SESSILE INVERTEBRATE COLONIZATION AND COMMUNITY

DEVELOPMENT IN THE SOUTH ATLANTIC BIGHT

by

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A Thesis Submitted to the Faculty

of the College of Graduate Studies

At Georgia Southern University

in Partial Fulfillment of the

Requirements of the Degree

Master of Science
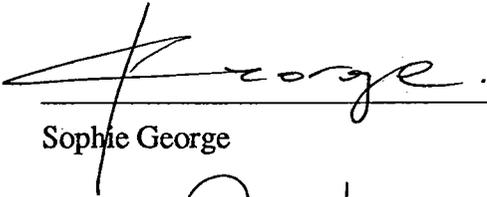
Statesboro, Georgia

1998

SESSILE INVERTEBRATE COLONIZATION AND COMMUNITY

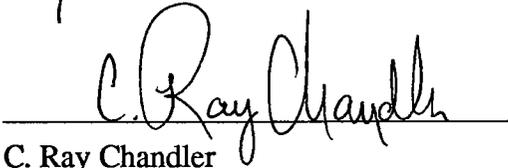DEVELOPMENT IN THE SOUTH ATLANTIC BIGHT

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ACKNOWLEDGMENTS

ABSTRACT

Invertebrate colonization of bare substrate was studied by placing rocks of similar composition to surrounding live-bottom outcrops on or near Gray's Reef National Marine Sanctuary. Colonization was measured over the course of one year. In one comparison, quarried rocks were placed on sand-bottom and hard-bottom areas to evaluate the effect of adjacent substrate type on community development. In a second comparison, quarried rocks were placed in open and in caged enclosures to examine the effect of grazing on colonization patterns. Bryozoans were dominant colonizers in all treatment types throughout the year. The highest species diversity was observed in the caged enclosures and the lowest on rocks placed above sand-bottom areas. There were significant differences among taxa in mean percent coverage between the open and caged enclosures, with open enclosures having higher coverage. Likewise, there were significant differences among taxa in mean percent cover between rocks placed on sand-bottom versus hard-bottom, with hard-bottom having higher coverage. Patterns of recruitment affected by seasonal changes for selected taxa will be discussed.

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INTRODUCTION

Biotic and abiotic factors that affect benthic community composition and diversity have long interested marine biologists. Colonization and subsequent community development have been studied in coral reef (Stoner, 1992) subtidal (Dean, 1981; Keough, 1983) and rocky intertidal habitats (Dayton, 1971). Less is known of these processes in hard-bottom habitats, also referred to as "live-bottom" (Stuhasker, 1969).

Hard-bottom habitats refer to areas of rocky outcrops of moderate height (1-2 m) separated by sandy flat-bottomed troughs. Hard-bottom areas are found along the continental shelf and cover approximately 29.8% of the seafloor of the South Atlantic Bight, which extends from Cape Hatteras, NC, to Cape Canaveral, FL (Parker et al., 1983; Figure 1). These hard-bottom patches provide substrate for many sessile organisms such as algae, corals, tunicates, bryozoans, and sponges (SCWMRD, 1984). The hard-bottom rock outcrops are composed of sedimentary lithified limestone and sandstone, embedded with fossilized organisms (Harding and Henry, 1994). The density and abundance of invertebrates increase with higher relief and are controlled on a large scale by the relative amount of sand veneer, sediment transport and water temperature (SCWMRD, 1982).

Factors previously identified as being important in controlling colonization and community development in other benthic marine habitats include: 1) substrate availability (Thorson, 1957), 2) larval recruitment densities (Connell, 1985, Gaines and Roughgarden, 1985, Stoner, 1994), 3) predation (Osman, 1977, Menge, 1991), 4) physical disturbance and environmental stress (Dayton, 1971, Menge and Sutherland, 1987), 5) natural

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mortality (Dayton, 1971), and 6) competition for space (Dayton, 1971, Connell, 1985, Menge 1991).

Two hypotheses are currently favored which explain the order of species colonization. One hypothesis suggests that larval colonizers are randomly distributed and settle onto available bare substrates. Initial colonization densities reflect densities of larvae (Gaines and Roughgarden, 1985). The first colonizers can affect subsequent larval recruitment, both positively or negatively depending on species, via physical and chemical changes of the substrate (Dean, 1981). Therefore, this hypothesis predicts that the first larvae to recruit are more likely to dominate until other biotic and abiotic factors allow for changes in community structure (Osman, 1977, Lubchenco and Menge, 1978, Sutherland, 1978, Dean, 1981, Keough, 1983, Dayton, 1984, Butler, 1986, Menge, 1987).

The second hypothesis suggests that larval recruitment and settlement are not random but represent a predictable pattern. This pattern is dependent on substrate type, chemical cues from previous settlers, and environmental conditions (Schoener, 1974, Schmidt, 1982, Roughgarden et al., 1988, Stoner, 1992, Rodriguez et al., 1993, Stoner, 1994, Walters, 1996). This hypothesis predicts an organized colonization process that eventually reaches an expected and repeatable climax community as described by Odum (1969). It is unknown which of these two hypotheses is more appropriate for the recruitment of marine epifaunal organisms on live-bottom reefs in the South Atlantic Bight.

Marine colonization studies have made use of artificial substrates so that field experiments could be controlled. Flat panels, such as Plexiglas plates, which are easy to transport and collect are the method of choice in epifaunal studies (Sutherland, 1978, Dean, 1981, Schmidt, 1982, Keough, 1983, SCWMRD, 1984, Butler, 1986). However, use of these plates has not resulted in epifaunal communities that represent the natural surrounding biota in live-bottom reefs (SCWMRD, 1984, Gilligan, 1985).

In this study, quarried limestone rocks were used because of their similarity in structure and composition to the natural limestone outcrops that characterize hard-bottom areas in the South Atlantic Bight. This is the first study using natural rock to describe colonization in hard-bottom habitats. Two comparisons were made using the quarried rock. First, quarried rocks were placed directly on a sand substrate or on hard-bottom substrate. This comparison evaluates the effect of the surrounding habitat on colonization and community development. Second, to examine the effect of large predators and grazers, a predator exclusion study was conducted. Colonization and development of the epifaunal community in cages excluding large predators and grazers were compared to open cages. These cages were set on platforms to eliminate potential problems of sand moving over, and covering the rocks. Qualitative differences between rocks in the first and second experiments were evaluated to examine the effect of sediment and sand transport. This is particularly important in live-bottom areas, since sediment and sand transport are constantly exposing and covering hard-bottom patches (SCWMRD, 1982). Furthermore, a comparison of rocks in all treatments can be used to evaluate hypotheses of random or systematic recruitment.

The outcomes of this study have implications for the feasibility of live-rock culture in the South Atlantic Bight. Harvesting of "wild" live rock has been increasing for the past decade worldwide. The South Atlantic and Gulf of Mexico Fisheries Management Councils have prohibited wild rock harvest in the South Atlantic Bight starting in 1994, as a result of increased harvest and destruction of live-bottom habitat. Harvest of naturally occurring live rocks still occurs in other areas of the world to supply the US demand. Due to this destructive practice, there is an interest in the cultivation of live rock for conservation and commercial purposes.

The main goals of this study were to: (1) document the process of recruitment and colonization of benthic communities in live-bottom habitats over a one year period, (2) test the effect of the surrounding substrata on species composition and percent cover, (3) test the effect of predation by large predators on patterns of species composition and percent cover, (4) use data to evaluate the two hypotheses on benthic recruitment, and (5) assess the feasibility of culturing visually attractive "live rock" in the SAB.

LITERATURE REVIEW

Overview

Knowledge of benthic marine ecology is closely tied to insights derived from studies of terrestrial ecology. Ecological theory has been heavily influenced from the thorough study of land plants distributions (Smith, 1990). Terrestrial communities are distinguishable through patterns observed in the vegetation in relation to the soil conditions and temperature of a given area. Terrestrial plant communities show a vertical stratification. The relationship between tree canopy, understory, and the animals in an area are all interdependent and affect one another. For example, thicker canopies on trees limit the number of shrubs and density of herbaceous grasses.

Aquatic communities are similarly stratified due to light penetration. Autotrophic organisms are in areas of high light availability. Heterotrophic species, however, thrive and use energy acquired from the autotrophs (Smith, 1990). Organisms in sessile communities must compete for space that is limited both vertically and horizontally. The resulting competition results in an orderly progression to a climax community where biotic interactions predominate. Ecological succession is defined as a sequential change in species dominance over time. Odum (1969) describes succession as an orderly sequential process resulting from changes in the environment from previous colonizers, and stabilizing eventually as a climax community. Succession studies are often descriptive accounts of population changes in a community over time. These studies detail

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the order of species colonization in an area and allow the logical prediction of an ultimate teraform based on ecological principles derived from these observations. Variables in the rates of community succession have been shown to exist and depend on factors such as predation, space, inter- and intra-specific competition, and limiting nutrient resources.

Three differing theories have been proposed to explain successional patterns: the facilitation model, the tolerance model, and the inhibition model (Connell and Slatyer, 1964). The facilitation model describes an autogenic approach where primary colonizers change the environment guaranteeing the success of subsequent species. The tolerance model, instead, suggests that the later colonizers are not affected by previous species. Species establish and outcompete the previous colonizer if they are more efficient in obtaining nutritional resources. The inhibition theory shows competition itself driving community succession, with no predisposed pattern but a random first come first serve pattern.

