categorized taphonomically in order to determine the level of post-mortem alteration. Tests were described as pristine, good, altered, or extremely altered. “Pristine” foraminifera are those with a test in “life condition” (Fig. 5A). This allows for some damage that fragile foraminifera may experience during life, but surface details are retained. “Good” foraminifera are generally in good condition, but show mild post-mortem alteration such as slight test breakage. Surface detail is retained (Fig. 5B). “Altered” specimens have noticeable damage to the test, particularly along their peripheries (Fig. 5C). Delicate ornamentation is be gone by this stage, but coarse features are still visible. Coloration is absent or weak in those foraminifera whose tests are colored in life (e.g., *Homotrema rubrum*). “Extremely altered” tests have a large amount of outer wall damage. Many individuals may be preserved as only the core of the test (e.g., *Archaias angulatas*.) All but the strongest ornamentation and test pigmentation will be obliterated (Fig. 5D).

Picked sediments were weighed to determine the amount of sediment yielding the target number of tests. Specimen counts for each species and each taphonomic category in each size fraction were then divided by the weight of sediment picked to produce the density of foraminifera per gram of sediment. This number was then multiplied by the

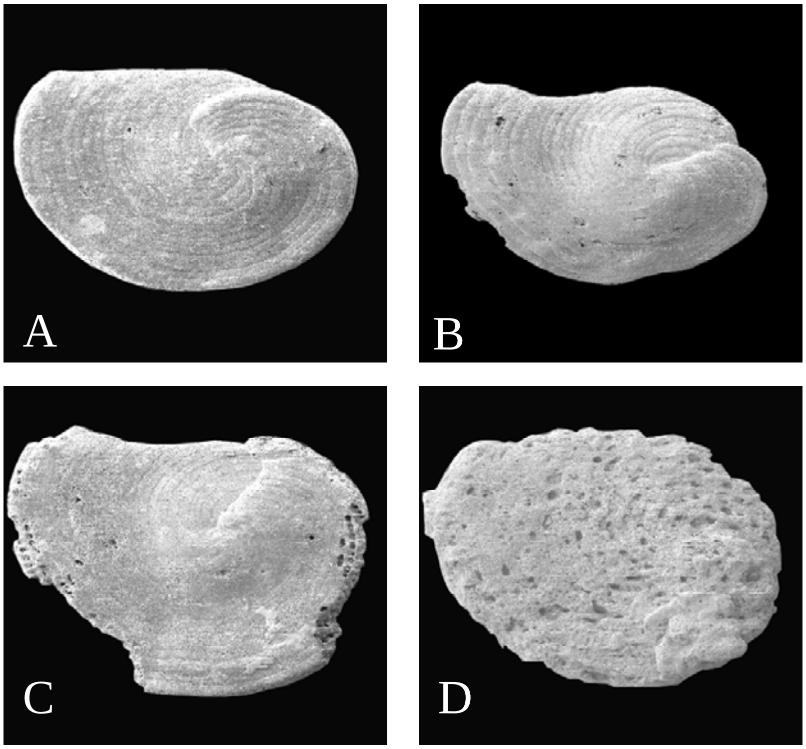


FIGURE 5—SEM photographs of the four taphonomic states used in this study. A = “pristine,” B = “good,” C = “altered,” and D = “extremely altered.” All specimens (*Archaias angulatus*) are approximately 1 mm across.

weight of the size fraction to produce the "adjusted number." The adjusted number for each of the 3 fractions was added to produce the "total adjusted number." This number was then used to calculate the final relative percent of each category and to make histograms. The raw data and calculations are given in the appendix (see CD).

The picking procedure described above is a modification of Martin and Liddell's (1988) "sieve method." Martin and Liddell also picked sediment fraction by fraction, but they totaled all size-fraction counts without considering the weight of each fraction. According to these authors, this method showed biofacies more effectively. In the present study, foraminifera were picked by separate size fractions for several reasons. First, looking for objects of the same size makes picking more efficient and less prone to error. Also, this allows for comparison of species assemblages found in different fractions. The modification in this procedure was made so that each size fraction was accurately represented as it was in the original sediment sample. Finally, Martin and Liddell's method could be easily replicated with the data as collected.

Data Analysis

Initially, foraminiferal assemblages on vegetation were compared to foraminiferal assemblages in the sediment at each site. Next, because *Thalassia* is one of the predominant vegetation types in most grass beds, the foraminiferal density in the sediment was compared to the *Thalassia* density at each site. Foraminiferal density is defined as the number of foraminifer tests per gram of sediment, and *Thalassia* density is defined herein as the number of blades per quadrat times the average blade length.

Controversy exists over whether to use the total foraminiferal assemblage or separate live and dead assemblages (Murray, 2000). This study compares both methods. Cluster analysis and non-metric multidimensional scaling (MDS) were used to group samples according to sediment and vegetation foraminiferal assemblages, using the PRIMER v5 software program (Clarke and Warwick, 2001). Since relatively rare taxa were included in the species groups, no species were deleted from the data set prior to analysis. First, each adjusted relative percent was transformed by the square root function in order to minimize the effects of dominance by a few highly abundant taxa (i.e., to equalize variance). In this way, similarities between two sites depend not only on the values of the abundant species but also the less common species. Cluster analysis was performed on samples (Q-mode) by using the Bray-Curtis similarity coefficient and using group average linking, following the recommendations of Clarke and Warwick (2001). The same similarity-coefficient matrix also was analyzed using non-metric multidimensional scaling (MDS). This technique emphasizes the relative, as opposed to absolute, values of similarities and uses the rankings to construct a map. The degree of fit between this two-dimensional map and the data matrix is termed “stress” (the lower the stress, the better the fit).

RESULTS

Site Descriptions

Six sites were selected for this project: three in Grahams Harbor at the north end of the island and three in Snow Bay at the southeast end (Fig. 6). Each site was selected based on water depth, water energy, and grass-bed density. In addition, water salinity, pH, temperature, and distance from shore were measured where possible for each site. Salinity and pH measurements are lacking for two sites because the water samples were lost. Distances from shore had to be estimated for some sites. Table 2 summarizes the various conditions at each site. Grain-size analysis was done for one sample per site (Fig. 7).

The Dump Reef site was located northeast of Dump Reef off Singer Bar Point at a distance of approximately 150 m from shore. This site had a moderately dense grass bed with both grass and calcareous algae. Energy levels here were low, and the depth ranged from 7 to 10 ft (2.1 to 3.0 m). Salinity was 36‰, pH was 8.1, and the water temperature was 88˚F (31.1˚C). The sediment at this site was relatively well sorted and coarsely skewed; coarser fractions were composed mostly of larger foraminifera.

The Gaulins site was located at the north end of the island approximately 1,100 m north of the island proper and 850 m from North Point. Gaulins Cay lay to the north. This site had a sparse grass bed adjacent to a denser bed to the south. Water energy

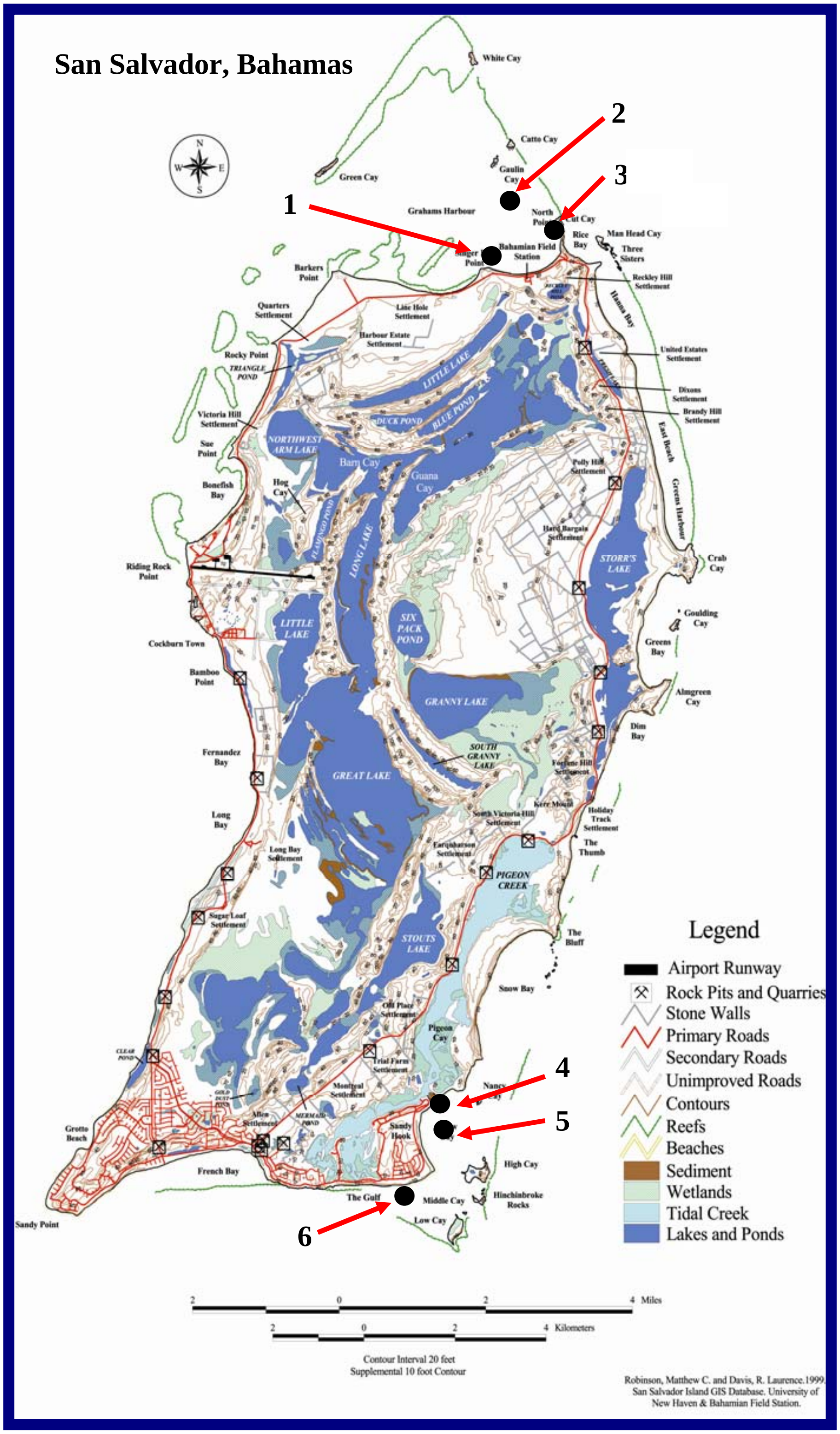


FIGURE 6—Map of San Salvador showing sampling sites (modified from Robinson and Davis, 1999). 1=Dump Reef, 2=Gaulins, 3=Cut Cay, 4=Snow Bay 1, 5=Snow Bay 2, 6=South

TABLE 2—Environmental data for each study site.

Site	Distance from shore (approx.)	Water Depth	Water Energy	Salinity	pH	Temp.	Vegetation Density
1. Dump Reef	150 m	7-10 ft (2.1-3.0 m)	Low	36‰	8.1	88˚F (31.1˚C)	Moderate
2. Gaulins	1100 m	11-15 ft (3.4-4.6 m)	Low	38‰	7.6	83˚F (28.3˚C)	Sparse
3. Cut Cay	5 m	1-5 ft (0.3-1.5 m)	Moderate	-	-	84˚F (28.8˚C)	Heavy
4. Snow Bay 1	10 m	2-4 ft (0.6-1.5 m)	High	40‰	8.0	88˚F (31.1˚C)	Heavy
5. Snow Bay 2	75 m	2-4 ft (0.6-1.2 m)	Moderate	38‰	8.0	88˚F (31.1˚C)	Heavy
6. South	10 m	5-6 ft (1.5-1.8 m)	High	-	-	86˚F (30.0˚C)	Sparse

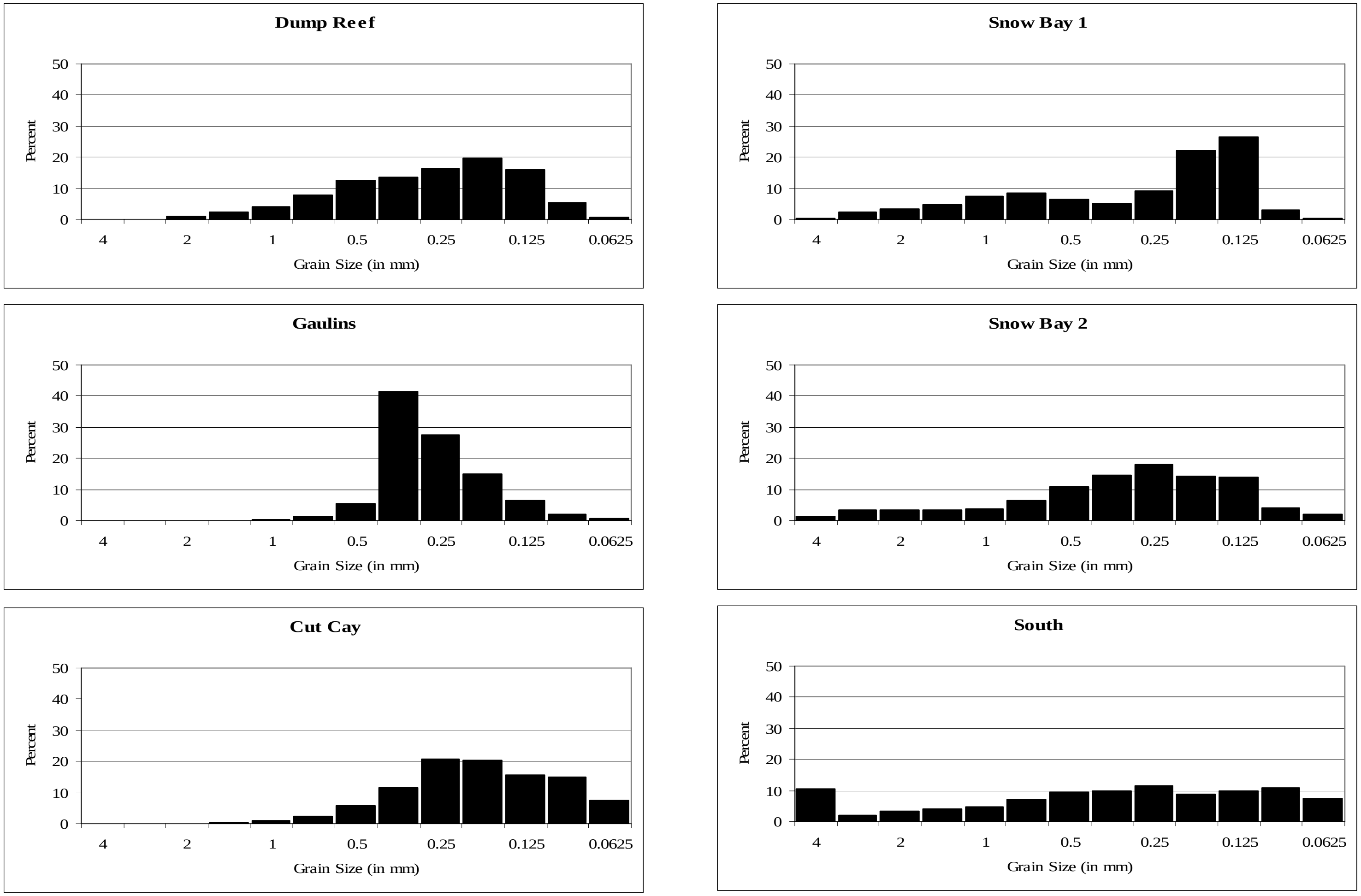


FIGURE 7—Grain-size distribution for each sample site.

was low, and depths ranged from 11 to 15 ft (3.4 to 4.6 m). Salinity was 38‰, pH was 7.6, and water temperature was 83˚F (28.3˚C). The sediment at this site was well sorted and finely skewed. The grains were slightly coarser than the other sites at the north end of the island.

The Cut Cay site was located at the north end of the island where the Atlantic Ocean has cut through the North Point peninsula linking Graham's Harbor with the Atlantic. The transect was located immediately north of the cut itself on the bay side. This site had a heavily vegetated grass bed dominated by *Thalassia*, a depth range of 1 to 5 ft (0.3 to 1.5 m), and a water temperature of 84˚F (28.8˚C). Due to exposure to higher energy currents through the cut, water energy at this site is considered to be moderate. The sediment at this site was well sorted and finely skewed. It has the largest fine fraction compared to sediments at all sites.

The remaining sites were located in Snow Bay, where a large estuary known as Pigeon Creek opens into a lagoon protected by cays and barrier reefs. Snow Bay 1 was located at the mouth of Pigeon Creek, immediately southeast of the private home known as "Ocean House." The transect was located in 2 to 4 ft (0.6 to 1.2 m) of water approximately 10 m from shore. Water energy was relatively high due to the flow of the creek. The grass bed was heavily populated with *Thalassia* and *Batophora*. Salinity was 40‰, pH was 8.0, and water temperature was 88˚F (31.1˚C).