As early as 1942, Lindeman postulated that the productivity in a community increases progressively with increased succession thus improving energy transfer. The first colonizer and successional organisms are usually small, sparse and encompass a wide spread area. It is followed by denser organisms with increased competition for space thus becoming a more vertical community (Odum, 1969).

Marine Benthic Communities

Marine invertebrate recruitment is affected by abiotic and biotic factors including, substrate type, species complexity, and seasonality (Thorson, 1957; Dayton, 1971; Connell, 1985; Butler, 1986, Menge, 1991; Rodriguez et al., 1993). Marine species interactions are not as visually distinguishable as their terrestrial counterparts (Barnes and Hughes, 1988). Sessile invertebrate competition often does not result in death of an organism, but is expressed by reductions in growth and reproduction rates. The most

common interaction between benthic invertebrate communities is when one organism changes a habitat making it unsuitable for other previous colonizer's to thrive in the area (Barnes and Hughes, 1988). Therefore, no one resource becomes the limiting factor but the presence of another individual prevents another from growing (Barnes and Hughes, 1988). Competition is an important principle and several ecological hypotheses have been derived from studies in marine ecosystems. These include the "predation hypothesis" by Paine (1966), the "stability/time hypothesis" by Sanders (1968), and the "competition synthesis" by Menge and Sutherland (1976) which contribute to the general ecological concept that a decrease in species richness is a result of competitive exclusion.

Benthic organisms are limited by substrate availability. Sessile marine organisms can be classified by substrate-organism interaction due to the inevitable association of both (Thorson, 1957; Rodriguez et al., 1993). Substrate can vary in quality for example, a rock is primary source of space but a biotic substrate such as oyster shell can serve as a secondary space (Barnes and Hughes, 1988). Unlike other resources, substrate space cannot usually be renewed suggesting it may be the most important factor in the settlement and recruitment of new individuals. Substrate can be limiting both physically as well as biologically. Physical limits include lack of area for attachment. Biological limits may be attributed to the reduction of light from other organisms or by chemical inhibition. Sessile invertebrates are also limited by their constraint to the immediate location of settlement which suggests wide tolerances to ranges of physical and biological factors.

Larval Recruitment

Availability of suitable substrate determines the occurrence of settlement in invertebrate larvae (Connell, 1985; O'Connor, 1993; Stoner, 1994). Studies of recruitment need to account for the fact that most marine invertebrates have the capability of dispersion by incorporation of larvae into the plankton. Larval settlement is critical to the recruitment

of sessile invertebrates in a habitat. The location of larval settlement determines where the adult will be present if conditions are favorable (O'Connor, 1993). Other factors such as growth, reproductive rates, mortality, and variation in different larval settlement rates combined can also contribute to seasonal diversity in benthic communities. Species life history characteristics play an important role in larval survivorship and distribution (Stoner, 1992). Larval dispersal patterns can be either an active or a passive process. This variation in the mode of dispersal can also attribute to the variation in settlement and resulting community structure.

Larval recruitment to a live bottom invertebrate community at Beaufort, North Carolina, was found to vary seasonally (Sutherland and Karlson, 1977). Generally, recruitment was low during winter months (December through March). Sponge recruitment had no seasonal pattern and seemed to occur randomly throughout the year. The hydroid, *Tubularia sp.*, recruited in Winter and early Spring when waters where cooler. The hydroid, *Pennaria sp.*, settled in the summer but not in extremely warm waters. Hydroids, *Bugula sp.* and *Schizoporella sp.*, generally settled throughout the year with a mild reduction in extreme winter conditions (Sutherland and Karlson, 1977). Solitary tunicates, *Styela sp.* and *Ascidia sp.*, recruited in late Spring and Fall, while the colonial tunicate, *Botryllus sp.*, did not follow an observable pattern.

Comparison between larval recruitment and subsequent community settlement and growth is hard to predict since no clear distinguishable pattern in benthic community structures has been observed (Menge, 1976; Sutherland and Karlson, 1977; Keough, 1983). Studies have shown no significant difference in recruitment patterns over repetitive samples and over time, thus suggesting that the larval recruitment into favorable ground is random and not directional (Sutherland and Karlson, 1977; Menge, 1991). Schmidt (1982) notes that larval settlement is not influenced by the presence of reciprocal juvenile species but by the larvae present. The recruitment into the rocky shores is limited by space,

predation, competition, and structure composition. These common limiting factors affect all organisms, yet sessile invertebrate abundance is variable and expresses no repeatable or predictable pattern. Sessile invertebrate variability is believed by many to be caused by randomness in larval recruitment that dictates the amount of settlement to rocky shores (Menge, 1991). In a subtidal community study, Keough (1983) observed high recruitment at one site and a very low recruitment in adjacent sites. Keough's study indicated that recruitment and settlement was not only variable yearly, but also over sample replicates.

Community Structure

There are two major views on live bottom community development: one expressing randomness of larval recruitment (Menge, 1976; Osman, 1977; Menge and Sutherland, 1987; Rodriguez et al., 1993), and the other on community structure reaching a point of equilibrium and expressing some successional pattern (Osman, 1977; Keough, 1983; Gilligan, 1985; Butler, 1986).

The benthic marine communities observed by Sutherland and Karlson (1977) do not follow a predictable successional pattern. Factors such as predation and interspecific competition are not recognized as influencing the successional pattern in benthic communities (Menge, 1976; Sutherland and Karlson, 1977). Community structure is variable initially in a barren substrate due to different larval densities (Sutherland and Karlson, 1977; Sutherland, 1978). Species however, do interact with one another, inhibiting or promoting colonization of other organisms. The hydroid, *Hydractinia sp.*, was found to survive the nearby settlement of other species. *Hydractinia sp.* was not found when the sponges, *Haliclona sp.* and *Halichondria sp.*, and ascidian, *Botryllus sp.*, were present. The bryozoan, *Schizoporella sp.*, inhibited other species to settle, but were not found among sponges, *Haliclona sp.* and *Halichondria sp.*, and ascidian *Botryllus sp.* Solitary tunicates, *Styela sp.*, were able to recruit in areas were there where previous

colonizers except for the hydroid *Hydractinia sp.* Thus mostly bryozoan, tunicate, and hydroid populations were tolerant to new recruits but varied within plate samples. Recruitment of invertebrates occurred twice a year in the Fall and Spring. Epifauna mortality allowed free substratum from 20-60% to be colonized through subsequent larval settlers. The addition of new organisms by continuous larval recruitment and continuous mortality of previously settled organisms emphasize the constant changes inherent to benthic communities. No repeatable pattern in the colonization plates was observed over a three year period (Sutherland and Karlson, 1977).

Other studies of benthic communities have shown a definite pattern of a climax community structure after initial settlement (Dayton, 1971; Osman, 1977; Keough, 1983; Butler, 1986). Competition for limited space produced predictable benthic community structure. Keough's (1983) study of a subtidal community demonstrated a spatial pattern of recruitment with the tunicates, *Didemnum sp.* and *Botryllus leachii.* The serpulids showed seasonal peaks throughout the year (Keough, 1983). Osman (1977) also demonstrated patterns of distribution in a marine epifaunal community living on rocks. Species composition was shown to be a direct result of larval abundance and that differentiation of the benthic community structure was related to substratum type. Community development was relative to the organism's substrate preference and to the associated larval abundance that varied seasonally (Osman, 1977; Sutherland and Karlson, 1977; Keough, 1983). The initial community was variable and resulted in one encrusting species dominating the rock. This encrusting benthic species was considered to dominate the climax community and will continue to dominate if not disturbed.

In a study of invertebrate recruitment on an artificial substrate, barnacles were the primary settlers, followed closely by hydroid colonies and serpulid worms. The serpulid worms were consequently grown over by colonial and branching bryozoans. Ascidian

colonies were observed to grow closely with the bryozoans but not above previous settled organisms (Gilligan, 1985).

Substrate Preference

Substrate structure plays an important role in the recruitment process since it provides the habitat for the sessile invertebrates to colonize. Previous colonizers influence the ability of other sessile invertebrates to colonize positively or negatively depending on the species (Dayton, 1971; Sutherland, 1974; Menge, 1976; Menge and Sutherland, 1976; Osman, 1977; Sutherland and Karlson, 1977; Lubchenco and Menge, 1978). For instance, dead barnacles can provide structure for other invertebrates to settle upon. Hydroids enhance the settlement of tunicates, and hydroid-tunicate assemblages enhance settlement of mussels. Barnacles and serpulid tube worms settle mostly on bare structures and are inhibited by the presence of other species (Dean, 1981). Dayton (1971) and Dean (1977) suggest that these interactions are seen in most benthic communities and are due to structural complexity influencing recruitment. Sessile organisms can also influence the colonization or presence/absence of motile invertebrates. Hydroids are thought to provide habitat for caprellid amphipods (Keith, 1971, Caine, 1979) and other relationships between marine motile and sessile species are still undetermined.

Carleton (1987) observed that an increase in species abundance is proportional to substrate irregularity. Greater species richness would therefore be related to the increased complexity of available substrates (Dayton, 1971; Dean, 1981). Sessile organisms can also influence the colonization or presence/absence of motile invertebrates. The structure produced by the first colonizers such as dead barnacles, tunicates, and hydroids, are essential for subsequent settlers by making the substrate suitable for other organisms, such as mussels and tunicates, to colonize successfully (Dean, 1981).

Conclusion

Benthic invertebrate communities are an important element in live bottom ecosystems, yet community development and organization remain largely unknown. Studies of marine benthic communities are important to gain knowledge on the ecological processes that affect live-bottoms and the associated fish community. The proposed research will be guided by the working hypothesis that "live-bottom" recruitment is sporadically seeded by the local community. The focus of this study will be on the newly recruited sessile organisms, which are the "foundation species" providing structure for other organisms, and how community succession progresses throughout time.

MATERIALS AND METHODS

Study Site Description

Gray's Reef National Marine Sanctuary (GRNMS) is a live-bottom reef located 34.2 km east of Sapelo Island, GA (Figure 1). The coordinates that mark the corners of the sanctuary are $31^0 21.45$N, $80^0 55.17$W; $31^0 25.15$N, $80^0 55.17$W; $31^0 25.15$N, $80^0 49.42$W; and $31^0 21.45$N, $80^0 49.42$W. GRNMS encompasses 42.9 km^2 of inner continental shelf hard-bottom, at depths of 18-20 m. Although located on the inner shelf, it has similar dense invertebrate communities as those of deeper live-bottom reefs found farther from shore along the southeastern United States (SCWMRD, 1982). In 1981, GRNMS was identified as the largest known nearshore live-bottom reef in the South Atlantic Bight (SCWMRD, 1982). The study site is centrally located within the sanctuary in an area of moderate ledge relief. The study site includes ledge, hard-bottom, and sand-bottom habitat (Figure 2).

GRNMS is a complex of limestone ridges and sand filled troughs (Hunt, 1974). The benthic habitats range from sparsely populated areas covered with a thin sand veneer, to densely populated outcrops and ledges of moderate to high relief (Table 1). There is approximately 58% of hard-bottom habitat, 24% of ledges with abundant epifauna, and 18% of sparsely populated sand-bottom habitat (Parker et al., 1983). Dredge and trawl collections indicate that dominant invertebrate fauna throughout the year are (in descending order of abundance): Porifera, Bryozoa, Cnidaria, Decapoda, Mollusca, Tunicata, Echinodermata, and Ciriipedia (SCWMRD, 1982). Within the various phyla,

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the number of species and percent cover vary little throughout the year (SCWMRD, 1982).

Greater relief and less sand veneer contribute to greater species richness (Hunt, 1974).

Moderate epifaunal densities are found on hard-bottom of <2.0 m relief and high epifaunal

densities are found on outcrops > 2.0 m (Henry, 1985). GRNMS surface water

temperatures range from winter lows of 12^0 C to summer highs of 29^0 C. Fall and Spring

temperatures range from 25^0 C to 29^0 C (Hunt, 1974). Bottom temperatures exhibit similar

extremes with winter lows of 16^0 C to summer highs of 26^0 C (Hunt, 1974). GRNMS is

affected by tidal cycles. The tidal currents are synchronized to the monthly semi-diurnal

tidal cycles at a 12.5 hour interval (Han et al., 1987). Salinity levels at GRNMS are

usually high ($\approx$36 ppt) in the summer and fall, and drop in the winter and spring ($\approx$34 ppt)

(SCWMRD, 1982). These fluxes have been correlated to offshore transport of low salinity

waters during high levels of riverine fresh water runoff. Turbidity levels vary widely in

response to oceanographic conditions. Secchi depths range from 6 m to 13 m with slight

seasonal variations (SCWMRD, 1982). Bottom visibility ranges from less then 1.5 m to

more than 13.5 m (Hunt, 1974).

Sediments of GRNMS are formed of carbonate and silicate sand that covers

approximately 50% of the sanctuary (Hunt, 1974). The process of sediment transport has

not been thoroughly studied at GRNMS. The limited knowledge of sediment transport was

obtained by hydrographic and diver observations. Ripple marks generated by bottom

currents up to 0.35 m have been observed on the surface of the sand (Hunt, 1974).

Geophysical surveys have also identified sand waves and sand ripples in the northwest and

southwest corners of the sanctuary (Henry, 1985). These ripples indicate the probability of

large movements of sediment throughout the sanctuary.

Preliminary Study

An earlier study conducted at GRNMS on live-bottom colonization in 1995, was hindered by sediment loads burying the rocks and killing the colonized biota. This study was located in the northwest corner of the sanctuary which has a substrate of loose sand sediments. Rocks were both loosely placed and grouped inside wire mesh baskets Three months after deployment, in September 1995, the rocks were still exposed with no visible physical disturbance. Epifauna had begun to colonize and were composed largely of bryozoans, tubularia, hydroids, and anemones. In April 1996, the loose and grouped rocks were partially covered by sediment that was evidently transported during winter storm events. Many of the loose rocks could not be located due to complete sand inundation. Due to these observations a modification of the experimental design was necessary to mitigate the effects of sediment transport if the experiment was to remain *in situ* during winter months.

Experimental Substrate

Limestone rocks were collected from a rock quarry in Wilmington, North Carolina. These rocks were chosen for their similarity to the natural hard-bottom found in GRNMS. The rocks were mostly limestone, embedded with fragmented calcareous fossil material, primarily molluscan. GRNMS hard-bottom is of a very similar calcareous sandstone and limestone with embedded fossilized organisms (Harding and Henry, 1994). The rocks ranged in size from 600 to 1200 cm^2 of surface area, with an average mass of 9.3 kg.

Using rocks as colonizing substrates imposed sampling problems. The rocks had to be deployed and recovered by SCUBA divers and were heavy and awkward to handle underwater. Moving the rocks during deployment and recovery was very strenuous due to the weight of the rocks and strong currents found at GRNMS. Replicates of treatment

types were kept to the minimum due to the difficult sampling effort. Although effort intensive, we felt that use of rocks was essential to closely mimic the natural reef for a colonization study of this type.

Limestone rocks were either loosely placed above the substrate or placed on PVC platforms. The study was divided into two experiments comparing: (1) individual rocks placed on the sand-bottom and live-bottom habitat to test the effect of the surrounding substrata in species composition, and (2) rocks on platforms with and without a wire mesh cover, to test the effect of predation by larger predators in species composition.

Effect of Surrounding Substrate

Loose rocks were placed both on live-bottom habitat of moderate relief (2 m) and on nearby sand-bottom (Figure 2). The sand-bottom habitat was not composed of loose sand, as described in the pilot study. It was a low relief (<0.5 m) hard-bottom area with a sand veneer cover of approximately 3 cm. The rocks were loosely placed to simulate newly uncovered hard-bottom habitat in the midst of a barren sand-bottom and newly uncovered rock on live-bottom. The rocks where placed approximately 0.3 m apart in a row of three in the sand-bottom and row of six in the hard-bottom (Figure 2). Twelve rocks were placed in sand-bottom and hard-bottom habitats. Three rocks from the sand and hard-bottom habitat were collected during each of three sample periods.

Effect of Predation

Covered and uncovered treatments were developed to contrast predator affected rocks versus covered rocks. Treatments compared were (1) raised rocks enclosed by wire mesh to exclude predation, and (2) raised rocks not excluding predation (Figure 3). The enclosed treatment (covered rocks) was created to prevent fish and invertebrate predators

from interacting with the colonizing epifauna, so the effects of predation on community development and growth of live-bottoms could be measured. Rocks were placed on top of PVC pipe platforms above a 5 cm nylon mesh (Figure 3). Six platforms (1.6 m x 1.4 m x 0.8 m) were used for the predation effect test. Twelve randomly selected rocks were placed on each stand (Figure 3). Three of the stands were covered by a $1cm^2$ wire mesh to prevent access to larger predators (Figure 4).

Rock Deployment and Collection

The study was initiated 18 June 1996, when rocks and the platforms and rocks where deployed. Rocks were placed inside mesh bags for deployment and released down a buoy line marking the study area. The platforms were individually carried by a diver to the desired location. Divers placed the rocks on the platforms and on the sand-bottom and live-bottom area (Figure 2). Efforts were made to leave the natural habitat undisturbed. After the rocks were placed in specified locations, the wire mesh covers of the three predator exclusion PVC stands were secured by tie wrapping all sides. A total of eight dives with groups of two divers was necessary for the deployment and set up of the experiments.

Sampling occurred every four months, which covered the range of seasonal temperature changes found at GRNMS. Samples were collected between Fall-Winter (October 1996), Winter-Spring (March 1997) and Spring-Summer (June 1997). Sampling surface temperatures were 21^0, 18^0, 24^0 Celsius, respectively.

During each sample period, three rocks were collected from both sand-bottom and live-bottom habitat for the surrounding substrate effect test, and three randomly selected rocks from each platform were collected for the predation effect test (Figure 4). Bare rocks, from the same rock quarry as the colonizing rocks and of the same dimensions, were used to replace the collected rocks in each platform. Rocks were replaced to maintain

the same physical configuration and orientation of the colonizing rocks to reduce

disturbance from sampling inside the grouped treatment. During each sampling cycle, the

mesh covers of the three covered platforms were carefully cleared of any benthic organisms

by divers using dive knives. The benthic organisms attached to the wire mesh cover could

affect light penetration and water movement.

During the second collection we discovered that one of the uncovered platforms

was missing. The colonizing rocks that originally were placed on the platform were located

on top of the ledge, suggesting the it was dragged by a boat anchor or fishing gear. The

first sample in October 1996 consisted of a total of 24 rocks. Due to the missing platform,

only 21 rocks were collected in March 1997 and June 1997.

Rocks were recovered by SCUBA divers to allow careful handling and control of

the rocks. This also prevented any possible damage to the colonized rock as well as to the

natural occurring live-bottom. The rocks were placed inside large labeled mesh bags

together by treatment type, and brought to the surface with an underwater 50 kg lift bag.

Once on the surface, the rocks were placed into labeled large plastic containers.