Snow Bay 2 was located approximately 180 m southeast of Snow Bay 1. This site was located farther offshore (approximately 75 m) in a heavily vegetated grass bed dominated by *Thalassia*. Grass blades were especially long here causing this bed to be the densest in terms of percent cover. The energy level was moderate, related to flow from Pigeon Creek. Depth ranged from 2 to 4 ft (0.6 to 1.2 m), salinity was 38‰, pH was 8.0, and water temperature was 88˚F (31.1˚C). The sediments at both Snow Bay sites were poorly sorted and coarsely skewed. The coarser fractions were dominated by large *Halimeda* plates.

The site we call South was located 10 m from shore along the southwestern margin of Snow Bay west of the point of Sandy Hook. Water depth ranged from 5 to 6 ft (1.5 to 1.8 m), and the energy level was high even though the study site was nearshore because it was not protected from the swell by an offshore reef. The grass bed was sparse and almost devoid of *Thalassia* and instead was dominated by calcareous algae. Water temperature was 86˚F (30.0˚C). Sediment at this site was the most poorly sorted and coarsely skewed of all sites. The coarser fractions contained mostly gastropod shells and fragments of other mollusc shells.

Distribution of Vegetation

Table 3 shows the total numbers of individual grass and algae counts and percentages per quadrat at each of the analyzed stations. "*Thalassia* density" was calculated by multiplying the number of *Thalassia* blades by the mean blade length for each station. The distribution of each vegetation type (genus) at each site is illustrated in Figure 8. Notice that *Thalassia* is the dominant genus at all sites except Dump, where *Syringodium* is more abundant, and South, which is dominated by algae and has very few *Thalassia* thalli. Figure 9 is a dendrogram showing the results of the Q-mode cluster analysis based on the taxonomic makeup of the grassbed at each site. Figure 10 shows the same data as a multi-dimensional scaling (MDS) plot. Cut Cay and Gaulins are

TABLE 3—Data for all vegetation at each station. D = Dump Reef; G = Gaulins; CC = Cut Cay; SB1 = Snow Bay 1; SB2 = Snow Bay 2; S = South.

	Number of Individual Counts per Quadrat at Each Station Analyzed								**Summary**	**Data**
STATION	*Thalassia*	*Syringodium*	*Halimeda*	*Penicillus*	*Udotea*	*Rhipocephallus*	*Batophora*	Total	Mean *Thalassia* Blade Length (cm)	Density= Number of *Thalassia* Blades x Mean Blade Length
D-1	204 (35.5%)	357 (62.1%)	1 (0.2%)	4 (0.7%)	2 (0.3%)	7 (1.2%)	0 (0%)	575	10.53	2148.12
D-2	223 (57.9%)	157 (40.8%)	1 (0.3%)	2 (0.5%)	2 (0.5%)	0 (0%)	0 (0%)	385	10.53	2348.19
D-6	101 (15.6%)	526 (81.3%)	8 (1.2%)	9 (1.4%)	3 (0.5%)	0 (0%)	0 (0%)	647	10.53	1063.53
G-2	65 (70.7%)	22 (23.9%)	0 (0%)	3 (3.3%)	2 (2.2%)	0 (0%)	0 (0%)	92	7.91	514.15
G-3	81 (75.0%)	22 (20.4%)	4 (3.7%)	1 (0.9%)	0 (0%)	0 (0%)	0 (0%)	108	7.91	640.71
G-6	15 (24.6%)	42 (68.9%)	1 (1.6%)	1 (1.6%)	2 (3.3%)	0 (0%)	0 (0%)	61	7.91	118.65
CC-1	559 (52.7%)	498 (47%)	0 (0%)	3 (0.28%)	0 (0%)	0 (0%)	0 (0%)	1060	12.43	6948.37
CC-2	374 (68.5%)	165 (30.2%)	4 (0.73%)	3 (0.55%)	0 (0%)	0 (0%)	0 (0%)	546	12.43	4648.82
CC-6	455 (82.1%)	92 (16.6%)	6 (1.1%)	0 (0%)	1 (0.18%)	0 (0%)	0 (0%)	554	12.43	5655.65
SB1-2	424 (51.5%)	118 (14.3%)	5 (0.6%)	1 (0.1%)	0 (0%)	0 (0%)	276 (33.5%)	824	10.83	4591.92
SB1-4	378 (66.0%)	41 (7.2%)	2 (0.3%)	2 (0.3%)	0 (0%)	0 (0%)	150 (26.2%)	573	10.83	4093.74
SB1-6	484 (78.2%)	4 (0.6%)	3 (0.5%)	0 (0%)	0 (0%)	0 (0%)	128 (20.7%)	619	10.83	5241.72
SB2-1	491 (90.9%)	25 (4.6%)	5 (0.9%)	1 (0.2%)	0 (0%)	0 (0%)	18 (3.3%)	540	14.57	7153.87
SB2-2	547 (83.1%)	74 (11.2%)	6 (0.9%)	4 (0.6%)	1 (0.2%)	0 (0%)	26 (4.0%)	658	14.57	7969.79
SB2-4	536 (88.7%)	47 (7.8%)	8 (1.3%)	1 (0.2%)	0 (0%)	0 (0%)	12 (2.0%)	604	14.57	7809.52
S-1	12 (21.8%)	16 (29.1%)	8 (14.5%)	2 (3.6%)	2 (3.6%)	0 (0%)	15 (27.3%)	55	0	0
S-2	0 (0%)	0 (0%)	12 (92.3%)	0 (0%)	0 (0%)	1 (7.7%)	0 (0%)	13	0	0
S-4	0 (0%)	0 (0%)	6 (26.1%)	11 (47.8%)	6 (26.1%)	0 (0%)	0 (0%)	23	0	0

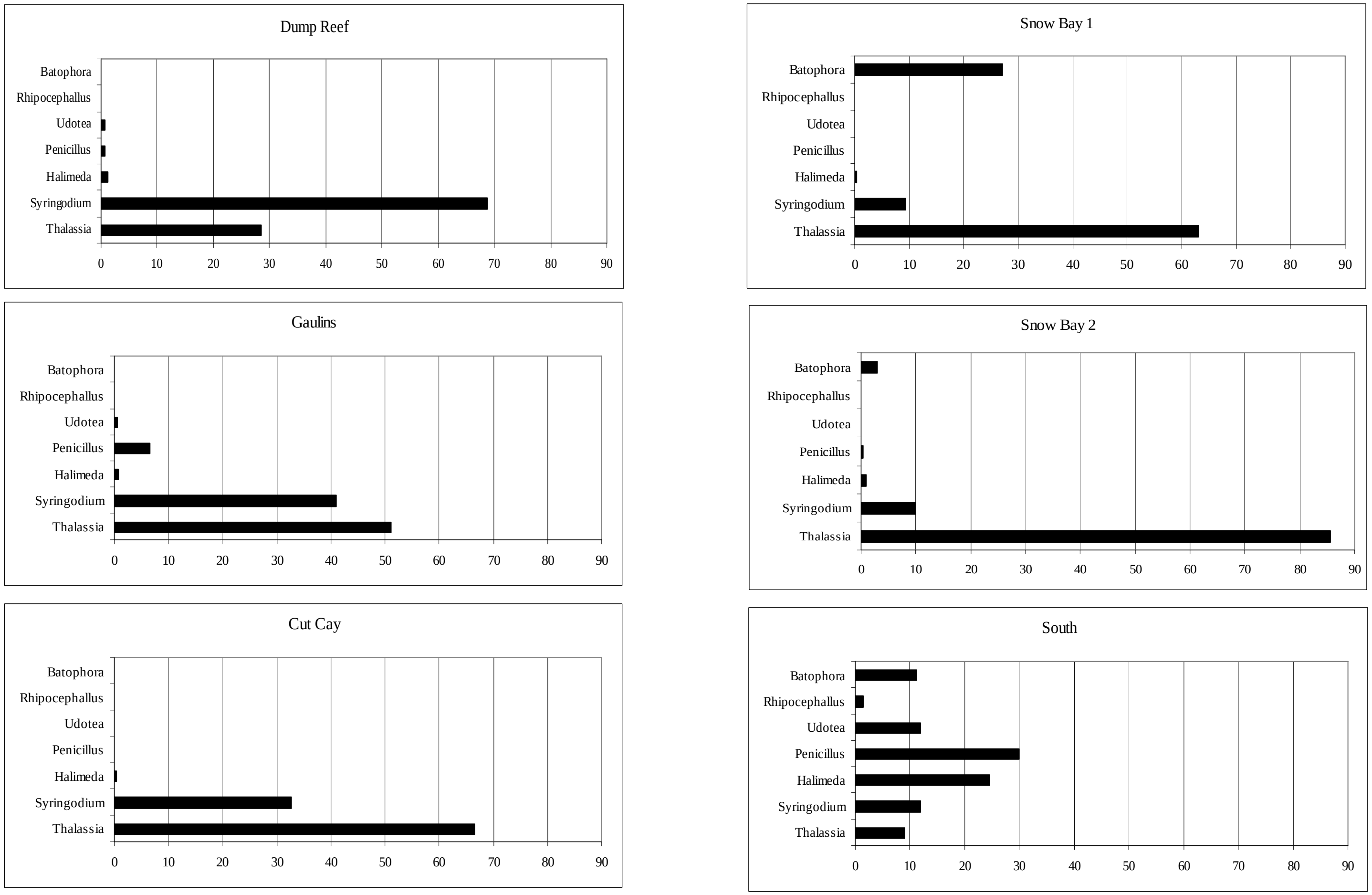


FIGURE 8—Percentages of each vegetation taxon at the six sites.

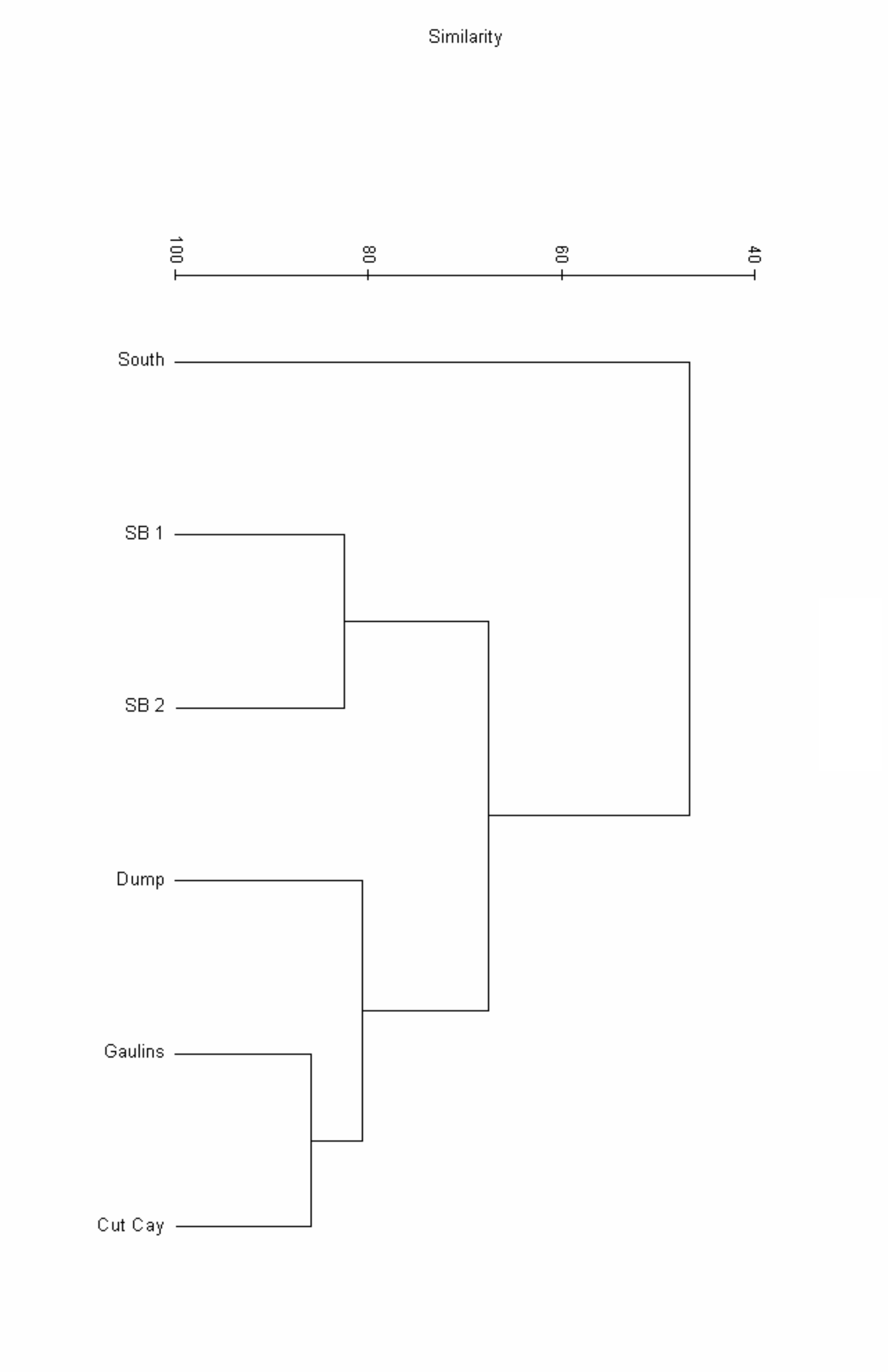


FIGURE 9—Hierarchical cluster analysis of the taxonomic makeup of each grassbed site. Analysis is based on the relative percents of each grass and algal genus as determined from quadrat counts (Table 2).

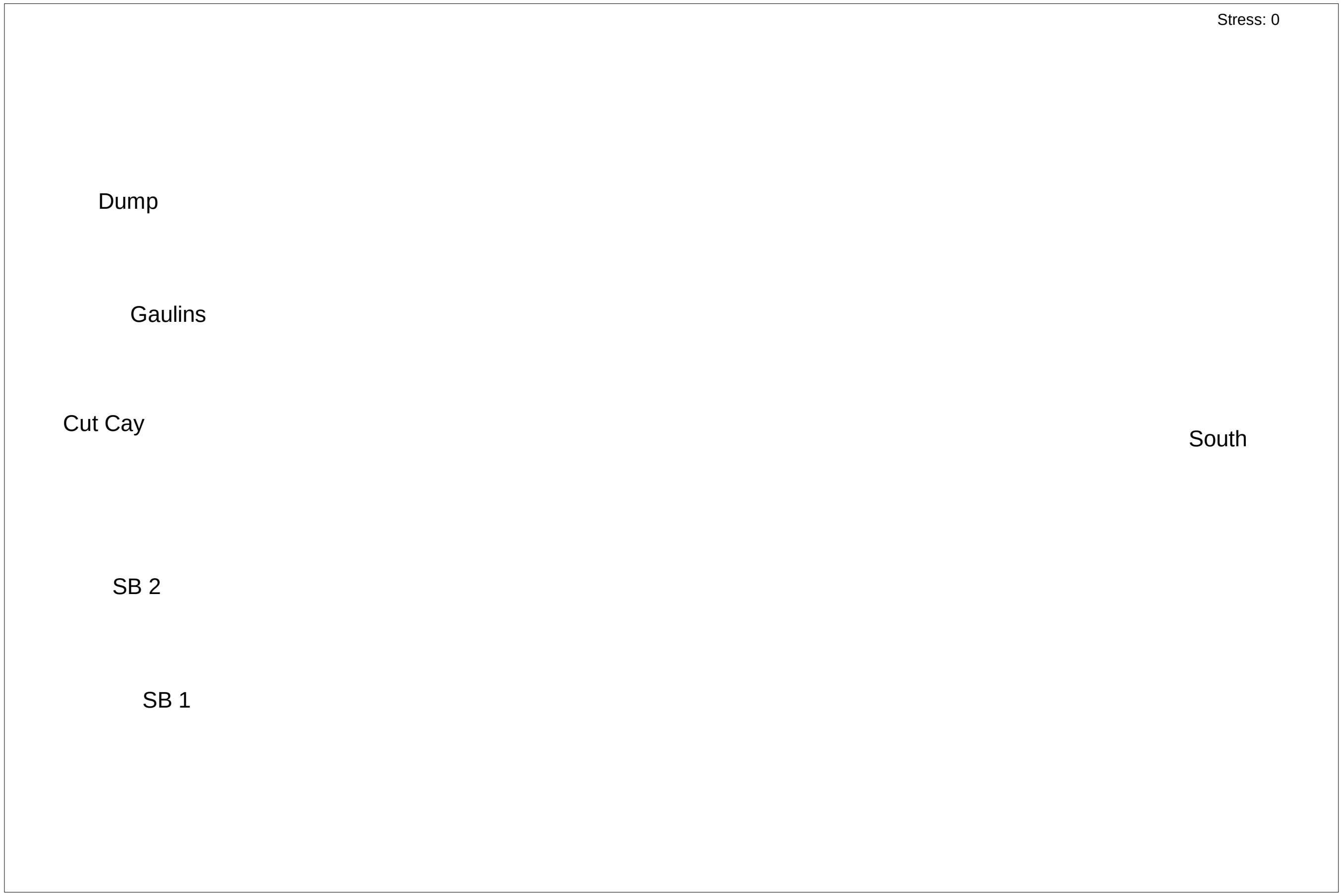


FIGURE 10—Multi-dimensional scaling (MDS) plot of the grassbed taxonomic makeup at each site. The closer the sites are placed together, the more similar the sites are to each other. Stress=0, which means that the diagram gives an excellent representation with respect to similarity coefficients.

closely related in their taxonomic makeup because both are dominated by *Thalassia* and have a significant amount of *Syringodium* (Table 3). Dump Reef is similar but is dominated by *Syringodium* instead of *Thalassia*. Snow Bay 1 and 2 are also similar, but *Syringodium* is not as abundant, while *Batophora* is present in significant amounts. South is the least similar to the other sites, with more calcareous algae and less grass. Gaulins and Cut Cay have similar taxonomic makeup, while Snow Bay 1 and 2 are closely related to one another. Note that, with the exception of South, the clustering reflects the geographic location of the areas studied (Figs. 9 and 10).