The containers were immediately filled with ocean water. Continuous water changes

during transport to land were made to prevent anaerobic conditions. Some rocks were kept

in ocean water for immediate sampling, while others where preserved in 10%

formaldehyde sea water solution. The sea water ($\approx$ 32 ppt) was made in the lab using an

artificial ocean salt mixture. All preserved rocks were analyzed within 60 days of

collection.

All rocks were weighed and surface area measured using a mesh overlay. Each

species was identified at least to family. Percent cover for individual species was obtained

for each rock with use of a $1cm^2$ mesh overlay.

Statistical Analysis

Multivariate analysis of variance, MANOVA, was used to compare substrate effects and predator effects. The MANOVA was chosen since it provided safeguards against the increase in the margin of error caused by multiple univariate tests (Sokal and Rohlf, 1995). These data are a comparison of epifaunal cover of the observed colonizing taxa by treatment and time, to show the effect of surrounding substrate and the effect of predation on species composition. These data were non-normal, both leptokurtic and skewed. An arcsine transformation was used for non-normal percentage and proportion data (Sokal and Rohlf, 1995). Some data remained non-normal regardless of the arcsine transformation. However, the MANOVA test was considered to be robust against some departures from normality (Sokal and Rohlf, 1995). The hypothesis tested was that species percent cover was not influenced by treatment and time variables. The species encountered were lumped into taxonomic groups for analysis. The taxa were algae, colonial ascidian, solitary ascidian, barnacle, bryozoa, hydroid, mollusk, polycheate, and porifera. The Pillai's Trace test was used for the MANOVA. The Pillai's Trace test was chosen because it is a preferred test with higher statistical power (SAS Institute, 1995). Individual taxon analysis by time and treatment were made using the Wilcoxon's test (Sokal and Rohlf, 1995). A two-way analysis of variance (ANOVA) was used to compare the most dominant species, *Schizoporella cornuta*, between covered and uncovered rocks, and loose rocks on the sand and live-bottom habitat. Qualitative comparisons of mean percent cover for all treatment types were made to determine differences in colonizing species. All data were analyzed with JMP® Statistical Discovery Software version 3.1 (SAS Institute, 1995).

RESULTS

Colonizing Species

Qualitatively, species composition on quarried rocks both in the surrounding substrate test and predator exclusion test, resembled the species composition of natural occurring live-bottom. Community organization appeared to have established a hierarchical order in species percent cover by four months of deployment. General species composition of the rocks were in decreasing order of coverage; bryozoans, porifera, algae, colonial ascidian, hydroids, mollusks, barnacles, solitary ascidians, and polycheates. This general pattern, with varying densities, was found throughout all sample periods and treatment types.

The most dominant species in percent coverage throughout all sample periods was the red encrusting bryozoan, *Schizoporella cornuta*. *Schizoporella cornuta* was present on all rocks sampled. *Mycale americana, Bugula turrita, Ascidia interrupta, Didemnum duplicatum, Chthamalus fragilis, Filograna implexa,* and *Chama macerophylla* were encountered in 4-month, 8-month, and 12-month samples (Table 2). *Aplysillia longispina* was encountered only in the 4-month and 8-month sample. *Plakortis angulospiculatus, Aplidium constellatum, Eudistoma hepacticum,* and *Styela plicata* were present in the 8-month and 12-month sample and none were observed in the 4-month sample (Table 2). *Clavelina* sp. was found in the 4-month sample and then only in the 12-month sample (Table 2). Two anthozoans encountered during the study were unique to the 8-month sample (Table 2). *Astrangia danae* was found only in the hard-bottom treatment and the

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Leptogorgia virgulata was found only in the sand-bottom treatment. No anthozoans were found in the grouped treatments. *Pteria colymbus* was found only in the 12 month sample. *Pteria colymbus* was dominant on the mesh covers of the covered raised treatment. They encrusted approximately 70% of the inside and outside of the mesh covers, but were not counted as part of the samples if not directly attached to the rock surface.

Effect of Surrounding Substrate

There was a significant difference in the percent cover of the nine taxa over the three collecting periods (MANOVA, p>0.004, 14, 18 d.f., approximate F = 4.28). The species percent cover was greater in the first sample period in the surrounding sand-bottom substrate and greater in the last sample in the surrounding hard-bottom substrate. Colonization was faster initially in the sand-bottom substrate, but higher in the hard-bottom substrate by the last sample (MANOVA, p<0.0001, 6, 9 d.f., exact F = 56.39). The overall difference between surrounding habitat effect was a higher localized recruitment on rocks placed directly above the hard-bottom. The rocks closely associated with the live-bottom in the had a higher percent cover (Figure 6).

Individual taxon analysis using the Wilcoxon's test, showed a significant difference in percent cover by treatment in the bryozoan and poriferan taxa (Table 3). The bryozoan percent cover was significantly higher in the live-bottom habitat than the sand-bottom habitat (p=0.05, chi-square = 5.89, 1 d.f.). The bryozoan covered 21.5% of the colonized surface area in the hard-bottom versus 18.73% in the sand-bottom habitat (Table 6). *Schizoporella cornuta* was the most prominent species, representing over 90% of the bryozoan taxon group. *Bugula turrita* represented less then 10% of the bryozoan taxon, and less than 1% was unidentified. The bryozoan percent cover did not differ significantly over time (p= 0.078, chi-square = 5.09, 2 d.f.). Although not statistically significant, the

percent cover for the bryozoans in the hard-bottom habitat was higher in the 8-month and 12-month sample than the first 4-month sample (Figure 6). The bryozoans in the sand-bottom habitat instead had a higher percent cover in the 8 month sample period then the 4-month and 12-month sample (Figure 6).

The poriferan percent cover varied significantly between the first two sample periods for both treatments, with a higher percent cover in the hard-bottom ($p < 0.01$, chi-square = 6.81, 1 d.f.) In June 1997, the poriferan *Mycale americana*, was 90% of the porifera taxon group. *Mycale americana* had similar coverage in both sand and hard-bottom habitats (Figure 6). Differences in the porifera cover might be correlated to seasonal variations associated with sediment transport, growth rates, and substrate selectivity. *Mycale americana* was often observed growing over *Schizoporella cornuta*. There was no significant difference in percent cover over time ($p = 0.42$, Chi-square = 1.74, 2 d.f.), but a steady increase in the densities of poriferans was detected.

Differences in algal percent cover over different sample periods was significant ($p = 0.001$, chi-square = 16.13, 2 d.f.). The algae percent cover was almost three times higher after 4-months than after 8-months and 12-months. There was no significant difference between treatment types for the algae coverage ($p = 0.87$, chi-square = 0.025, 1 d.f.).

Rocks on the hard-bottom habitat had higher percent cover of *Schizoporella cornuta* than the rocks on the sand-bottom habitat (2-way ANOVA, $p > 0.002$, F= 14.39, 1 d.f.). The percent cover of *Schizoporella cornuta* also differed throughout the three sampling periods (2-way ANOVA, $p > 0.004$, F= 8.43, 2 d.f.). The sand-bottom initially had a higher percent cover, but the rocks placed on hard-bottom habitats had a higher species density by the last sample (2-way ANOVA, $p > 0.0007$, F= 10.41, 3 d.f.). The

Schizoporella cornuta covered approximately 22% of rocks in the hard-bottom surroundings and 19% in the sand-bottom surroundings (Table 6).

Effect of Predation

The coverages on rocks exposed versus those enclosed by were significantly different by treatment and time (MANOVA, $p<0.0001$; 27, 114 d.f., approximate F $=6.17$). Number of species was higher in the covered treatments avoiding large predators, but the species percent cover was high in the uncovered treatments (MANOVA, $p<0.001$; 9, 36 d.f., exact F $= 4.66$). There was also a significant increase in percent cover by time (MANOVA, $p<0.0001$; 18, 74 d.f., approximate F $= 6.99$).

Individual taxon analysis showed a significant difference in percent cover by treatment for the bryozoans, poriferans, barnacles, and colonial ascidians (Table 4). Bryozoans and poriferans were the most common species encountered in the covered and uncovered treatments (Figure 7). Bryozoans had the highest species percent cover and differed significantly by treatment (Wilcoxon , $p<0.01$, chi-square $=5.47$, 1 d.f.). Bryozoans exhibited a significant gradual growth between sample periods for both the uncovered and covered treatments (Wilcoxon, $p=<0.002$, chi-square $= 12.28$, 1 d.f.). The most dominant bryozoan was *Schizoporella cornuta*, the red encrusting bryozoan. The least dominant bryozoan was the spiral tufted bryozoan, *Bugula turrita* . The highest percent cover of bryozoan was observed in June 1997 with the least cover in October 1996 (Figure 7).

Poriferan percent cover was higher in the uncovered treatment versus the covered treatment (Wilcoxon, $p= 0.01$, Chi-square $= 6.85$, 1 d.f). There was no significant difference in the poriferan percent cover over time (Wilcoxon, $p= 0.15$, chi-square $= 3.76$, 2 d.f.). Like the poriferans, the barnacle percent cover was higher in the uncovered

treatment (Wilcoxon, p=0.02, chi-square = 5.47, 1 d.f.). There was no significant difference in barnacle coverage over time (Wilcoxon, p=0.853, chi-square = 0.85, 2 d.f.). The colonial ascidian percent cover was higher in the covered treatment versus the uncovered treatment (Wilcoxon, p=0.035, chi-square = 4.46, 1 d.f.). The percent cover of the bryozoans, poriferans, and barnacles, was always higher in the uncovered treatment than the covered treatment (Figure 7).

There was no significant difference in the colonization of algae, solitary ascidians, hydroids, mollusks, and polycheates by treatment (Table 4). A significant difference over time was observed in the algae, solitary ascidians, bryozoans, and hydroids (Table 4). The percent algal cover for both the covered and uncovered treatments was four times higher in the 4-month sample then the 8-month and 12-month samples (Wilcoxon, p=0.0001, chi-square = 36.6, 2 d.f.). The solitary ascidian, and hydroid cover increased steadily over the sample periods (Table 4). The algae, solitary ascidians, bryozoans, and hydroids were growing significantly after attachment or differed by larval recruitment throughout the three sample periods. No significant difference over time was found in mollusks, polycheates, and poriferans.

Ascidian percent cover increased in the third sample period (Figure 7). The solitary ascidians percent cover *Styela plicata*, *Mogula manhattensis*, and *Ascidia* sp. increased significantly by time (Wilcoxon, p=0.015, chi-square = 8.441, 2 d.f.). The colonial ascidians percent cover also increased throughout time although not statistically significant (Wilcoxon, p=0.1630, chi-square = 3.6284, 2 d.f.).

The poriferans percent cover increased by the third sample period, although not statistically significant (Figure 4). *Mycale americana* was observed growing over the *Schizoporella cornuta*. Other poriferans such as *Cliona sp.*, *Aplysillia longispina*, and *Plakortis angulospiculatus*, had higher percent cover in the uncovered raised treatment.

Haliclona oculata was observed only in the covered raised treatment. Increase of the

solitary ascidians, *Styela plicata, Mogula manhattensis,* and *Ascidia interrupta,* also

occurred in the third sample period (Figure 8). These organisms were commonly attached

to the *Schizoporella cornuta.* Some poriferans were also observed covering *Schizoporella*

cornuta. The most commonly found poriferans throughout all treatments was *Mycale*

americana. *Mycale americana* had a higher percent cover in the uncovered raised

treatment. Similar densities of barnacles and polycheates were found throughout all

treatment and sample periods (Figure 8).

Results of a two-way ANOVA show that the percent cover of *Schizoporella cornuta*

differed significantly by treatment and time interaction (ANOVA, p<0.0001, F= 15.72, 3

d.f.). The uncovered treatment had a higher percent cover then the covered treatment

(ANOVA, p<0.0001, F= 29.07, 1 d.f). The percent cover of the *Schizoporella cornuta*

increased over the sample periods, with the 4-month sample having the least cover and the

12-month sample having the highest percent cover. The *Schizoporella cornuta* covered

approximately 45% of the rock surface area in the covered and uncovered treatments by the

end of 12-months of deployment (Table 6).

Qualitative Comparison Between Loose Rocks and Platform Treatments

There where some obvious visual differences in colonization density and species

composition between treatments (loose rocks in the sand and hard-bottom habitats, and

grouped rocks covered and uncovered). Both main treatments of loose versus grouped

rocks had the same dominant species and similar community organization, but differed in

densities and in the occurrence of rare species (Table 6). Although we cannot compare

these effects with statistical measures due to the experimental design, qualitative

comparisons are useful to show that two types of deployment resulted in different percent

cover for different species. The general trend for all species encountered throughout all sample periods was that loose rocks recruited less species with less density than the grouped rocks.

The total mean percent cover for all sample periods were 87.5% for the covered treatment, 88.0% for the uncovered treatment, 39.0% for the hard-bottom habitat, and 31.8% for the sand-bottom habitat (Table 6). Although all treatments increased in percent cover over time, the platform rocks epifaunal cover was almost three times the epifaunal cover of loose rocks (Figure 8). The grouped treatments effectively provided more surface area and were less affected by physical variables such as sediment transport. The loose rocks were more susceptible to extrinsic variables and had less surface area for overall recruitment and colonization to occur. It should be emphasized that when I calculated percent cover, the whole surface of the rocks was counted as possible substrate for organisms to colonize. The raised grouped rocks were placed on a mesh cover, thus probably allowed more recruitment of organisms on the underside than the rocks placed directly on the bottom. The underside of rocks that were loosely placed did have attached organisms but were less densely colonized.

The bryozoan *Schizoporella cornuta*, steadily increased in percent cover over time except on the sand-bottom treatment (Figure 8). The densities of *Schizoporella cornuta* in the sand-bottom decreased in the third sample period (Figure 8). The uncovered raised treatment rocks had the highest mean percent cover of the *Schizoporella cornuta*, 46.8%, and the sand-bottom had the fewest, 18.7 % (Table 6). The bryozoan, *Bugula turrita*, had the least percent cover (1.5%) in the uncovered treatment (Table 6).

The uncovered raised treatment had the highest mean percent cover for the bryozoan *Schizoporella cornuta*, the poriferan *Mycale americana* , the solitary ascidians *Styela plicata* and *Mogula manhattensis*, the colonial ascidians *Aplidium constellatum* and *Eudistoma*

hepacticum, and the hydroid *Pennaria tiarella* (Table 6). The covered raised treatment had the highest mean percent cover for the poriferans *Cliona sp.* and *Aplysillia longispina*, the colonial tunicate *Botryllus planus*, and the algae *Cladophora sp.* and Phaeophyta (Table 6). The hard-bottom habitat had the highest mean percent cover for the spiral tufted bryozoan *Bugula turrita*, and the mollusk *Pteria colymbus* and *Chama macerophylla* (Table 6). The sand-bottom habitat did not exceed in mean percent cover for any species encountered throughout the 12 month study compared to the other treatments, except for the rare occurrence of the anthozoan *Leptogorgia virgulata* that was present in one rock in the 8 month sample.

Increase in densities in the sand-bottom treatment of colonial ascidian, *Aplidium constellatum*, was observed in the 12-month sample (Figure 8). An association with the decrease in the *Schizoporella cornuta* might indicate exclusion competition. The *Aplidium constellatim* was noted growing over the *Schizoporella cornuta*. (Figure 8).

Descriptive Appearance of the Colonizing Rocks

The colonizing rocks were extremely colorful and attractive after only four months of deployment. The densities or the epifaunal organisms increased over time, and became even more attractive after 12 months of deployment. The variety of the color on the rocks ranged from bright red and orange (*Schizoporella cornutta, Mycale americana*, and the *Cliona sp.*), to different shades of whites and purples (*Aplidium constellatum, Didemnum duplicatum*, and *Eudistoma hepacticum*). The visually appealing purple and yellow royal tunicate, *Botryllus planus*, were only found in the 4-month sample in October 1996. The hydroid *Pennaria tiarella* was larger and denser after 12 months of deployment. After 12 months deployment, larger solitary ascidians such as the *Mogula manhattensis* and the *Styela plicata* increased in density on the colonizing the rocks.

DISCUSSION

The colonization of invertebrates on the rocks exhibited similar characteristics to the sessile live-bottom community, except for the occurrence of large sponges and corals that are commonly found on live-bottom reefs (Henry and Van Sant, 1982). One would not expect presence of these species in this study since they are very slow growing and are known to be slow colonizers (SCWMRD, 1984; Wendt et al., 1989). Species composition became more complex over time, but in general, the first colonizing species predominated throughout all the sampling periods. The most common species encountered was the red encrusting bryozoan, *Schizoporella cornuta*. Common species by percent cover included the spiral tufted bryozoan (*Bugula turrita*), red encrusting sponge (*Cliona sp.*), sulfur sponge (*Aplysillia longispina*), flabby orange sponge (*Mycale americana*), sea liver tunicate (*Eudistoma hepactimum*), and constellation tunicate (*Aplidium constellatum*). Rare species encountered included the sea whip (*Leptogorgia virgulata*), the star coral (*Astrangia danae*), and the finger sponge (*Haliclona oculata*). All species observed are typically found in GRNMS live-bottom areas (SCWMRD, 1982).

The present study clearly indicates that the type of seeded artificial substrate plays an important role in benthic recruitment. Results show similarities between species composition on natural live-bottom reefs and the quarried rocks. Our study demonstrates superiority of a quarried rock to artificial made substrates used in previous studies. One study on live-bottom colonization used Plexiglas and textured Formica plates as the colonizing substrate (SCWMRD, 1984). After 9 months of recruitment, barnacles and

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algae dominated the colonizing plates (SCWMRD, 1984). After one year of recruitment the colonizing rocks were composed mainly of barnacles and colonial hydroids on sand-bottom areas, and colonial ascidians and hydroids on hard-bottom areas (SCWMRD, 1984). Another study conducted on the colonization of invertebrates on a concrete surface also resulted in barnacle dominance (Gilligan, 1985). Barnacles dominated most of the substrate with a few other organisms (bryozoans, sponges and hydroids) growing over the barnacles after 5 months of deployment (Gilligan, 1985). These previous studies do not replicate the community composition found in the natural bottom but favored barnacle colonies. In our study, barnacles covered less then 1% of the rock surface throughout all three sample periods (Table 6). Dominance of barnacles and hydroids in previous studies indicate differences in substrate preference by benthic invertebrates. Barnacles and serpulid tube worms settle mostly on bare smooth structures and are inhibited by the presence of other species (Dayton, 1971; Dean, 1981). The main difference in the present study was using a substrate similar to the natural bottom. Colonizing substrate is shown to be a key factor in recruitment studies and should be looked at closely when similar studies are designed. Similarities in species composition to the natural habitat allow inferences to be made of biotic processes on the natural live-bottom, such as recovery rates and growth assessments.