Foraminifera Found on Vegetation

Table 4 shows the taxonomic categories used in this study and the species contained in each. These taxonomic categories are shown as genus names and are used in the following tables and figures. Note that these names may represent single species, such as *Archaias angulatas,* or groups of species. For example "*Quinqueloculina*" includes several species of *Quinqueloculina* and *Triloculina*. "*Planorbulina*" includes species of *Acervulina*, and "*Peneroplis*" includes *Levipeneroplis* species. Table 5 shows the foraminifera, live and dead, found on *Thalassia* and *Halimeda* at each site. Table 6 shows the total foraminifera found on vegetation at each site, and Table 7 shows substrate preferences (*Thalassia* or *Halimeda*) of the phytal foraminifera when all sites are considered together. Figure 11 shows the substrate preferences on a site-by-site basis.

TABLE 4—Taxonomic categories used in this study and corresponding species. Species marked with * indicate rare species.

CATEGORY	**SPECIES**
SUBORDER TEXTULARIINA	
Clavulina	*Clavulina tricarinata* d'Orbigny, 1839 **Clavulina difformis* (Brady), 1844
Valvulina	*Valvulina oviedoiana* d'Orbigny, 1839
SUBORDER MILIOLINA	
Quinqueloculina/Triloculina	*Quinqueloculina tricarinata* d'Orbigny, 1839 **Quinqueloculina bidentata* d’Orbigny, 1839 **Quinqueloculina tenagos* Parker, 1962 *Triloculina bicarinata* d'Orbigny, 1839 *Triloculina linneiana* d'Orbigny, 1839 *Triloculina trigonula* (Lamarck), 1804 **Spiroloculina antillarum* d’Orbigny, 1839
Peneroplis	*Laevipeneroplis proteus* d'Orbigny, 1839 **Peneroplis pertusus* (Forskal), 1775
Broeckina	*Broeckina orbitolitoides* (Hofker), 1930
Archaias	*Archaias angulatus* (Fichtel and Moll), 1803
Cyclorbiculina	*Cyclorbiculina compressa* (d'Orbigny), 1839
Sorites	*Sorites marginalis* (Lamarck), 1816
SUBORDER ROTALIINA	
Amphistegina	*Amphistegina gibbosa* d'Orbigny, 1839
Planorbulina	*Planorbulina acervalis* Brady, 1884 **Acervulina spp.*

TABLE 5—Data of live and dead large benthic foraminifera found on *Thalassia* and *Halimeda* at each site (except South site because *Thalassia* was extremely rare and was not collected). T = *Thalassia*; H = *Halimeda*; L = Live; D = Dead; Clav = *Clavulina*; Valv = *Valvulina*; Quinq = *Quinqueloculina*; Pen = *Peneroplis*; Bro = *Broeckina*; Arch = *Archaias*; Cyclo = *Cyclorbiculina*; Sor = *Sorites*; Amp = *Amphistegina*; Plan = *Planorbulina*.

FORAM NAME	**D T**	**D H**	**G T**	**G H**	**CC T**	**CC H**	**SB1 T**	**SB1 H**	**SB2 T**	**SB2 H**	**S H**	**Total on Veg.**	**Total on *Thalassia***	**Total on *Halimeda***
Valv., L	0	0	0	0	0	0	0	0	0	0	2	2	0	2
Valv., D	0	0	0	0	0	0	0	0	0	0	2	2	0	2
Arch., L	0	5	2	26	0	0	0	1	1	17	59	111	3	108
Arch., D	0	1	1	12	0	0	0	4	1	0	6	25	2	23
Cyclo., L	0	11	0	0	0	0	0	0	1	0	0	12	1	11
Cyclo., D	0	1	0	0	0	0	0	5	0	0	0	6	0	6
Sor., L	19	61	235	253	3	0	24	13	0	10	69	687	281	406
Sor., D	0	2	31	40	0	2	0	8	0	0	14	97	31	66
Amp., L	1	0	0	0	0	0	0	0	0	0	0	1	1	0
Amp., D	0	0	0	3	0	0	0	0	0	1	0	4	0	4
Plan., L	7	51	80	340	3	0	15	22	8	146	174	846	113	733
Plan., D	0	3	3	4	0	0	0	0	0	61	1	72	3	69
TOTAL	**27**	**135**	**352**	**678**	**6**	**2**	**39**	**53**	**11**	**235**	**327**	**1865**	**435**	**1430**

TABLE 6—Total numbers of live and dead large benthic foraminifera found on *Thalassia* and *Halimeda* at each site.

	Number of Foraminifera Found on Vegetation					
SITE	***Thalassia* Live**	***Thalassia* Dead**	***Halimeda* Live**	***Halimeda* Dead**	***Thalassia* Total**	***Halimeda* Total**
Dump Reef	27	0	128	7	27	135
Gaulins	317	35	622	60	352	682
Cut Cay	6	0	0	2	6	2
Snow Bay 1	39	0	36	17	39	53
Snow Bay 2	10	1	173	62	11	235
South	N/A	N/A	304	23	N/A	327

TABLE 7—Assemblages of large benthic foraminifera found on *Thalassia* and *Halimeda* at all sites. Note that *Sorites* dominates the *Thalassia* assemblage, whereas *Planorbulina* is more abundant than *Sorites* when *Halimeda* is the substrate.

Foraminifera Found on Vegetation	**Live+Dead on *Thalassia***	**Live+Dead on *Halimeda***
Valvulina	0 (0%)	4 (0.3%)
Archaias	5 (1.1%)	131 (9.2%)
Cyclorbiculina	1 (0.2%)	17 (1.2%)
Sorites	312 (71.7%)	472 (33.0%)
Amphistegina	1 (0.2%)	4 (0.3%)
Planorbulina	116 (26.7%)	802 (56.1%)
TOTAL	435	1430

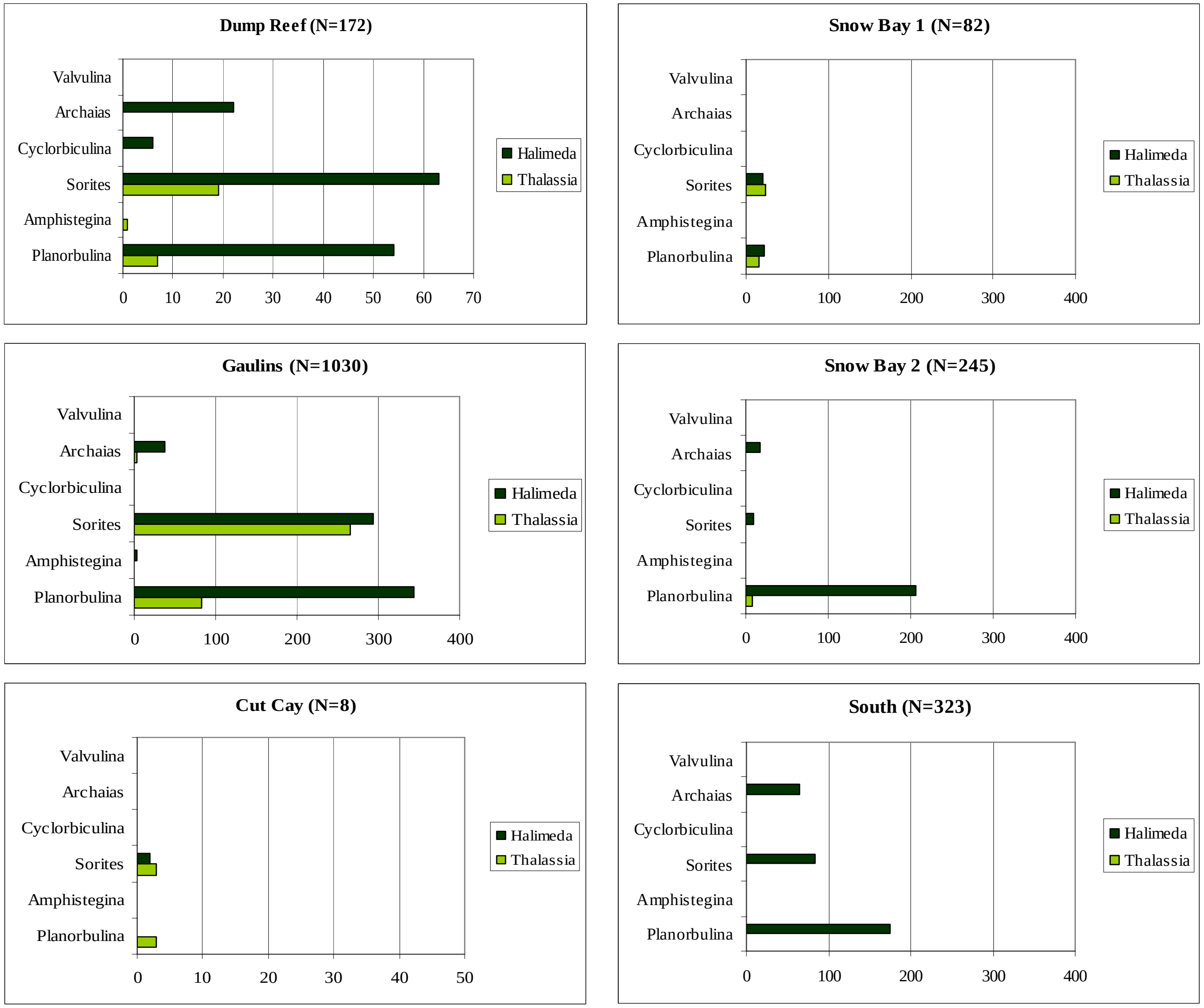


FIGURE 11—Total number of foraminifera found attached to *Thalassia* and *Halimeda* at each site.

Figure 12 illustrates assemblages of live and dead foraminifera found attached to 20 *Thalassia* blades and 20 *Halimeda* thalli at each site. *Sorites* and *Planorbulina* are the dominant foraminifera that live on the vegetation at all sites. *Sorites* is the dominant foraminifer found living on vegetation in sites at the northern end of the island (Dump Reef, Gaulins, and Cut Cay), whereas *Planorbulina* is the dominant taxon living on vegetation at 2 of the 3 sites at the southern end of the island (Snow Bay 2 and South). *Cornuspiramia* was found in various quantities at all sites but was not included due to the difficulty of determining where one individual began and another ended. Its fragile test and encrusting nature precludes its preservation in sediment samples.

Figures 13 and 14 show the relationships between the number of foraminifera on the *Thalassia* and *Thalassia* variables such as blade length and density. Figure 13 shows the sum of the lengths of 20 *Thalassia* blades at each site versus the total number of foraminifera found on those 20 blades. Data show that the number of tests found on *Thalassia* was not determined by the sum of the blade lengths examined. Most total blade lengths examined were between 200 and 300 cm. The number of foraminifera tends to decrease as blade length increases. Figure 14 shows *Thalassia* density (mean number of *Thalassia* times the average blade length) versus the number of foraminifera per cm of *Thalassia*. The number of foraminifera found on *Thalassia* (20 blades per site) was not a function of *Thalassia* density. Gaulins (lowest density) had the highest total foraminiferal abundance by far. Other localitites do not show a consistent trend. The two sites with the highest *Thalassia* density (Cut Cay and Snow Bay 2) had the lowest foraminifera per cm.

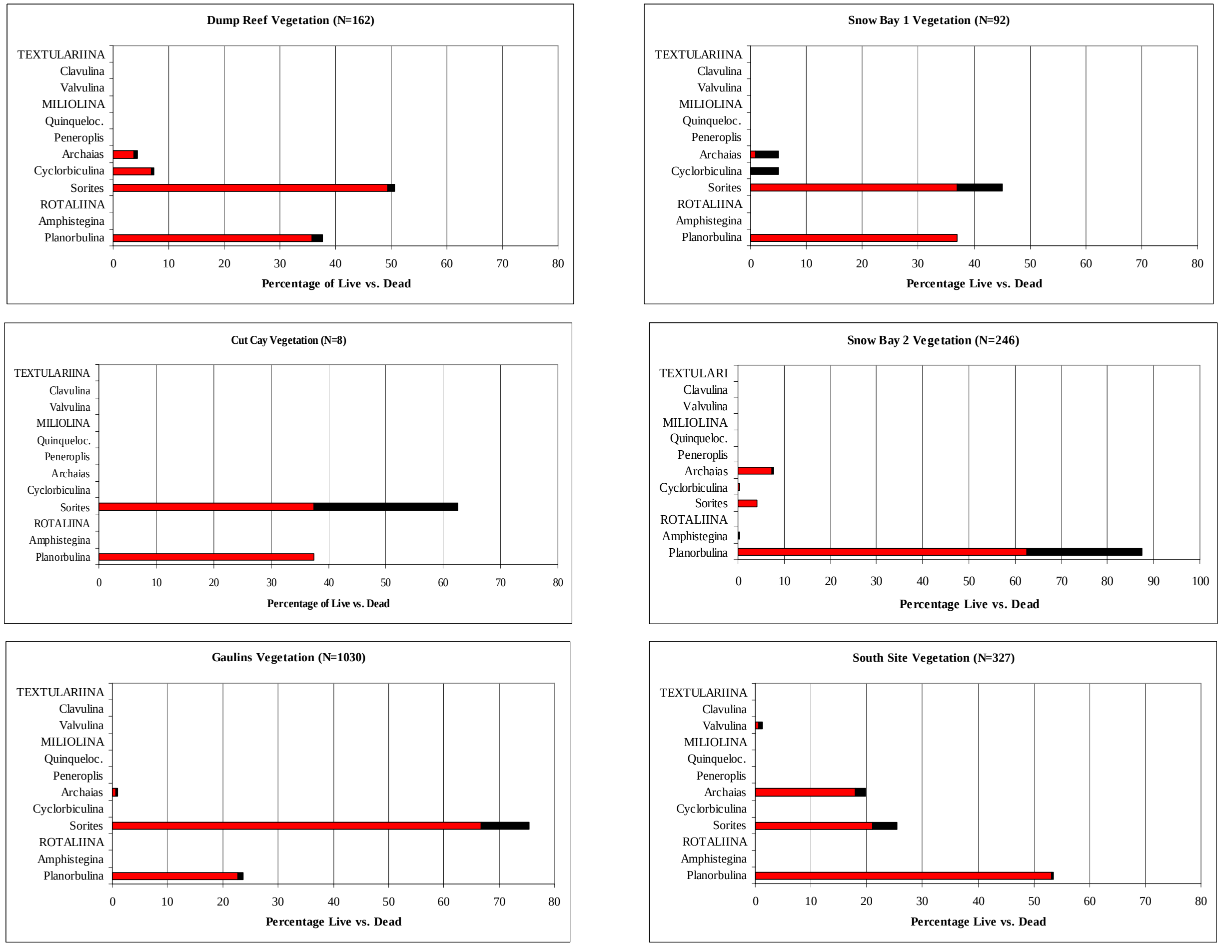


FIGURE 12—Assemblages of large benthic foraminifera found attached to vegetation (*Thalassia* and *Halimeda*) at each site. Live foraminifera are indicated by red, and dead tests by black. Note that only a few taxa are found on vegetation, principally *Sorites* and *Planorbulina*.

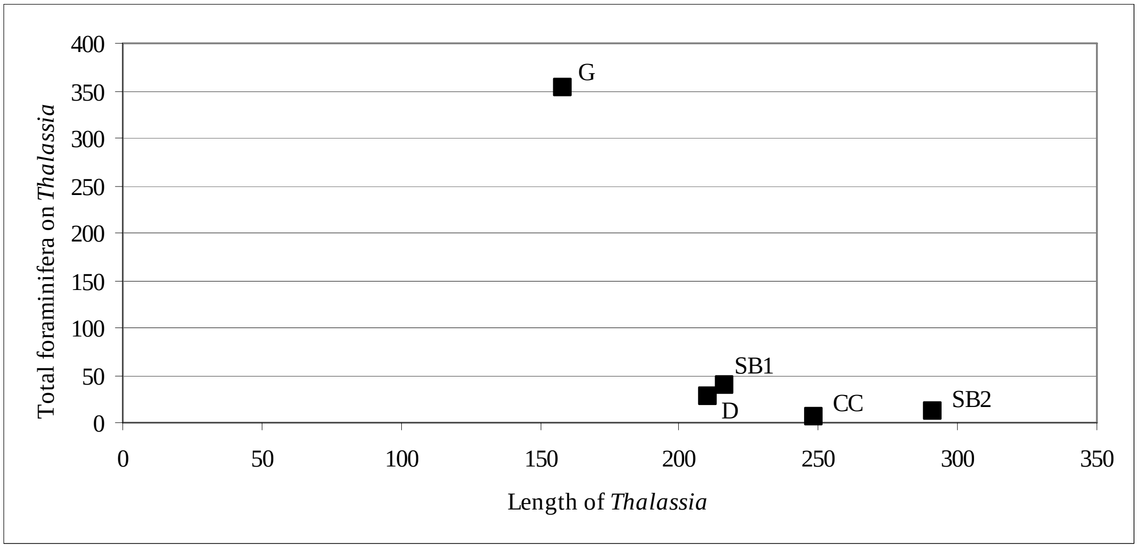


FIGURE 13—Relationship between combined lengths of 20 *Thalassia* blades at each site versus total number of foraminifera on those 20 blades.

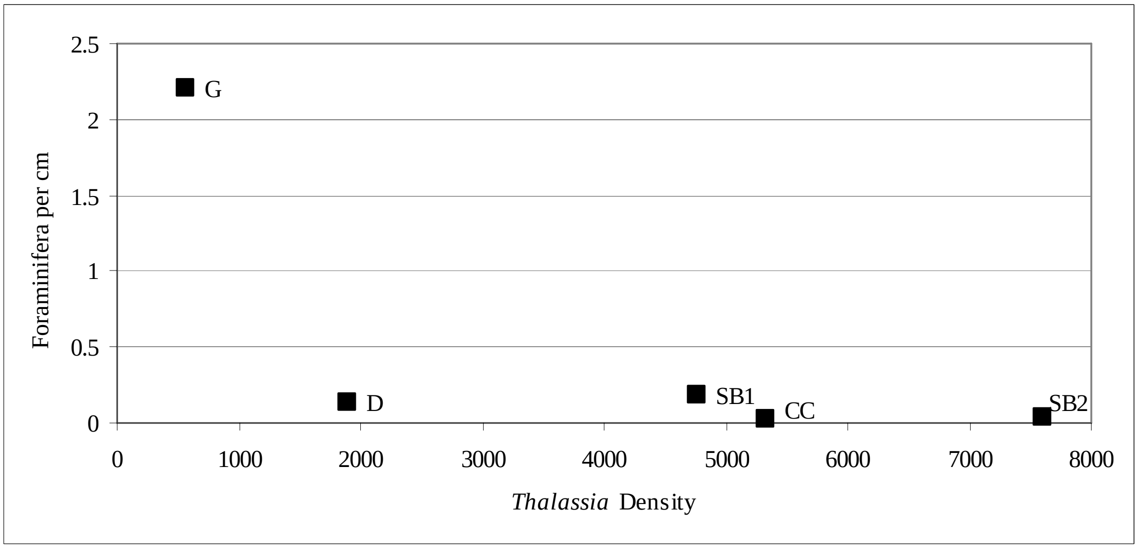


FIGURE 14—Number of foraminifera per cm of *Thalassia* as a function of "*Thalassia* density," which is defined in this study as the mean number of *Thalassia* blades per quadrat times average blade length.

In order to approximate the standing crop of foraminifera on vegetation, the number of foraminifera on both *Thalassia* and *Halimeda* per m^2 was totaled. This differs from true standing crop because dead as well as live tests were used. Empty tests were included to show the total number of foraminifera that will be deposited to the seafloor upon the death of the phytal substrate; thus I use the term “phytal standing crop.” Figures 15 and 16 show the relationships between the phytal standing crop of foraminifera on *Thalassia* and *Halimeda* at each site. Figure 15 compares the phytal standing crop to the total counts of all vegetation per m^2. It shows that the quantity of vegetation does not control the standing crop of foraminifera. Comparison of standing crop to mean *Thalassia* density at each site (Fig. 16) shows a slightly clearer trend. With the exception of Gaulins, grassbeds with the lowest and highest *Thalassia* densities have smaller standing crops, whereas those with moderate *Thalassia* density (Snow Bay 1) have a much larger standing crop.

Foraminifera in the Sediment

Total foraminifera counts per station recovered from sediment samples are provided in the appendix (see enclosed CD). The foraminiferal assemblages found on vegetation are compared to sediment assemblages at each site in Figures 17 through 22. Comparison of these graphs shows that the assemblages do not match. At each site, the vegetation assemblage was dominated by *Sorites* and *Planorbulina*, but these taxa were among the least abundant in the sediment. In addition, vegetation assemblages were dominated by live individuals, whereas very few live specimens were found in the sediment.

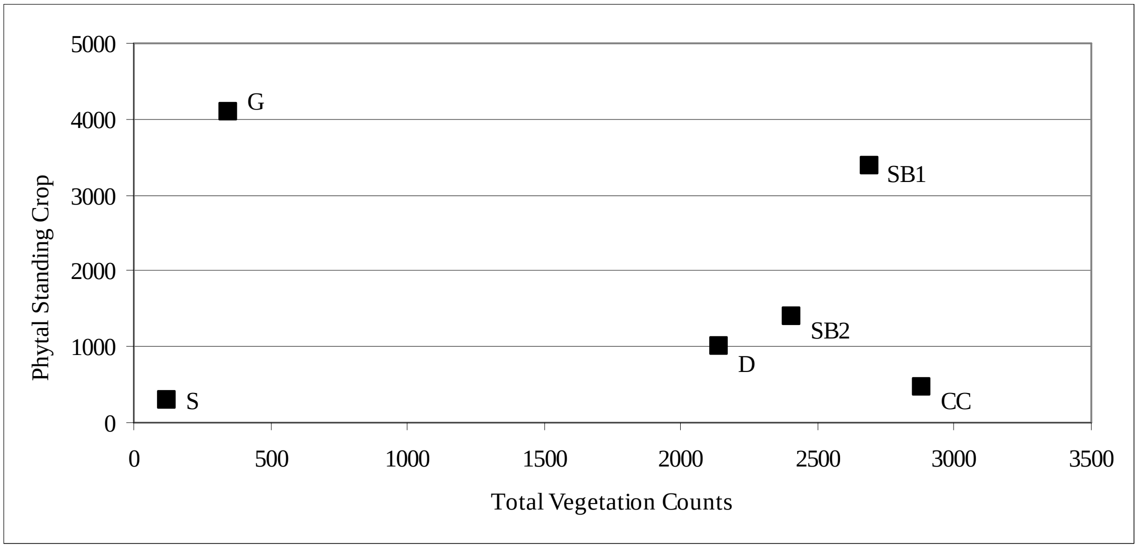


FIGURE 15—“Phytal standing crop” (number of foraminifera on *Thalassia* and *Halimeda* per m^2) versus total counts of vegetation per m^2.

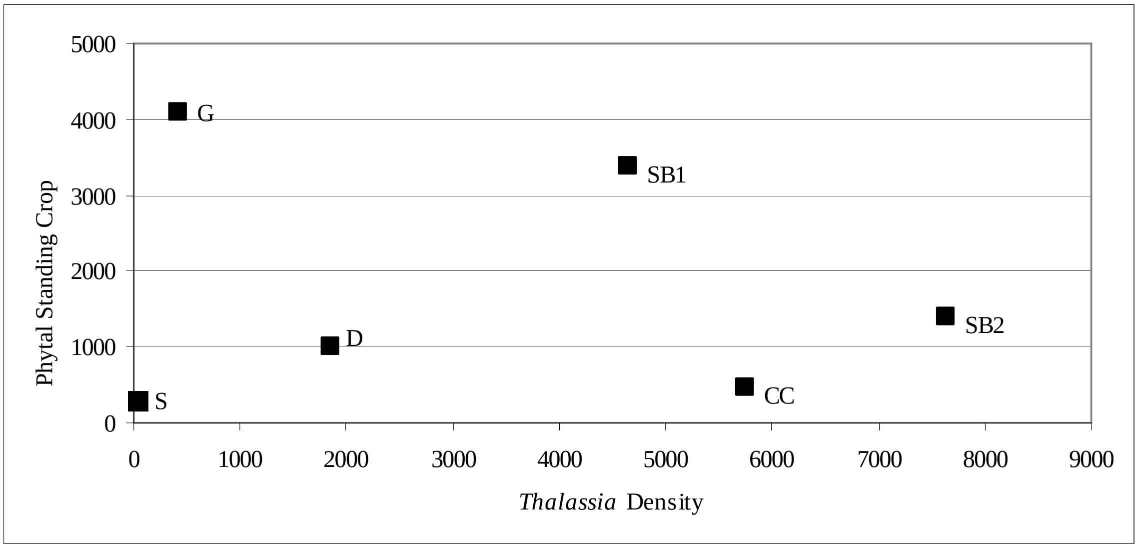


FIGURE 16—“Phytal standing crop” of foraminifera versus mean *Thalassia* density at each site.

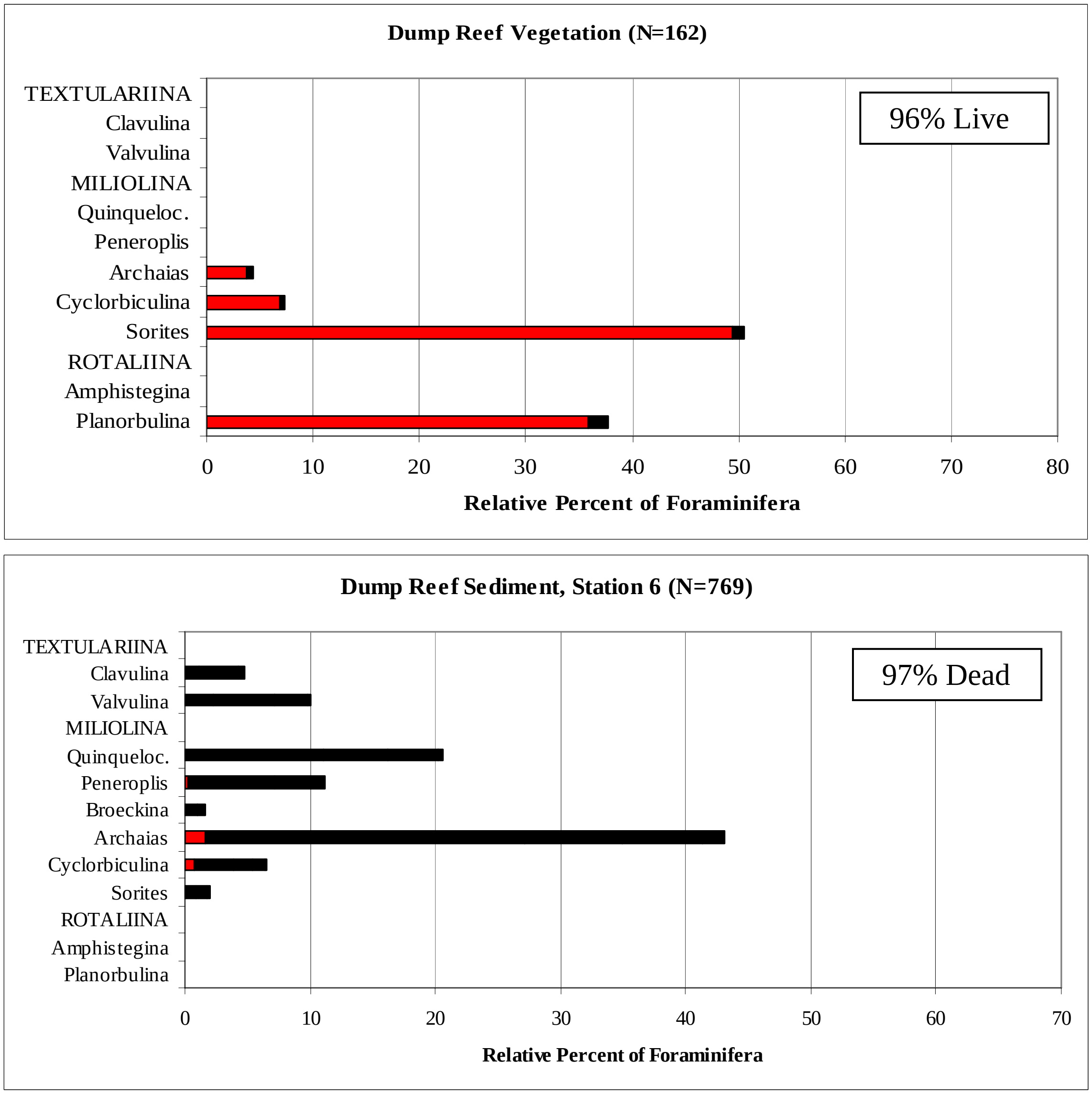


FIGURE 17—Comparison of foraminiferal vegetation assemblage (upper) with sediment foraminiferal assemblage (lower) for the Dump Reef site. Red indicates live individuals, black represents empty tests or dead individuals.

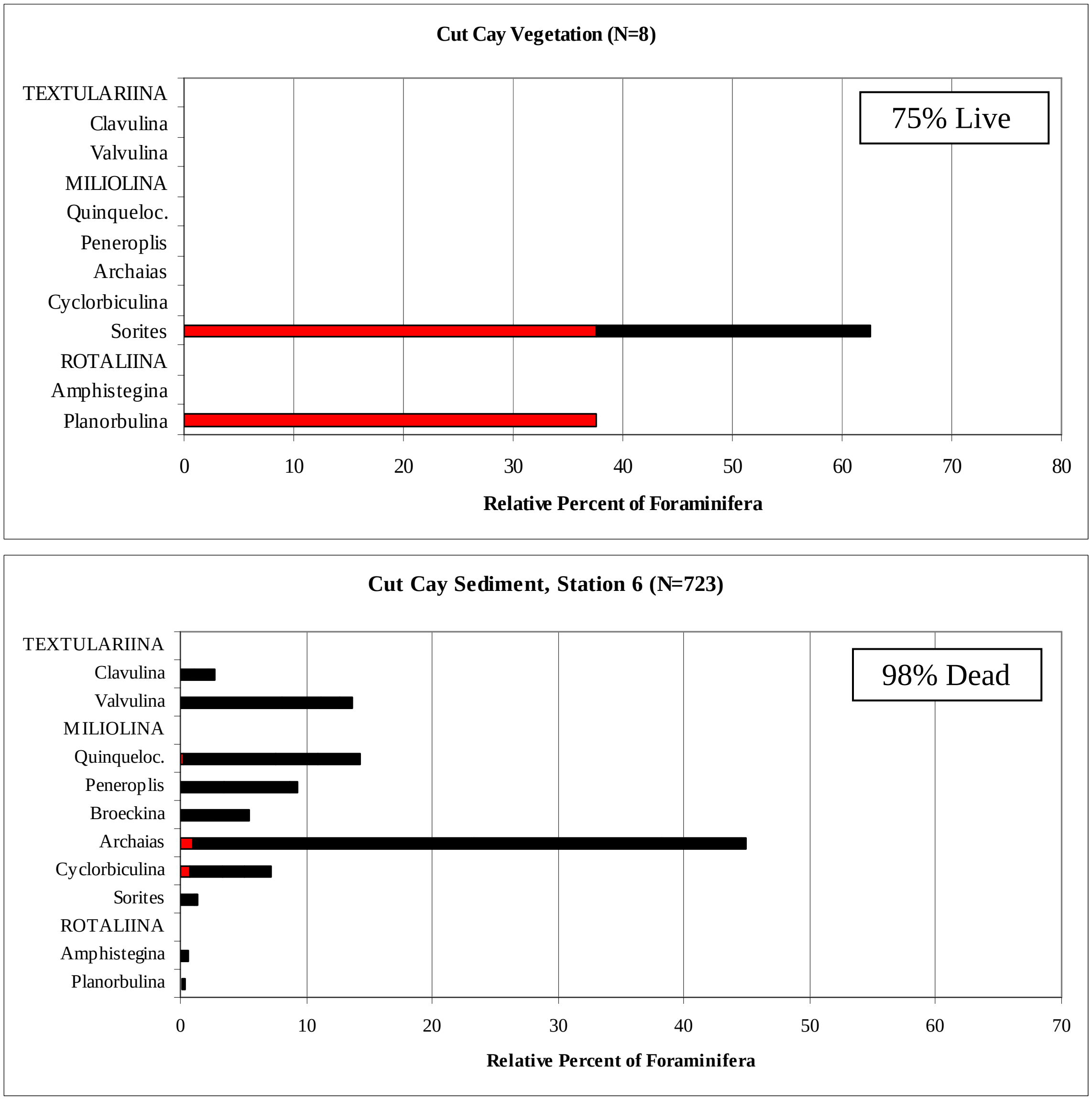


FIGURE 18—Comparison of foraminiferal vegetation assemblage (upper) with sediment foraminiferal assemblage (lower) for the Cut Cay site. Red indicates live individuals, black represents empty tests or dead individuals.