The primary colonizers observed in this study were bryozoans, followed by hydroids, porifera, and colonial ascidians (Figure 6). Sessile community organization is dependent on the substrate type and on the previous colonized biota (Dayton, 1971; Osman, 1977; Sutherland and Karlson, 1977, Dean, 1981). Since the quarried rocks contained embedded fossilized shells, it provided a suitable substrate for colonization without a preliminary barnacle-hydroid community. It has been known that dead barnacles provide an acceptable physiochemical habitat for other invertebrates to settle

upon (Dean, 1981). Hydroids enhance the settlement of ascidians, and ascidian-hydroid assemblages enhance the settlement of mussels (Dean, 1981). Colonial invertebrates outcompete solitary species, therefore dominating the hard substratum in live-bottom habitats (Jackson, 1977). Hydroids and bryozoans also provide refuge for ascidians and sponges from predation by fish (Sutherland, 1974). These secondary colonizers are therefore, lower in density than the primary colonizers and use the refuge provided by hydroids and bryozoans. The physical structure provided by other sessile organisms was an influencing factor in abundance of both sessile and motile organisms (Dean, 1981). In this study we observed dominance in the bryozoans throughout all samples, with a slight increase in the poriferan and colonial ascidian cover in the 12-month sample (Figure 8). The physical structure created by the bryozoans enabled other organisms to successfully colonize. Solitary tunicates, *Styela sp.* and *Ascidia sp.*, have been observed to recruit in late spring and in the fall, when an increase in density was noted in our study (Young, 1989). Higher species diversity would be encountered following at least a 12 month period where sessile communities would have become well established by a dominant bryozoan cover where other species would settle. Thus the composition of the substrate and physical structure created by colonizing organisms play a very important role in determining the species composition and development of live-bottoms (Osman, 1977).

The encrusting bryozoan, *Schizoporella cornuta*, was the dominant species throughout all sample periods. It has been reported that *Schizoporella sp.* settle throughout the year with only mild reductions in extreme winter waters (Sutherland and Karlson, 1977). Our results indicated constant growth of *Schizoporella cornuta* over time and throughout treatments, except for a small decrease in the density after 12 months in the sand-bottom habitat (Figure 8). Any notable decreases in the dominance of this species might be caused by inter- or intraspecific competition and not related to seasonal

variations in larval distributions. Encrusting bryozoans have been observed to exclude

other species from the space it occupies and becomes the dominant species (Stoner,

1994). Dominance of these species in the colonizing rocks is therefore, not unusual

especially since each rock is a "habitat island" existing as a discrete ecological unit where

colonization and dominance can occur (Osman, 1977). The size and surface area of the

rocks would therefore affect the species dominance. The larger the available area for

recruitment, the less dominance by one species and the higher species diversity is

encountered (Osman, 1977). In our study, there was limited surface area by the rocks

resulting in one species dominating, especially in the individual rocks (Figure 6). The

grouped rocks were dominated by the bryozoans, but had a higher species diversity than

the individual rocks on the sand-bottom and hard-bottom (Figure 7). Grouping the rocks

on platforms created a larger surface area for recruitment compared to the individual

rocks. Once substrate availability became limiting, as seen after 12 months, sponge

overgrowth on the bryozoans was observed. Approximately 20-50% of the previous

colonized bryozoan was covered by *Mycale americana* (Figure 6&7). Overgrowth is

commonly seen in sessile organisms were space is limiting and usually results in the death

of the underlying organism (Jackson, 1979; Osman, 1977; Sutherland and Karlson,

1977).

The differences in percent cover on the rocks placed in different habitats (sand-

bottom versus live-bottom) were probably caused by the amount of disturbance created by

sediment transport. The percent cover of sessile organisms was higher in the rocks

placed directly on the live-bottom than the rocks placed on the sand-bottom. The

difference in colonization and growth associated with the location of the loose rocks was

partially due to the associated bottom relief. Sessile epifaunal communities are influenced

by the topography and amount of sediment present (Hunt, 1974). The rocks on the sand-

bottom most closely represented a low relief, <0.5 m, community (Table 1). These low relief areas are affected by sediment transport that is constantly covering newly colonized areas, thus reducing the density of organisms. As the level of sediment cover increases, epifaunal density decreases (Henry and Van Sant, 1982). The proximity to the natural live-bottom habitat might have also influenced the percent cover established on the rocks. Rocks placed on the live-bottom could have been colonized by cloning of the sessile organisms nearby instead of a planktonic larval distribution. Some ascidians, colonial bryozoan, sponges, and cnidarians have short dispersal ranges due to cloning and brooding (Svane and Young, 1989). Higher species diversity and density would therefore be expected in the rocks placed on the live-bottom community.

Rocks placed on the live-bottom also represented a higher relief bottom than the rocks on the sand-bottom. This moderate relief habitat of approximately 2 m, holds medium to abundant epifauna (Henry and Van Sant, 1982). In the present study, rocks placed on the live-bottom represented a moderate relief habitat (Table 6). Ten percent more epifaunal cover was observed on the live-bottom rocks than on the sand-bottom (Table 6). The difference density might be due to physical disturbance. The higher the bottom relief, the less physical disturbance on the colonizing biota occurs by sediment transport. Sediment transport studies have not been conducted in GRNMS. Studies indicating the fluctuations and amount of sediment transport during different times of the year would be useful in the assessment of live-bottom communities.

The density of the colonizing epifauna was significantly higher in the uncovered platforms than the covered platforms. Preventing large predators from grazing on the rocks had a negative effect on the density of the epifauna. The mesh not only excluded large predators from grazing on the colonizing epifauna, but predation of fish on other smaller associated fish and motile invertebrates. The covered rocks had a variety of

predators associated with them, such as sea urchins, sea cucumbers, sea stars, brittle stars, arrow crabs, and other mollusks. These predators can affect the density of newly founded bottom communities (Thorson, 1957, Connell, 1964). Predation can reduce the density of species and the competition for space (Dayton, 1984). The mesh cover also served as a refuge for the associated motile invertebrates that were feeding on the colonizing epifauna on the rocks. Thus, instead of decreasing predation on the covered rocks, it probably increased the concentration of smaller invertebrates and subsequently net predation was higher.

The mesh covers became highly encrusted between sample periods. Although divers attempted to clear the covers between samples, encrusting organisms on the cover affected the colonization of invertebrates on the rocks below. The encrusted mesh could have reduced current flow inside the covered platform, and therefore reduced overall larval recruitment. The encrusted mesh also reduced light availability to the rocks, selecting against photosynthetic organisms. Some larvae have been found to settle on a substrate that has a favorable light environment for growth and reproduction (Stoner, 1994). The most common species encountered above the mesh covers were solitary ascidians, winged oysters, barnacles, and sparse bryozoans.

Algal cover, throughout all samples, was much higher in October than in the March and June samples. Concentration of algae was influenced by extrinsic factors rather then by the underlying substrate type. Factors affecting algal concentration were probably seasonal variations in temperature and light availability, and competition for space.

Higher percent coverages for the bryozoan, porifera, and barnacle taxa were observed for the uncovered treatment (Figure 7). Conversely, colonial ascidian taxa coverage was higher in the covered treatment (Figure 7). The covered treatment

prevented predators but also reduced the amount of species cover. Our results indicated that the wire mesh cover not only prevented predators but also prevented some recruitment and growth for certain species. Observed differences indicate that different species vary in the susceptibility to large predators. There was no significant difference in the colonization of algae, solitary ascidians, hydroids, mollusks, and polycheate by treatment indicating that the above taxa are not affected by the mesh cover.

Differences in density of the colonizing community were affected by treatment and time. The highest density of organisms was observed in the uncovered platforms. Mean total percent cover differed slightly between the covered and uncovered platforms; 87.5% and 88.0% respectively (Table 6). Hard-bottom and sand-bottom rocks were significantly lower in percent cover then rocks on the platforms; 39.0% and 31.8% respectively. These differences can be explained by low recruitment rates. Successful recruitment was lower in the loose treatment versus the grouped rocks. Data on the amount of larvae present would be useful in determining if there was a difference in possible larval recruits in the different areas. Previous studies have shown that many colonial marine organisms, such as bryozoans, sponges, and ascidians, have short larval dispersal distances and depend more on brooding or cloning (Svane and Young, 1989). Since there is a daily flux in tidal currents in GRNMS, stratification of larvae in such a small area is not expected. The rate at which larvae successfully recruited could have been dependent on the appropriate substrate (Stoner, 1994). The loose rocks were susceptible to a larger amount of physical disturbance such as sediment cover. The loose rocks were also susceptible to higher predation then the grouped rocks on the platforms. Predators within the grouped treatment had a larger area upon which to graze versus individually placed rocks. Therefore, predation may have had a higher effect on the loose

rocks. This relationship with adjacent areas of lower colonized densities has been explained by high predation and high biotic disturbances (Menge, 1991).

An important interaction between the colonizing species was competition for space. Sessile marine invertebrates are limited in growth and succession by the total available surface area (Connell, 1985; O'Connor, 1993; Stoner, 1994). Fast growing encrusting species, such as the *Schizoporella cornuta*, could outcompete most other species for space resulting in dominance by one species as seen in our study (Osman, 1977). Sessile species compete for space resulting in either interspecific competition for space or coexistence (Menge and Sutherland, 1987). Observation of coexistence was noted between the *Mycale americana*, *Aplidium constellatum*, and the *Schizoporella cornuta*. *Mycale americana* and *Aplidium constellatim* were observed growing over the *Schizoporella cornuta* after 12 months. Another common result of competition between encrusting organisms is overgrowth. Studies have shown that bryozoan zooid deterioration increases the chances on settlement by other organisms and by other fouling larvae (Jackson, 1979). Competition for space and overgrowth would become more influential in community development after the rocks were 100% colonized. In our study, the surface of the rocks was never completely covered, indicating availability of more space for recruitment without intensive competition if nutrient resources are not limited (Table 6). The percent cover of the poriferans was not significantly different over time, but they were noticed to be numerous after 12 months. This might suggest that poriferans are slow growing organisms and need more time to grow.