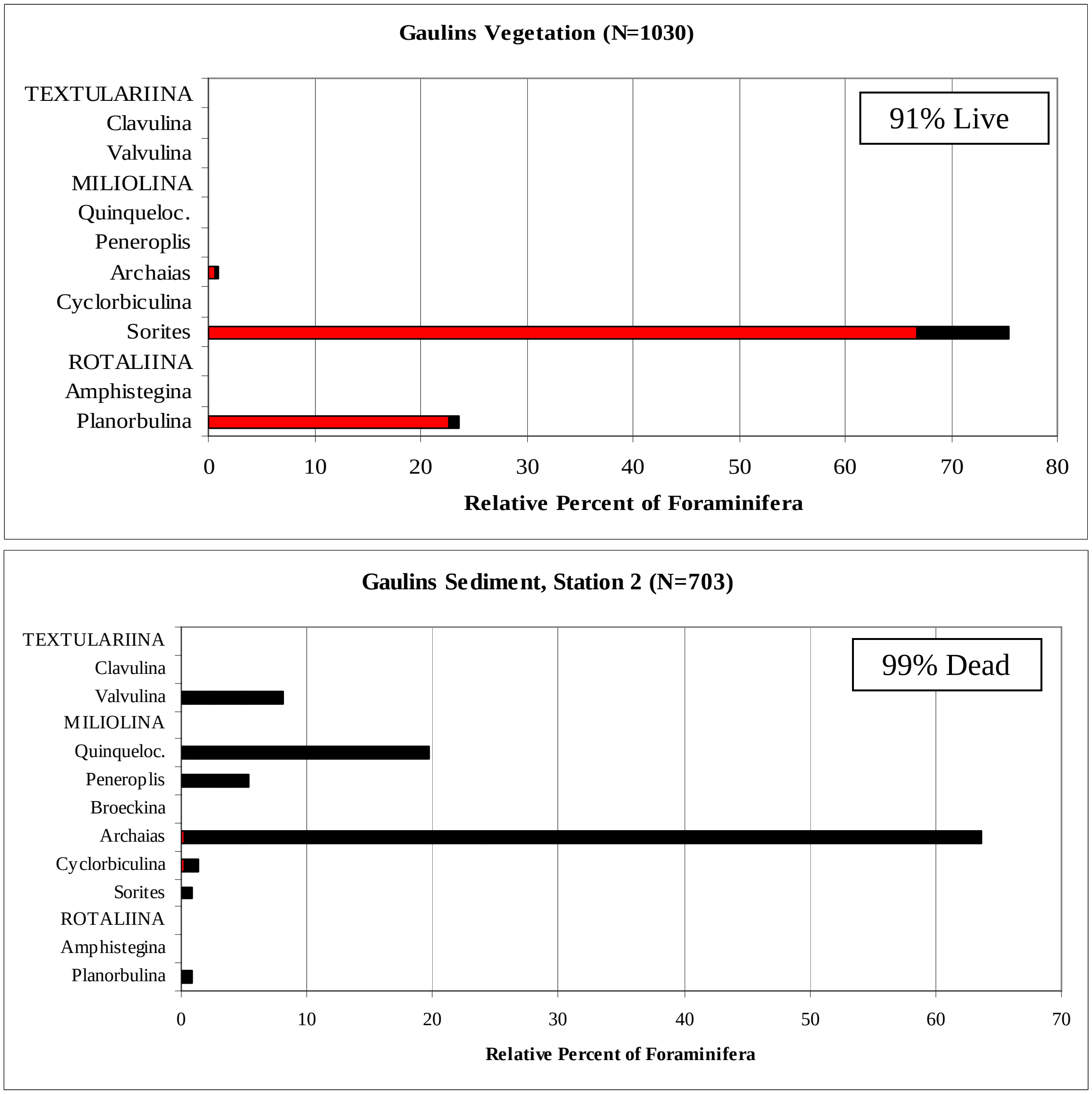


FIGURE 19—Comparison of foraminiferal vegetation assemblage (upper) with sediment foraminiferal assemblage (lower) for the Gaulins site. Red indicates live individuals, black represents empty tests or dead individuals.

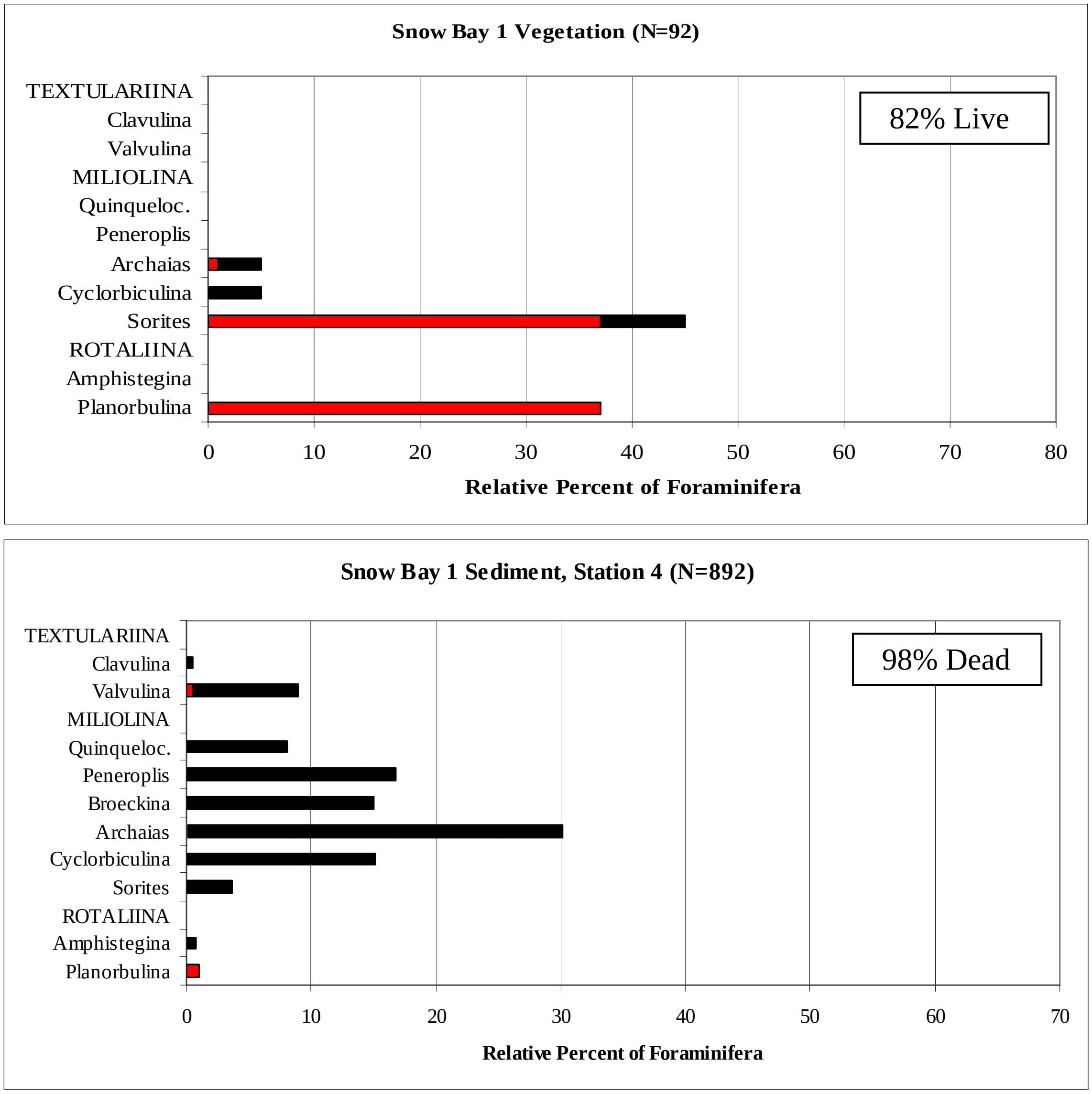
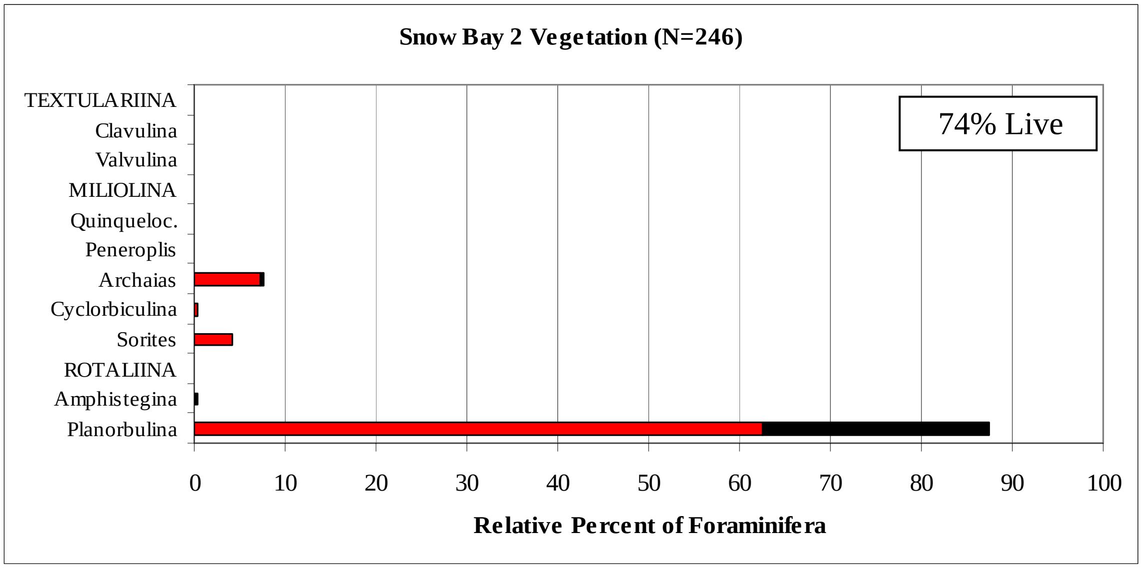


FIGURE 20—Comparison of foraminiferal vegetation assemblage (upper) with sediment foraminiferal assemblage (lower) for the Snow Bay 1 site. Red indicates live individuals, black represents empty tests or dead individuals.



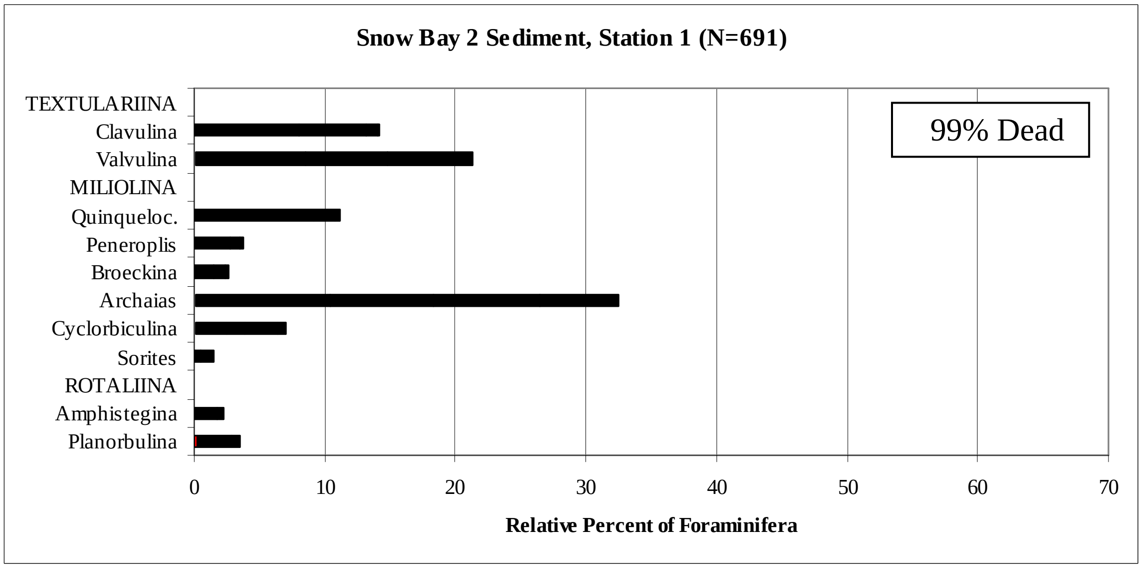
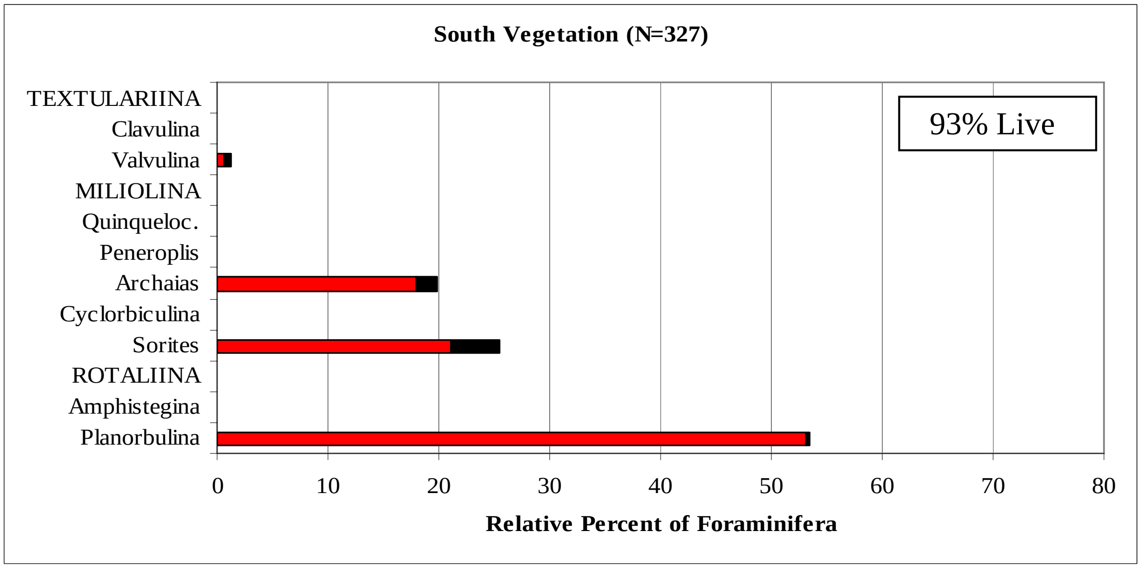


FIGURE 21—Comparison of foraminiferal vegetation assemblage (upper) with sediment foraminiferal assemblage (lower) for the Snow Bay 2 site. Red indicates live individuals, black represents empty tests or dead individuals.



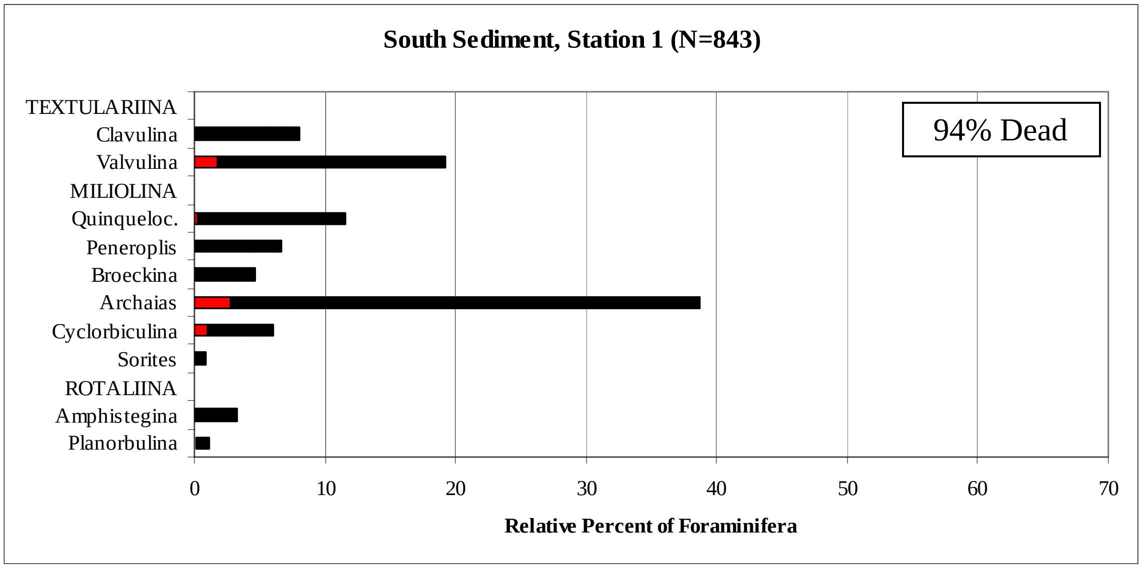


FIGURE 22—Comparison of foraminiferal vegetation assemblage (upper) with sediment foraminiferal assemblage (lower) for the South site. Red indicates live individuals, black represents empty tests or dead individuals.