Both random larval settlement and a predetermined settlement pattern theory could be argued for the results in community development in this study. Random settlement theory might apply in this study since some species were only encountered in one sample, such as *Astrangia danae*, and *Leptogorgia virgulata* A predetermined settlement pattern

theory fits this study since the same dominant organisms were encountered throughout all samples. Results indicate a primary bryozoan colonizer throughout all sample periods followed by steadily increasing secondary colonizers, poriferans and ascidians. After one year the colonizing rocks did not appear to have achieved a climax community. A longer study would help determine whether a stable community is ever reached in live-bottom habitats, or whether constant changes in community structure take place. Seasonal and annual fluctuations in larval supply contribute to variations in community establishment (Connell, 1985; Gaines and Roughgarden, 1985). Higher recruitment of different species, during different seasons, altered the composition of the community, particularly on small surfaces like our limestone rocks (Keough, 1981; Butler, 1986). Osman (1977), attributes 5 main factors influencing benthic community variation: (1) larval selectivity, (2) seasonal fluctuations, (3) biological interactions, (4) size of colonizing surface, and (5) physical disturbance. Further studies differentiating between the amount of larvae present, settlement ratios, and survivorship over a longer time would help determine the type of community establishment present in live-bottom habitat.

This study suggests that culturing of artificial "live rock" is feasible in the SAB. The rocks were approximately 50% covered after only 4 months of deployment. The rocks were colorful and appealing for the hobbyist. Perhaps the most interesting observation made during this effort was the significant difference in community composition of the experimental units used in this study to the manufactured units of previous investigations. My rocks quickly established a population of "target" species coveted for their intricate morphologies and color variations while previous studies were dominated by the more mundane fouling barnacles. These data suggest that substrate type may be a more critical factor in the establishment of live-bottom invertebrate communities than previously thought. Future studies could be easily designed to address this issue.

Some rocks were placed in aquariums for display after the 8-month sample period. The epifaunal organisms seemed to become well established after a few days. The most dominant species, the *Schizoporella cornuta*, was mostly affected by the retrieval procedures. The *Schizoporella cornuta* is very fragile and brittle and was very hard to handle underwater during recovery. It was inevitable that many branches of the *Schizoporella cornuta* were broken off during recovery, which probably affected the overall health of the organism. Ways to preventing damage to *Schizoporella cornuta* might reduce the transplant shock of the organism.

Design of careful handling strategies for rock recovery would likely improve the survivability of some species after removal. This was not an objective of the present study as the majority of samples were immediately preserved in a formaldehyde solution for analysis. The small sub-sample transferred to aquaria maintained varying levels of viability dependent on species. Additional effort would be required to determine the feasibility of maintaining healthy assemblages of sessile invertebrates in aquaria. Light regimes, food types, salinity levels, and filtration systems would need to be manipulated through careful experimental design and subsequent analysis to allow a rational means for supporting feasibility.

LITERATURE CITED

Barnes, R. S. K., Hughes, R. N. (1988) An introduction to marine ecology. Oxford, Blackwell Scientific Publications.

Butler, A. J. (1986) Recruitment of sessile invertebrates at five sites in Gulf St. Vincents South Australia. J Exp Mar Biol Ecol 97:13-36.

Connell, J. H., Slatyer, R. O. (1964) Mechanisms for succession in natural communities and their role in community stability and organization. Am Nat 111: 1119-1144.

Connell, J.H. (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. J Exp mar Biol Ecol 93:11-45.

Cummins, R., Jr., Rivers, J. B., Struhasker, P. (1962) Snapper trawling explorations along the southeastern United States. Commercial Fisheries Review 24:1-7.

Dayton, P. K. (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol Monog 41:351-388.

Dayton, P. K., Ed. (1984) Processes structuring some marine communities: are they general? Ecological communities: conceptual issues and the evidence. Princeton, NJ, Princeton University Press. pp 181-197.

Dean, T. A. (1981) Structural aspects of sessile invertebrates as organizing forces in an estuarine benthic community. J Exp Mar Biol Ecol 53:163-180.

Gaines, S.D., Roughgarden, J. (1985) Larval settlement rate: a leading determinant of structure in ecological communities of marine intertidal zone. Proc Natl Acad Sci USA 82: 3707-3711.

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Gilligan, M. (1985) Colonization and utilization of concrete artificial reef off the Georgia
coast by invertebrates and fishes. Proceedings of the 1985 habitat symposium:
reconstruction growth impacts on coastal N.E. Florida and Georgia, Ed. Demort,
C.L. and White, A.Q., Florida Sea Grant Project Number IR-84-4, pp 231-241.

Han, G.C., Calvert, J.O., Blanton, J.O. (1987) Current velocity measurements at Gray's
Reef National Marine Sanctuary. NOAA Technical Memorandum NOS MEMD 8.
NOAA, OCRM: Washington, DC. pp 32 + appendices (pp 67).

Harding, J.L., Henry, V.J., Jr. (1994) Geological history of Gray's Reef National Marine
Sanctuary: A final report to the National Oceanic Atmospheric Administration,
Marine Estuarine Management Division under cooperative agreement NA-87-AA-
H-CZ033. pp 58.

Henry, V.J., Jr., Giles, R.T. (1979) Distribution and occurrence of reefs and
hardgrounds in the Georgia Bight. A draft final report to U.S. Geological Survey,
Office of Marine Geology, Woods Hole, MA. pp 55.

Henry, V.J., Jr., Van Sant, S.B. (1982) Results of reconnaissance mapping of the Gray's
Reef National Marine Sanctuary. A report prepared for the Georgia Department of
Natural Resources, Coastal Resources Division, Brunswick, GA, under
cooperative agreement with the Sanctuaries Programs division of NOAA. pp 21.

Henry, V.J., Jr. (1983) Ocean bottom survey of the US South Atlantic OCS region: Final
report. US Geological Survey Office of Marine Geology, Woods Hall, MA. Marine
Geology Program, University of Georgia, Athens, GA.

Henry, V.J., Jr. (1985) Final Report: Results of Gray's Reef National Marine Sanctuary
hydrographic and geophysical survey. Unpublished Report submitted to NOAA,
pp 53.

Hunt, J. L., Jr. (1974) The geology and origin of Gray's Reef, Georgia Continental Shelf. MS thesis. University of Georgia, Athens, GA. pp 83.

Jackson, J.B.C. (1979) Overgrowth competition between encrusting Cheilostome Ectoprocts in a Jamaican cryptic reef environment. Jour of Animal Eco. 48: 805-823.

Jackson, J.B.C. (1977) Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. Am Nat 111:743-767.

Keough, M. J. (1983) Patterns of recruitment of sessile invertebrates in two subtidal habitats. Exp Mar Biol Ecol 66:213-245.

Leonard, G. H.,Clark, R. P. (1993) Point quadrat versus video transect estimates of the cover of benthic red algae. Mar Ecol Prog Ser. 101: 203-208.

Lubchenco, J., Menge, B. A. (1978) Community development and persistence in a rocky intertidal zone. Ecological Monographs 59:67-94.

Menge, B. A. (1976) Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecol Monogr 46:355-393.

Menge, B. A. (1991) Relative importance of recruitment and other causes of variation in rocky intertidal community structure. J Exp Mar Biol Ecol 146: 69-100.

Menge, B. A., Sutherland, J.P. (1987) Community regulation: variation in disturbance competition, and predation in relation to environmental stress and recruitment. Am Nat 130: 730-757.

O'Connor, N. J. (1993) Settlement and recruitment of the fiddler crabs *Uca pugnax* and *U. pugilator* in a North Carolina, USA, salt marsh. Mar Ecol Prog Ser 93: 227-234.

Odum, E.P. (1969) The strategy of ecosystem development. Science 164: 262-270.

Osman, R. W. (1977) The establishment and development of a marine epifaunal community. Ecol Monogr 47: 37-63.

Paine, R. T. (1966) Food web complexity and species diversity. Am Nat 100: 65-75.

Parker, R. O. J., Colby, D. R., Willis, T. D. (1983) Estimated amount of reef habitat on a portion of the US South Atlantic and Gulf of Mexico continental shelf. Bull Mar Sci 33: 935-940.

Rodriguez, S., R, Ojeda, F. P., Inestrosa, N. C. (1993) Settlement of benthic marine invertebrates. Mar Ecol Prog Ser 97:193-207.

Roughgarden, J., Gaines, S., Possingham, H. (1988) Recruitment dynamics in complex life cycles. Science 241:1460-1466.

SAS Institute (1996) JMP Start Statistics: A guide to statistics and data analysis using JMP and JMP IN® Software. Duxbury Press, Belmont, CA. pp 521.

Schmidt, G. H. (1982) Random and aggregative settlement in some sessile marine invertebrates. Mar Ecol Prog Ser 9, 97-100.

Schoener, A. (1974) Colonization curves for planar marine islands. Ecology 55: 818-827.

Schoener, A., Greene, C. H. (1980) Comparison between destructive and nondestructive sampling of sessile epibenthic organisms. Limnol Oceanorg 26:770-774.