Because *Thalassia* is one of the predominant vegetation types in most grass beds, foraminiferal densities in the sediment were compared to *Thalassia* densities at each site (Fig. 23). Foraminiferal density is defined as the number of foraminiferal tests per gram of sediment, and *Thalassia* density is defined as the number of blades per quadrat times the average blade length. With the exception of South site (where there was virtually no *Thalassia* present), foraminiferal density correlates to *Thalassia* density to a degree. Low density *Thalassia* beds such as Gaulins had a low sediment foraminiferal density, and moderate density beds such as Snow Bay 1 and Cut Cay had higher foraminiferal density. However, the highest density *Thalassia* beds, such as at Snow Bay 2, produced lower foraminiferal densities. Thus, the foraminiferal density in the sediment seems to peak at moderate *Thalassia* density. It is interesting to point out that two of the Cut Cay stations have similar *Thalassia* densities and foraminiferal densities, but the one Cut Cay station with a higher *Thalassia* density also has a lower foraminiferal density and clusters with the Snow Bay 2 stations.

The dendrograms in Figure 24 are Q-mode cluster diagrams of the stations studied as determined by taxonomic composition of the foraminiferal assemblages recovered from the sea floor. The left diagram shows the relationship between samples with live individuals as well as dead tests (“total” assemblages), and the right diagram shows assemblages of dead tests only. Notice that, because the proportion of foraminifera found as living individuals is so low, the two dendrograms are nearly identical. The stations for each site cluster together at high levels of similarity except for Dump Reef (dead assemblage), showing the similarities of the foraminiferal assemblages along each

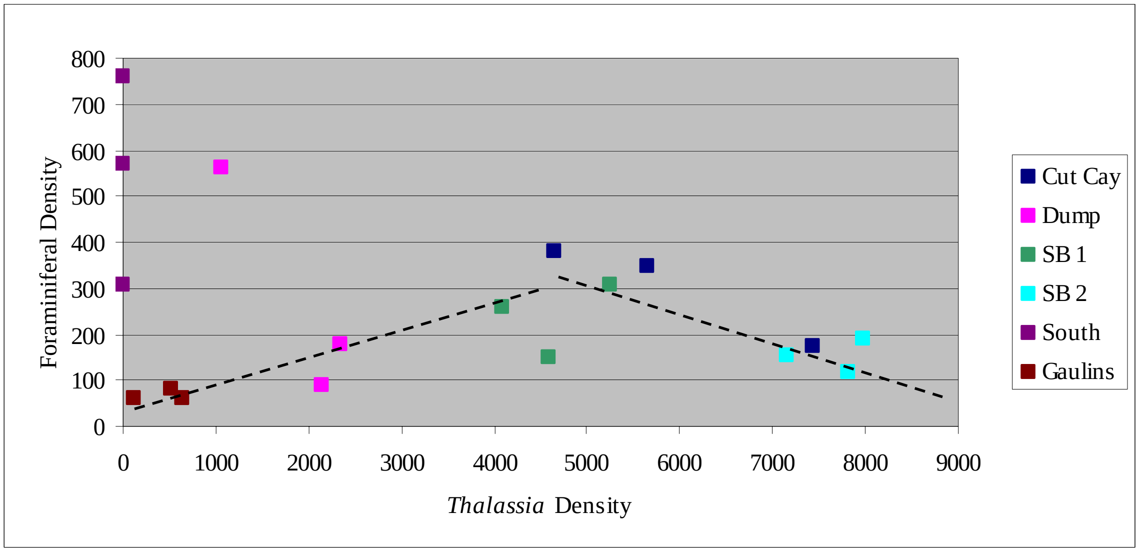


FIGURE 23—Foraminiferal density versus *Thalassia* density at each station. With the exception of South site, where there was virtually no *Thalassia* present, foraminiferal density generally peaks at moderate *Thalassia* density (~5000 cm/quadrat). Dashed lines are subjective and were added to illustrate the perceived trend.

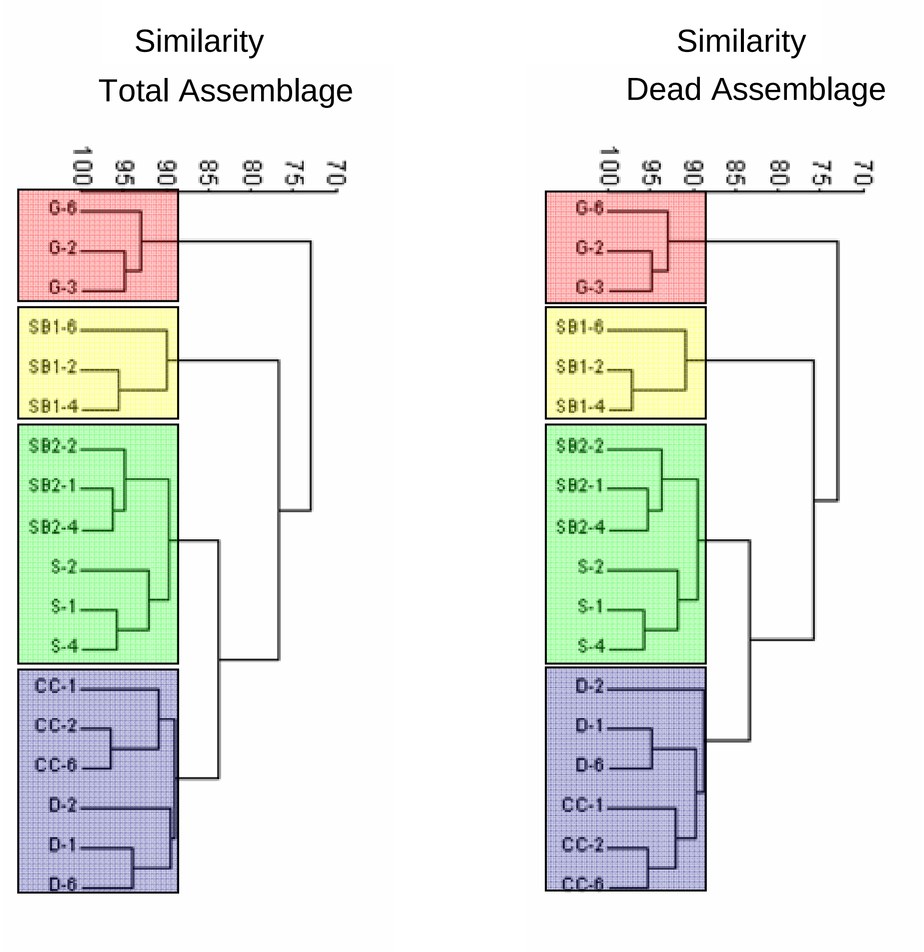


FIGURE 24—Hierarchical cluster analyses of sediment foraminiferal assemblages. Live plus dead (total) assemblages and dead only (right) are virtually identical.

transect. However, neighboring stations (10 m apart) are not necessarily the most similar at any site. In both analyses, four clusters (biofacies) are revealed. The first cluster consists of the Gaulins site, which has sparse vegetation and a very distinct sediment assemblage. Snow Bay 1, one of the densest beds, forms the next cluster, which is not closely related to Snow Bay 2 even though they are less than 200 m apart. Snow Bay 2 and South (cluster 3) are closely related, although they differ greatly in vegetation types and vegetation density. The Cut Cay and Dump Reef sites form the fourth cluster.

Figure 25 shows the results of a cluster analysis of the vegetation taxa found at each station (based on quadrat data) and compares this with the (total) foraminiferal assemblage recovered from the seafloor (from Figure 24). The South site assemblages plot apart from the others because of the lack of *Thalassia* and abundance of calcareous algae at this site.

Sediment foraminiferal assemblages were analyzed further based on the taphonomic condition of each specimen. It is preferable theoretically to use only dead assemblages: in the absence of catastrophic burial, it is the post-mortem assemblages that will become part of the rock record (Murray, 2000). However, the total assemblage was used in the present study because the taxa found as live specimens have a high preservation potential (e.g., *Archaias*). Because the transect stations from each site clustered together, one station per site was selected as typical for further comparison. Taphonomic states were summarized for each site by using a “preservation index” (PI), which is defined here as the relative percent of *live* plus *pristine* plus *good* foraminifera. Gaulins, the first cluster, had a mean PI of 37.6% (Fig. 26). Snow Bay 1 (cluster 2) had a

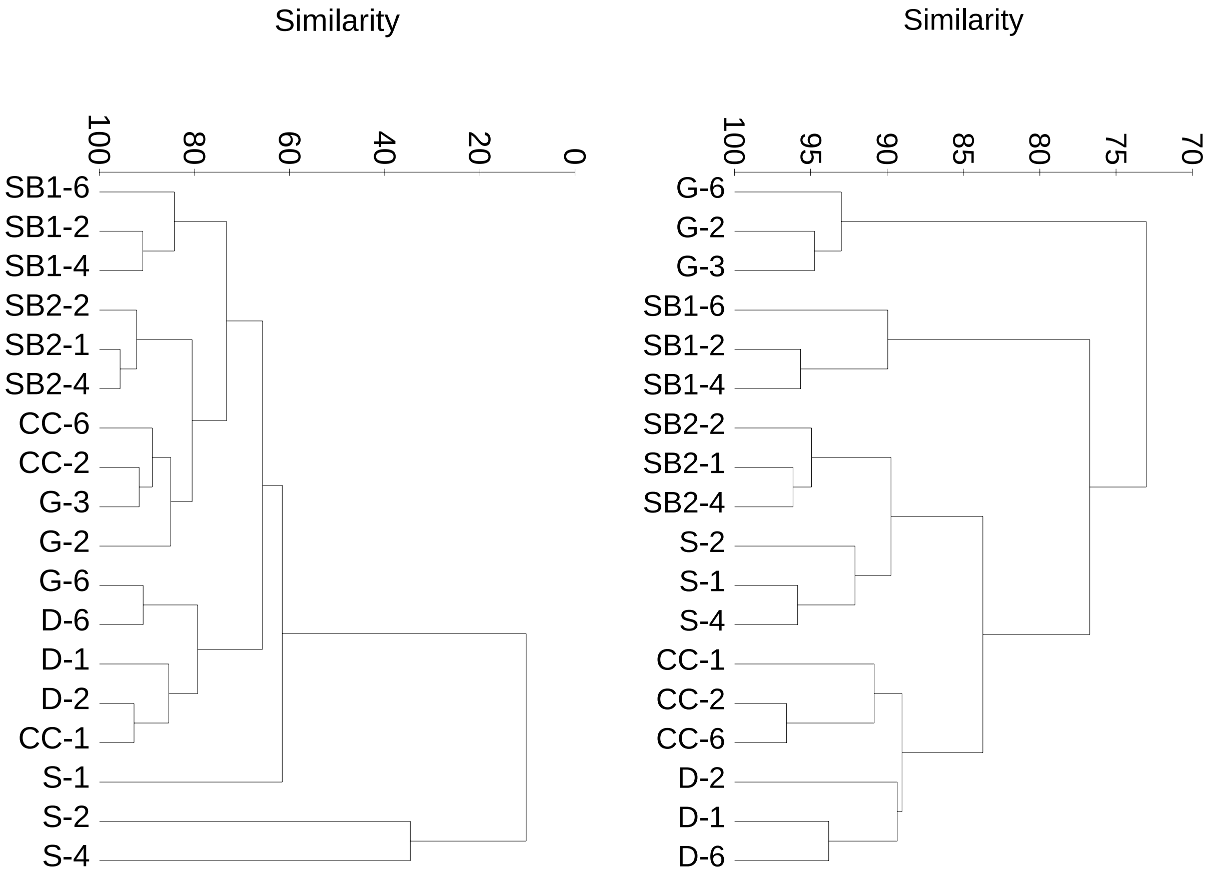


FIGURE 25—Hierarchical cluster analysis of the vegetation assemblage versus the foraminiferal sediment assemblage (total) at each site. Note the lack of agreement between the two diagrams.

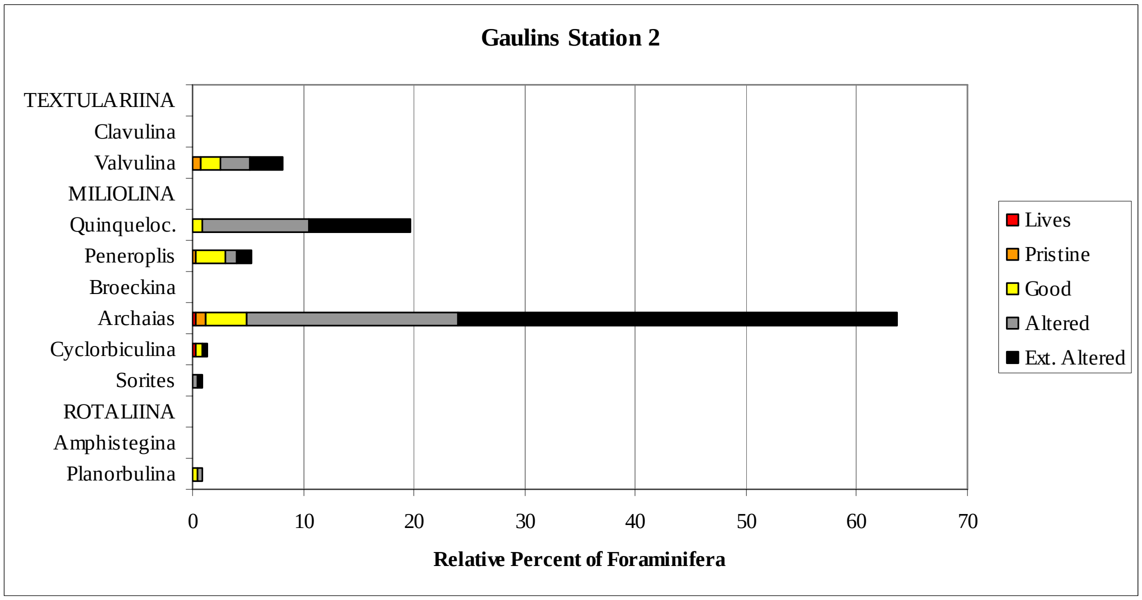


FIGURE 26—Taphonomic breakdown of the sediment foraminiferal assemblage at a typical station from the Gaulins site. PI=37.6%.

mean PI of 85.9% (Fig. 27). Figure 28 shows that Snow Bay 2 and South site's assemblages are similar causing them to form cluster 3. However, comparison of these sites taphonomically shows that they are different (Fig. 29). Snow Bay 2 has a PI of 85.4%, whereas South site has a mean PI of only 53%. Figure 30 shows the taphonomic comparison of cluster 4, which is composed of Cut Cay (PI = 87.1%) and Dump Reef (PI = 84.6%) sites. Figure 31 shows the four main alteration states for each site; note that Gaulins is dominated by abrasion. All sites have relatively high levels of breakage, but Snow Bay 2 has a high percentage of foraminifera that have been cemented (grains cemented to the exterior of the test) and encrusted with organisms.

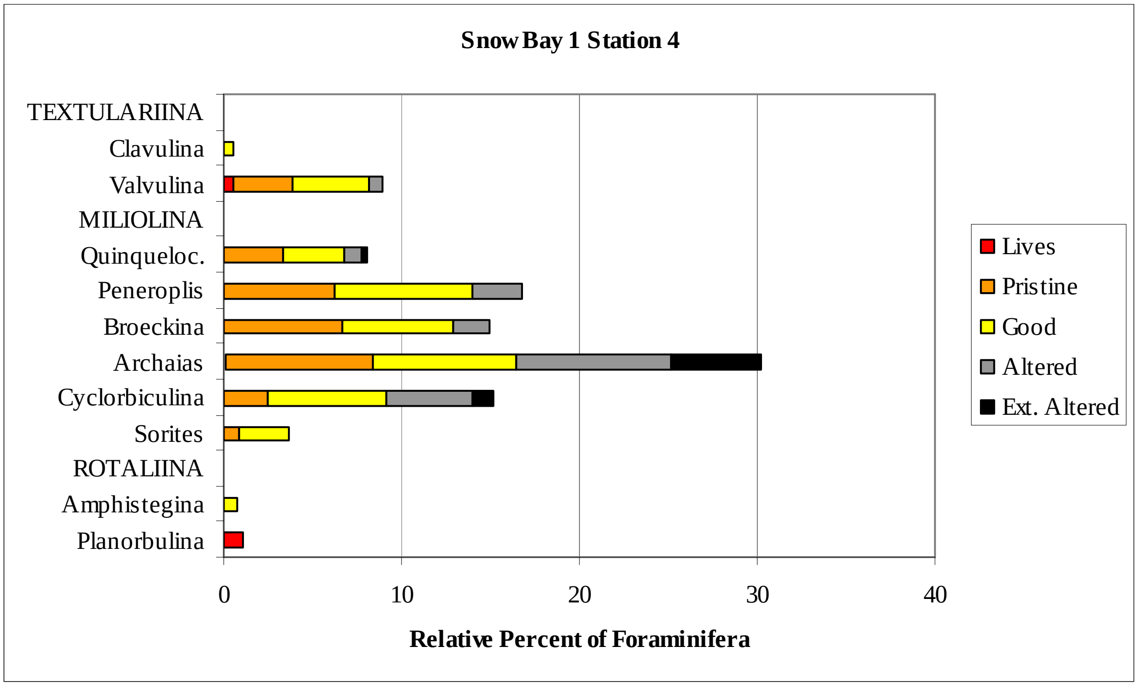
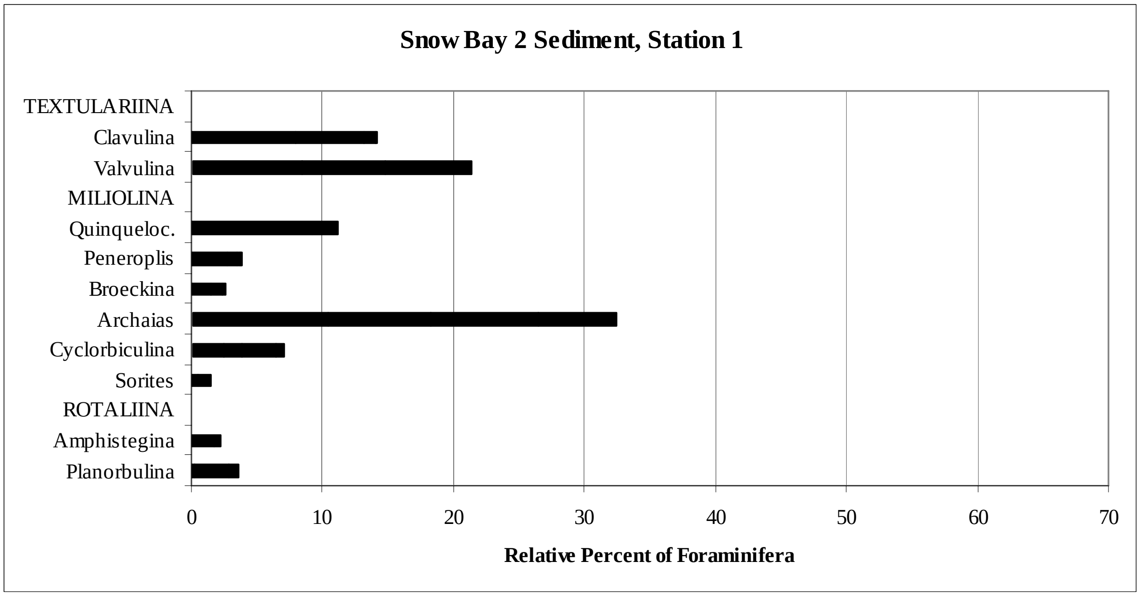


FIGURE 27—Taphonomic breakdown of the sediment foraminiferal assemblage at a typical station from the Snow Bay 1 site. PI= 85.9%.



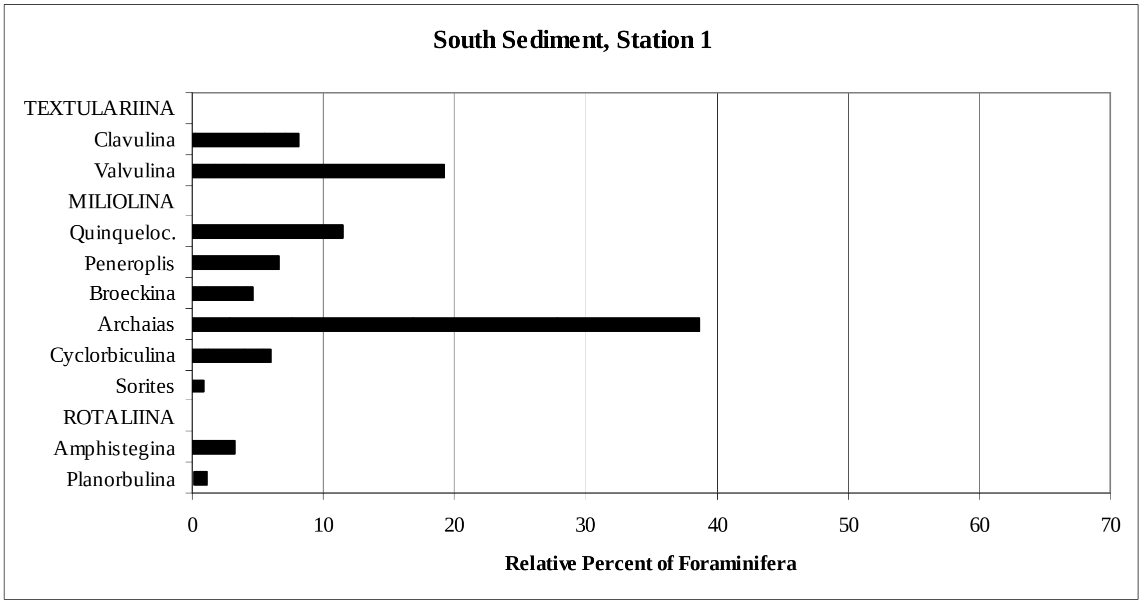
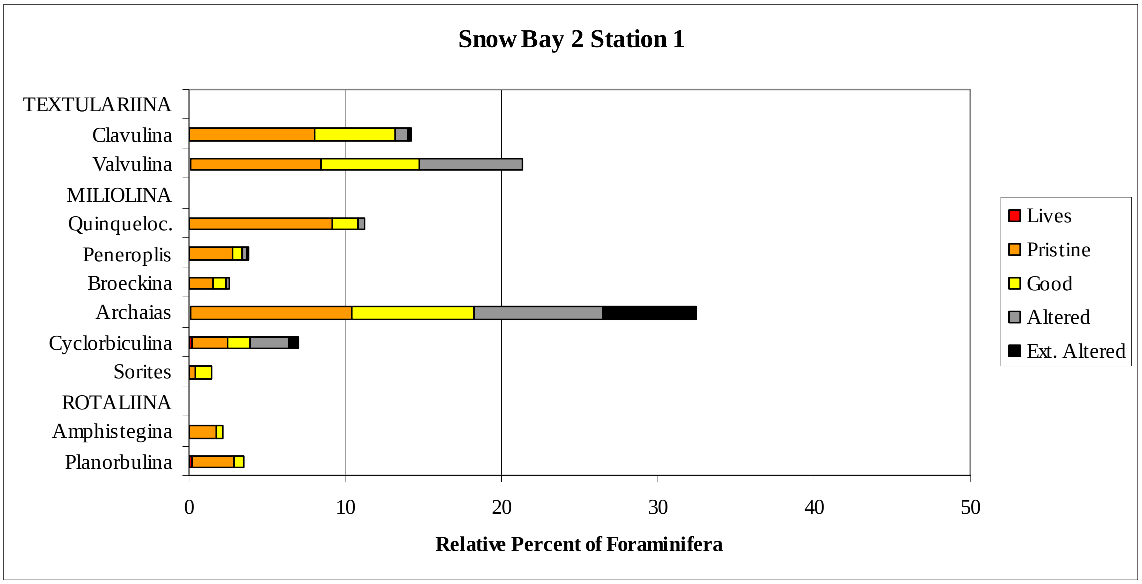


FIGURE 28—Comparison of the Snow Bay 2 and South sites based only on sediment foraminiferal assemblages. Note the strong similarity between the sites when taphonomy is not used.



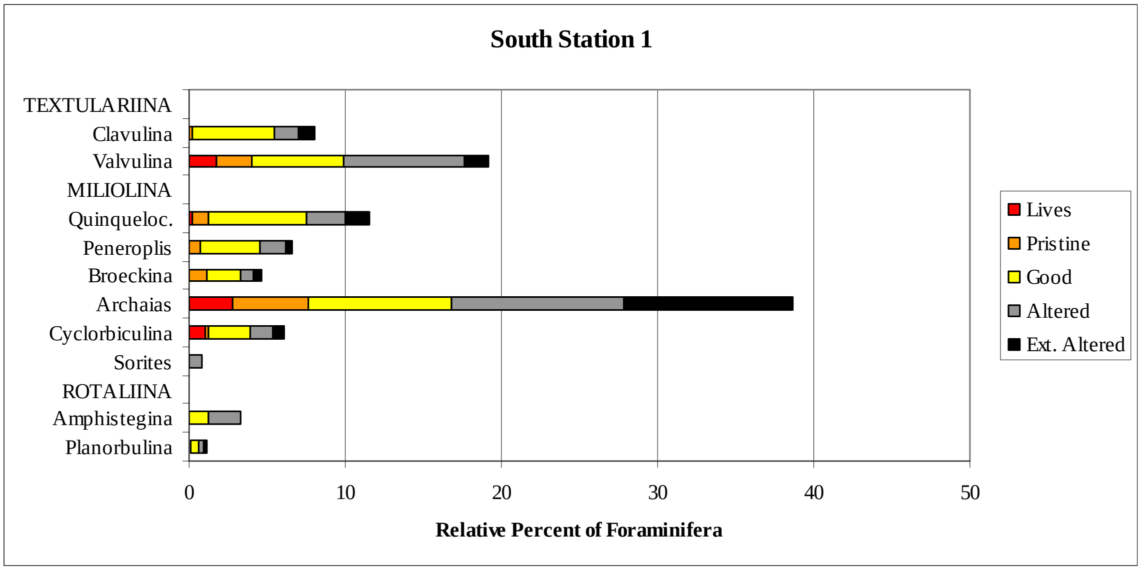
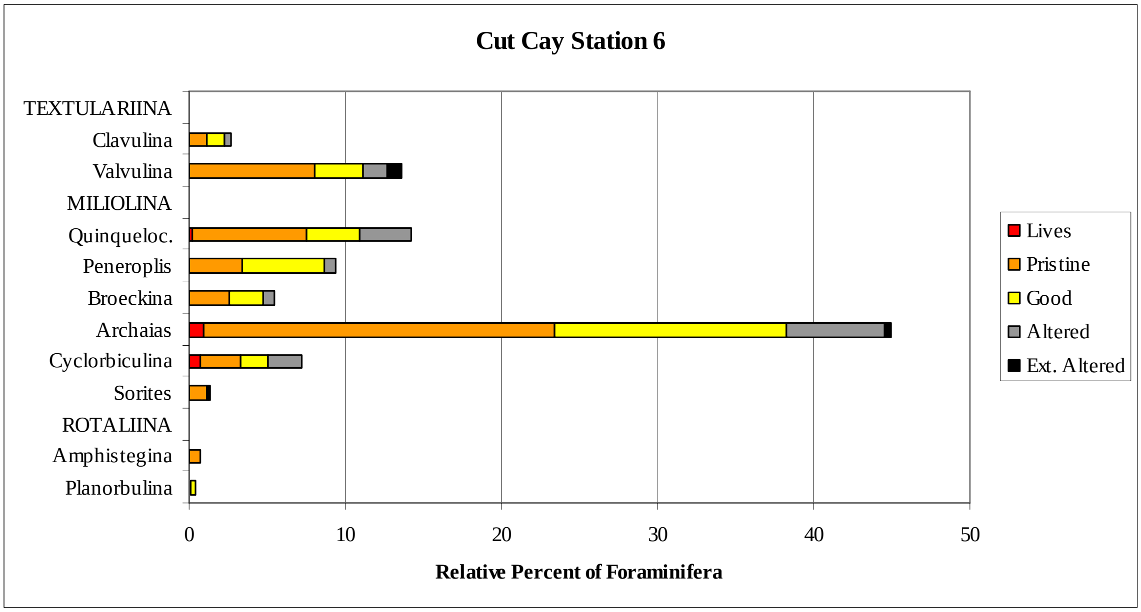


FIGURE 29—Taphonomic breakdown of the sediment foraminiferal assemblages at Snow Bay 2 (PI=85.4%) and South (PI=53%) sites.



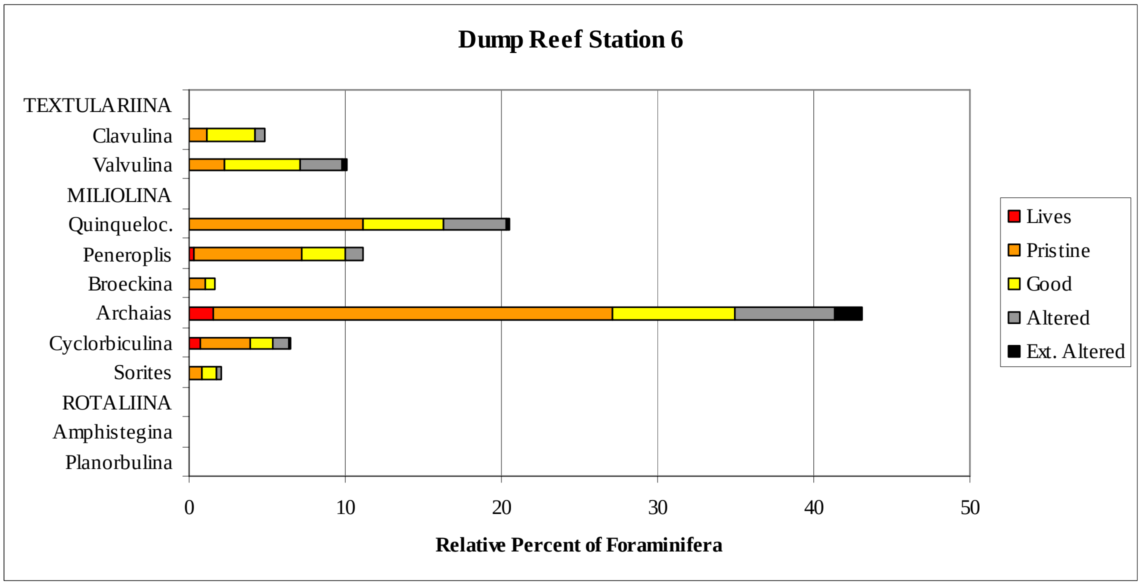


FIGURE 30—Taphonomic breakdown of the sediment foraminiferal assemblages at typical stations from the Cut Cay and Dump Reef sites. Cut Cay PI=87.1% and Dump Reef PI=84.6%.

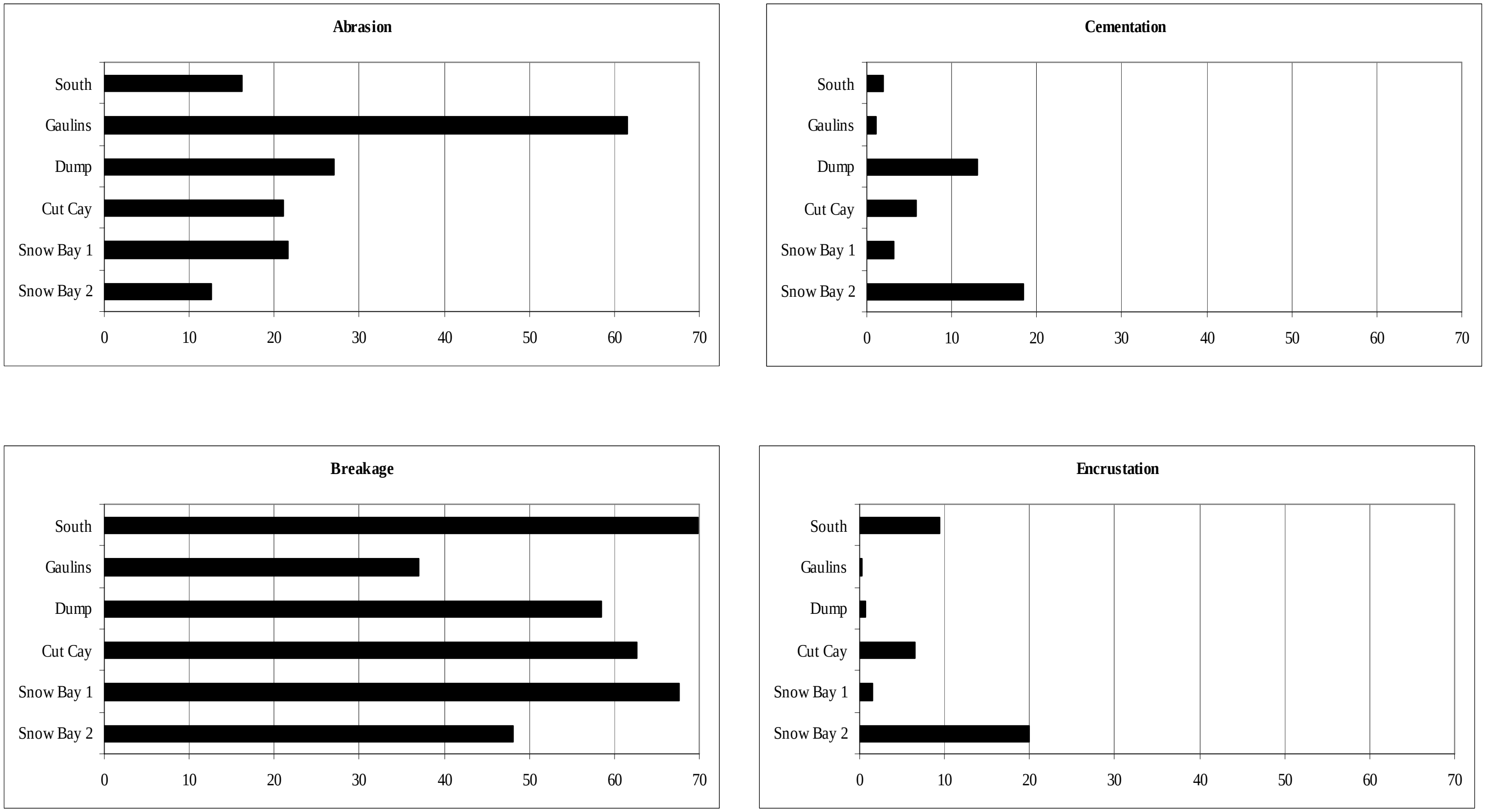


FIGURE 31—Four major taphonomic states for each site. Breakage and abrasion are dominant modes of alteration.

DISCUSSION

Vegetation and Attached Foraminifera

Vegetation assemblages and their epiphytic foraminifera do not appear to be controlled simply by geographic location, or solely by any one environmental variable. Salinity, pH, and temperature were similar among all sites, although vegetation and foraminiferal assemblages differed greatly. Water depths and energies were different from site to site, but neither was the principal factor controlling the vegetation assemblages. *Thalassia* was the dominant vegetation type at each site except Dump Reef and South (Fig. 8), but these two sites have little in common (Table 2). However, *Batophora* was only present at sites at the southern end of the island, especially South and Snow Bay 1, and therefore may prefer sites with higher energy levels and coarser substrates.

Sites that clustered together according to vegetation assemblages (Fig. 9) did not necessarily have similar foraminiferal assemblages on the vegetation or similar densities of foraminifera. For example, Gaulins and Cut Cay were both dominated by *Thalassia,* but Gaulins is a sparse grassbed with a high foraminiferal count on grass blades, while Cut Cay is a dense grassbed with very few foraminifera living on the blades. Dump Reef was dominated by *Syringodium* rather than *Thalassia*, but the grasses were still the dominant vegetation in the grassbed (as opposed to benthic macroalgae). Thus, all of the Graham's Harbor sites clustered together as determined by vegetation type. The Snow

Bay sites clustered together due to their relatively low proportions of *Syringodium* and the presence of *Batophora*. South was the least similar site with almost no *Thalassia* and an abundance of calcareous algae. This is probably due to the fact that South site had a very high energy level that may have been unsuitable for *Thalassia*, which prefers low energy environments (Bock, 1969). As a result, the algae could grow in greater abundance.

The foraminifera attached to *Thalassia* and *Halimeda* were examined in an effort to determine substrate preference. The two most abundant foraminifera living on vegetation were *Sorites* and *Planorbulina* (Fig. 12). Although higher counts of both *Sorites* and *Planorbulina* were found on *Halimeda* than on *Thalassia* (Fig. 11) at most sites, single blades of *Thalassia* cannot be compared with the complex branching thalli of *Halimeda*. However, the total percentages of each foraminifer on *Thalassia* versus *Halimeda* shows a clearer relationship (Table 7). On *Thalassia* blades at all sites, 72% of the foraminifera living on blades were *Sorites*, whereas 27% were *Planorbulina*. On *Halimeda* thalli, 33% of the foraminifera living on algae were *Sorites*, whereas 56% were *Planorbulina*. This suggests a strong relationship between *Sorites* and *Thalassia* and between *Planorbulina* and *Halimeda*.

Sorites was the most abundant foraminifer on the vegetation at the northern sites, whereas *Planorbulina* was the most abundant foraminifer at the southern sites except for Snow Bay 1 (Fig. 12). Since the energy level in general was higher at the southern sites, the higher populations of *Planorbulina* over *Sorites* could be due to the fact that *Sorites* was not as securely attached. According to Langer (1993), *Planorbulina* is a permanently attached foraminifer belonging to Morphotype A. In this category, foraminifera have a distinct attachment surface in continuous contact with the substrate and secrete a "glyco-glue" to assist in permanent attachment. *Sorites* has also been placed in this category because of its discoidal growth pattern, although it lacks an attachment surface and does not produce a "glycol-glue" (Langer, 1993). In addition, I noted that *Sorites* was easily removed from its substrate with a small brush during examination of vegetation. Comparison of the Gaulins assemblage (the site with the lowest energy and dominated by *Sorites*), with the assemblage at South (the site with the highest energy and dominated by *Planorbulina*), further supports the hypothesis that *Planorbulina* is more firmly attached that *Sorites* (Fig. 12).

It is well known that *Archaias angulatus* is commonly associated with *Thalassia* blades (Wright and Hay, 1971; Steinker and Steinker, 1976a, b; Hallock et al., 1986; Hallock and Peebles, 1993). However, in this study, *Archaias* seemed to prefer *Halimeda* thalli over *Thalassia* blades at most sites (Table 5, Fig. 11). According to Hallock et al. (1986), *Archaias* prefers a lush epiphytic growth on the primary substrate. The samples examined in the present study generally lacked the abundant epiphytic growth that is prevalent in the Florida Bay. Apparently on San Salvador, the individual blades of *Thalassia* did not provide enough epiphytic growth for *Archaias*, whereas the branching *Halimeda* thalli provided more shelter and allowed more epiphytes to establish a suitable surface for *Archaias*. Martin (1986) states that *Archaias* prefers relatively low energy environments because of its weak means of attachment by reticulopodia only. This could also help to explain the low numbers of *Archaias* found living on the vegetation in the present study.

South site was dominated by *Planorbulina*, which is consistent with higher energy environments. Although the South site is characterized by extremely high energy, some other factor must control the foraminiferal assemblage at this location because it is consistently the exception. South site had a higher percentage of live foraminifera in the sediment despite the low-density grassbed. Perhaps oxygen and inorganic nutrients were supplied in high abundance by the open ocean on this narrow shelf.

Gaulins had an extremely high density of attached foraminifera compared to other sites. It plotted well above other sites when compared with cumulative blade length (Fig. 12) and when plotted against *Thalassia* density (Fig. 13). Since *Thalassia* was virtually absent at South site, Gaulins was the only sparse grassbed where *Thalassia* was examined. The higher foraminiferal density at Gaulins could be due to the lack of available *Thalassia* blades. Because the grassbed was sparse, all the phytal foraminifera in the area lived on the few blades that were available. The lack of available living space at Gaulins was probably also combined with recruitment of foraminifera from the grassbed to the south. Foraminiferal densities of the denser grassbeds are nearly equal on both graphs.

Vegetation density combined with phytal foraminiferal density (Fig. 15) provided an estimate of the number of foraminifera attached to seagrass and algae per m^2 of seafloor. There is no clear relationship between the “phytal standing crop” (total number of foraminifera on *Thalassia* and *Halimeda* in one m^2) and the total vegetation count in per m^2. Again, Gaulins has a high standing crop, producing over 4000 tests of phytal large benthic foraminifera even though it has sparse vegetation. Denser grassbeds have total vegetation counts that range between 2000 and 3000 plants, but the standing crop numbers do not show a proportional relationship. With the exception of Gaulins, the phytal standing crop seems to peak at a moderate *Thalassia* density (Snow Bay 1) then decreases again as the *Thalassia* density continues to increase (Fig. 16). This could be due to competition between *Thalassia* and the foraminifera for available inorganic nutrients (e.g., phosphorus and nitrogen), or the lush grassbed could block out sunlight that foraminiferal symbionts require for photosynthesis.

Foraminifera in the Sediment

When assemblages of foraminifera attached to *Thalassia* and *Halimeda* were compared to assemblages found in seafloor samples, it was clear that they do not match. Vegetation assemblages were mostly live and dominated by *Sorites* and *Planorbulina*, but these taxa were among the least common in sediment assemblages (Fig. 12). Martin (1986) also reported finding large populations of *Planorbulina* on vegetation but noted that living *Planorbulina* were not found in any sediment sample. He attributed the lack of *Sorites* and *Planorbulina* in the sediment to their low preservation potential. In this study, the only living *Planorbulina* found in the sediment were still attached to dead *Halimeda* plates at the Snow Bay 2 site. The accumulation of *Halimeda* plates in the sediment most likely offered some protection to the fragile *Planorbulina*. Martin (1986) also found that *Archaias* was the dominant foraminifer in the sediment at all sites but varied in relative percent from site to site. This is likely due to the robustness of the *Archaias* test and its ability to withstand taphonomic processing that would destroy more fragile tests.

Comparing the *Thalassia* density to sediment foraminiferal density at each site (Fig. 23) shows an interesting relationship. Ignoring South because of the lack of *Thalassia*, foraminiferal density correlates to *Thalassia* density to a degree. Gaulins, a sparse grassbed, had a low foraminiferal density. The moderate density beds, Cut Cay and Snow Bay 1, had the highest foraminiferal density. However, the highest density grassbed, Snow Bay 2, had a low foraminiferal density. Thus, the foraminiferal densities appear to peak at approximately 5000 cm/blade. This could be because the highest density beds may be too crowded for a dense foraminiferal community. The extremely high foraminiferal numbers at South probably was controlled by other factors such as nutrient levels in the water. In short, foraminiferal density can be an indicator of grassbed density, except for very dense grassbeds, and high foraminiferal density can also result from other causes, as the South site shows.

In the cluster diagrams of the total and dead foraminiferal assemblages at each site (Fig. 24), stations from each site cluster together, showing that all stations at each site are closely related in their foraminiferal assemblages. It is interesting to note that Snow Bay 1 and South sites cluster together, but South is a sparse bed with little *Thalassia* and Snow Bay 1 is a dense grassbed. Again, there appears to be some other, currently unrecognized, external factor controlling the South foraminiferal population. Cluster analyses show that the site-to-site foraminiferal assemblages are not controlled simply by geographic location or by any of the water variables measured. In addition, the sediment and vegetation clusters show that foraminiferal assemblages in the sediment are not controlled by vegetation assemblages (Fig. 25).

Taphonomic Data

Grassbed types from site to site are not easily differentiated based on vegetation or sediment foraminiferal assemblages. Taphonomic analysis was used to add data beyond the taxonomic compositions of the sediment assemblages. The preservation index (PI), which is the relative percent of live plus pristine plus good foraminifera, was defined in order to compare sites. Figure 24 shows that Gaulins clustered alone, but examination of the taphomomic make up of tests from that site (Fig. 26) reveals a dominance by poorly preserved foraminifera. Gaulins has a mean PI of 37.6%, and *Archaias* alone has a PI of 11.2%.

Snow Bay 1, a relatively dense grassbed, clustered alone based on its foraminiferal assemblage. The relative percent of *Archaias* is lower than some of the other sites, whereas the percent of the other foraminifera is relatively high (Fig. 27). Therefore, Snow Bay 1 formed a separate cluster. However, looking at taphonomy, it has a PI of 85.9%. Thus, the relatively dense Snow Bay 1 site has far better preserved foraminifera than Gaulins, a sparse grassbed.

Snow Bay 2 clusters with South, and the graphs of foraminiferal assemblages initially appear very similar (Fig. 28). Each foraminiferal genus occurs in roughly the same abundance at both sites. However, once taphonomic states are differentiated, the differences between the sites become obvious (Fig. 29). Snow Bay 2, the denser bed, has a PI of 85.4%, whereas the sparse South site has a PI of only 53%. The vegetation at Snow Bay 2 protects the foraminiferal tests, whereas the sparsely vegetated South site leaves the foraminifera relatively unprotected, which results in more broken tests.

Cut Cay and Dump Reef clustered together based on their foraminiferal sediment assemblage (Fig. 30). However, unlike the previous cases, these sites are characterized by have very similar taphonomic states, apparently because the grass beds have a similar density and composition. Cut Cay has a PI of 87.1%, and Dump Reef has a PI of 84.6%.

Finally, the type of alteration can give additional information about the type of grassbed at a given site (Fig. 31). For example, all sites experienced high amounts of breakage, especially South, which had the highest water energy. Gaulins had the highest amount of abrasion. Apparently this sparse grassbed did not offer enough protection to hold the tests in place and allowed them to abrade easily. Cementation and encrustation were mainly seen in the dense Snow Bay 2 site. Other dense grassbeds also experienced some cementation and encrustation. However, the sparse grassbeds showed little of this type of alteration. Most likely, the dense beds held foraminiferal tests in place for a longer period of time, allowing the grains to cement together and providing time for encrustation of the tests by other organisms.

CONCLUSIONS

Vegetation and sediment foraminiferal assemblages do not appear to be strictly controlled by geographic location or any one water variable. Vegetation assemblages varied from site to site and were not controlled by the density of the grassbed or the grassbed composition. *Sorites* has a preference for *Thalassia* and was the dominant foraminifer at the northern sites, whereas *Planorbulina* has a preference for *Halimeda* in the southern sites. While it has been well established that *Archaias* prefers *Thalassia* as a substrate, this study shows that *Archaias* prefers the *Halimeda* thalli instead. This may be explained by the low levels of epiphytes on *Thalassia* at San Salvador as opposed to the Florida coast.

Foraminiferal assemblages on vegetation at each site do not match the assemblages in the sediment. While vegetation is dominated by *Sorites* and *Planorbulina*, these taxa are very rare in sediment samples, which are dominated by *Archaias* instead. Sediment assemblages were also not determined solely by geographic location, water depth, or distance from shore. Foraminifera from the sediment sample sites at the north end of the island did not cluster separately from those at the south end, and those that did cluster together had a wide range of water variables. Foraminiferal density in the sediment correlates to some degree with the average *Thalassia* density. Foraminiferal number is low in low density beds, peaks at a moderate *Thalassia* densities, then drops again at the stations with the highest *Thalassia* density.

The use of taphonomic states allows recognition of well-developed grass beds. Dense grass beds had an average preservation index of approximately 85%, whereas sparse grassbeds had a much lower preservation index. Certain types of alteration (e.g., cementation and encrustation) can also be useful in determining grass-bed coverage. Thick coverage and longer blades trap foraminifera and allow them to become cemented and encrusted. In sparse grassbeds, grains are more easily transported and can experience higher levels of abrasion and breakage.

Significance

Seafloor samples of lagoonal large benthic foraminifera are dominated by soritids such as *Archaias*, *Cyclorbiculina*, and *Peneroplis* (e.g., Hallock and Glenn, 1986; Martin and Liddell, 1991) mobile epiphytes (Langer, 1993) flourishing in grassbed settings. However, previous studies have not quantified the density of vegetation beds, or compared vegetation density with the foraminiferal density in the sediment. In addition, very few studies have considered the taphonomic conditions of the dead individuals. The present study shows that, in spite of the contrast between standing populations of epiphytic foraminifera and sediment assemblages, seafloor samples can be used as proxies for the presence and density of seagrass beds. While sediment foraminiferal assemblages alone can be used to recognize zones such as lagoon versus fore-reef, taphonomic analysis can help distinguish between microhabitats within certain zones, such as the lagoonal settings in this study.

SUGGESTIONS FOR FURTHER STUDY

Foraminiferal assemblages on vegetation and at the sediment-water interface are similar to those recognized in previous studies by other authors. Associations of certain foraminifera with phytal substrates has been well established. The current study further confirms the substrate preferences of several large benthic foraminifera. However, no two grassbeds are alike. In this study, comparisons between two sites were based on the relative similarity between the grassbeds (composition and density) and not on the environmental variables at each site. Still, the environmental variables play an important role in the foraminiferal assemblages on the vegetation and in the sediment. Because of this, further studies should be performed to evaluate the relative importance of these variables.

In order to maximize the use of foraminifera as proxies for the existence (or lack of) grassbeds further comparisons should be performed. Comparisons between grassbeds with similar composition and densities, as well as similar environmental variables would help to verify the main results of this study. In addition, comparative studies of sparse grassbeds and sand flats that completely lack grass are needed. Also, variables such as nutrient levels (e.g., nitrogen, phosphorus, oxygen) in the water should be measured to determine their controls on the foraminiferal population. Finally, to make this use of foraminifera universally applicable, grassbeds in other areas of the Caribbean and even other parts of the world should be examined in detail.

Sites such as Gaulins and South are unique in that they both had high densities of foraminifera in the sediment, but were the lowest density grassbeds. In addition, Gaulins was a low energy site, whereas South was high energy. Further studies could help to determine what factors are controlling the high foraminiferal population despite the differences in water energy.

Taphonomic analysis appears to be a useful tool in differentiating between various types of grassbeds, and its use should be continued. The use of a preservation index helped to distinguish between high and low density grassbeds in lagoonal settings. However, it is possible that a high preservation index could be found in assemblages in deeper waters. In this case, the foraminiferal species composition of the assemblage would help to determine the zone (e.g., lagoon, fore-reef), while the preservation index could distinguish between grassbed densities.

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