Smith, R. L. (1990) Ecology and Field Biology, 4th edition. Harper and Rowe, Publishers, New York.

Sokal, R.R., Rohlf, F.J. (1995) Biometry: the principles and practice of statistics in biological research 3rd ed. State University of New York at Stony Brook. W.H. Freeman and Company, New York. pp 887.

South Carolina Wildlife and Marine Resources Department (SCWMRD) (1984) South Atlantic OCS Area Living Marine Resources Study: Phase III-Volume I. Prepared for Minerals Management Service, Washington, DC. pp 223.

South Carolina Wildlife and Marine Resources Department (SCWMRD) (1982) South Atlantic OCS Area Living Marine Resources Study: Year II-Volume I- An investigation of live bottom habitats off South Carolina and Georgia. Prepared for the Minerals Management Service, Washington, DC. pp 190.

Stoner, D. S. (1992) Vertical distribution of a colonial ascidian on a coral reef : the roles of larval dispersal and life-history variation. Am Nat 139:802-824.

Stoner, D. S. (1994) Larvae of a colonial ascidian use a non-contact mode of substratum selection on a coral reef. Mar Biol 121: 319-326.

Struhsaker, P. (1969) Demersal fish resources: composition distribution and commercial potential of the continental shelf stocks off the southeast United States. Fishery Industrial Research. 4(7): 261-287.

Sutherland, J. P. and Karlson, R. H. (1977) Development and stability of the benthic community at Beaufort, North Carolina. Ecol Monogr 47: 425-446.

Sutherland, J. P. (1978) Functional Roles of *Schizoporella* and *Styela* in the benthic community at Beaufort, North Carolina. Ecology 59: 257-264.

Svane, I.B. and Young, C.M. (1989) The ecology of and behaviour of ascidian larvae. Oceanogr. Mar. Biol. Annu. Rev. 27:45-90.

Thorson, G. (1957) Bottom communities (Sublittoral or Shallow Shelf). In "Treatise on Marine Ecology and Paleoecology." (J. W. Hegpeth, Ed.), pp. 461-534 Geological Society of America, New York.

Wendt, P.W., Knott, D.M., Van Dolah, R.F. (1989) Community structures of the sessile biota on five artificial reefs of different ages. Bull Mar Sci 44(3):1106-1122.

Young, C.M.(1990) Larval predation by epifauna on temperate reefs: scale, power and the scarity of measurable effects. Austr Jour of Eco 15:413-426.

Table 1. Morphological classification of hard-bottom reefs in the Georgia Bight (after Henry and Giles, 1979).

Classification	Relief	Live-bottom Community	Location & Distribution
Low-Relief Hard-bottom	<0.5 m	Sparse to moderate occurrence of sessile epibenthos, principally sponges and octocorals.	Widely distributed across the shelf.
Moderate-Relief Hard-bottom	Up to 2 m	Moderate to abundant occurrence of epibenthos, principally sponges, octocorals, and algae.	Generally restricted occurrence, but more common off northeast Florida to the Carolinas in inner and middle shelf locations.
Shelf-Edge Reef	Up to 15 m	Moderate to abundant occurrence of epibenthos, principally sponges, octocorals, hard corals, and algae.	Occur as a discontinuous ridge or ridges at or near the shelf edge.

Table 2. List of species groups resulting from analysis of taxa covering the quaried rocks sumberged for 4, 8, and 12-months. (A=Algae, An= Anthozoa, As= Ascidians, Ba= Barnacles, B= Bryozoans, H= Hydroids, M=Mollusks, P= Polycheate, Po= Porifera)

4 Month Sample		8 Month Sample		12 Month Sample	
Aplysilia longispina	(Po)	Aplysilia longispina	(Po)	Cliona sp.	(Po)
Cliona sp.	(Po)	Cliona sp.	(Po)	Mycale americana	(Po)
Haliclona oculata	(Po)	Mycale americana	(Po)	Plakortis angulospiculatus	(Po)
Mycale americana	(Po)	Plakortis angulospiculatus	(Po)	Bugula turrita	(B)
Bugula turrita	(B)	Bugula turrita	(B)	Schizoporella cornuta	(B)
Schizoporella cornuta	(B)	Schizoporella cornuta	(B)	Ascidia interrupta	(As)
Ascidia interrupta	(As)	Ascidia interrupta	(As)	Aplidium constellatum	(As)
Botryllus planus	(As)	Aplidium constellatum	(As)	Clavelina sp.	(As)
Clavelina sp.	(As)	Didemnum duplicatum	(As)	Didemnum duplicatum	(As)
Didemnum duplicatum	(As)	Eudistoma hepaticum	(As)	Eudistoma hepaticum	(As)
Chthamalus fragilis	(Ba)	Styela plicata	(As)	Mogula manhattensis	(As)
Filograna implexa	(P)	Pennaria tiarella	(H)	Styela plicata	(As)
Chama macerophylla	(M)	Astrangia danae	(An)	Pennaria tiarella	(H)
Cladophora sp.	(A)	Leptogorgia virgulata	(An)	Chthamalus fragilis	(Ba)
Phaeophyta	(A)	Chthamalus fragilis	(Ba)	Filograna implexa	(P)
Green Algae	(A)	Filograna implexa	(P)	Chama macerophylla	(M)
		Chama macerophylla	(M)	Pteria colymbus	(M)
		Phaeophyta	(A)	Cladophora sp.	(A)
		Green Algae	(A)	Phaeophyta	(A)

Table 3. Comparison of percent cover of the taxonomic groups present by time, and sand-bottom and hard-bottom habitat. Wilcoxon's test.
*= not significant

Taxonomic Group	Treatment Sand vs. hard-bottom	Time
Algae	*	p<0.001
Colonial Ascidian	*	*
Solitary Ascidian	*	*
Barnacle	*	*
Bryozoa	p=0.05	*
Hydroid	*	*
Mollusks	*	*
Polycheate	*	*
Porifera	p<0.01	*

Table 4. Comparison of percent cover of the taxonomic groups present over time, and by covered and uncovered treatment. Wilcoxon's test.
*=not significant

Taxonomic Group	Treatment Covered vs. uncovered	Time
Algae	*	$p < 0.001$
Colonial Ascidian	$P < 0.05$	*
Solitary Ascidian	*	$p < 0.01$
Barnacle	$p = 0.035$	*
Bryozoa	$p = 0.01$	$p = 0.002$
Hydroid	*	$p < 0.001$
Mollusks	*	*
Polycheate	*	*
Porifera	$p < 0.01$	*

Table 5. *Schizoporella cornuta* percent cover in sand-bottom and hard-bottom habitat over three sampling periods; the result of testing the null hypothesis that the treatment and time do not differ in percent cover of the most dominant species, *Schizoporella cornuta.*
** $P \leq 0.005$.

Source of Variation	df	SS	F_s
Treatment	1	351.03667	14.3892**
Time	2	411.3098	8.4262**
Interaction	3	762.1676	10.4139**
Error	17	1103.7106	

Two-Way Model I ANOVA

Table 6. Area per species as a percentage of total organisms encountered throughout the different treatment types. (A= Algae, An= Anthozoa, As= Ascidians, Ba= Barnacles, B= Bryozoans, H= Hydroids, M= Mollusks, P= Polycheate, Po= Porifera)

Species List	Hard-bottom Mean Percent Cover	Sand-bottom Mean Percent Cover	Covered Raised Mean Percent Cover	Uncovered Raised Mean Percent Cover
Schizoporella cornuta (B)	21.50	18.73	43.18	46.79
Bugula turrita (B)	2.65	2.05	2.52	1.46
Plakortis angulospiculatus (P)	0.57	0.20	0.11	0.23
Cliona sp. (P)	1.39	0	2.73	1.77
Mycale americana (P)	3.03	1.73	1.11	9.64
Aplysillia longispina (P)	0.10	0	2.18	0
Haliclona oculata (P)	0	0	0.03	0
Ascidia interrupta (As)	0	0.06	0.10	0.10
Mogula manhattensis (As)	0	0.23	0	0.35
Styela plicata (As)	0.15	0.35	0	1.93
Aplidium constellatum (As)	0.11	1.95	0	7.26
Eudistoma hepacticum (As)	3.50	2.44	0	9.81
Didemnum duplicatum (As)	0.16	0.03	0.48	0.12
Botryllus planus (As)	0	0	3.73	0
Clavelina sp. (As)	0	0.19	0.56	0.37
Pennaria tiarella (H)	0.18	0.22	0.04	0.48
Astrangia danae (An)	0.1	0	0	0
Leptogorgia virgulata (An)	0	0.1	0	0
Chthamalus fragilis (Ba)	0.09	0	0.40	0.26
Filograna implexa (P)	0.12	0.16	0.62	0.43
Cladophora sp. (A)	0.06	0	4.68	0.05
Phaeophyta (A)	3.5	3.2	23.90	5.2
Pteria colymbus (M)	0.50	0.03	0	0.48
Chama macerophylla (M)	1.38	0.21	0.98	1.29
Green algae (A)	0	0	0.17	0
Mean Percent Total Cover	39.0	31.79	87.53	88.03

Table 7. *Schizoporella cornuta* cover in covered and uncovered raised treatment over three sampling periods; the result of testing the null hypothesis that the treatment and time do not differ in percent cover of the most dominant species encountered, *Schizoporella cornuta* . *** P≤0.0001.

Source of Variation	df	SS	F_s
Treatment	1	1520.4408	29.0742***
Time	2	1162.1243	11.1112***
Interaction	3	2466.0016	15.7185***
Error	44	2399.9853	

Two-Way Model I ANOVA
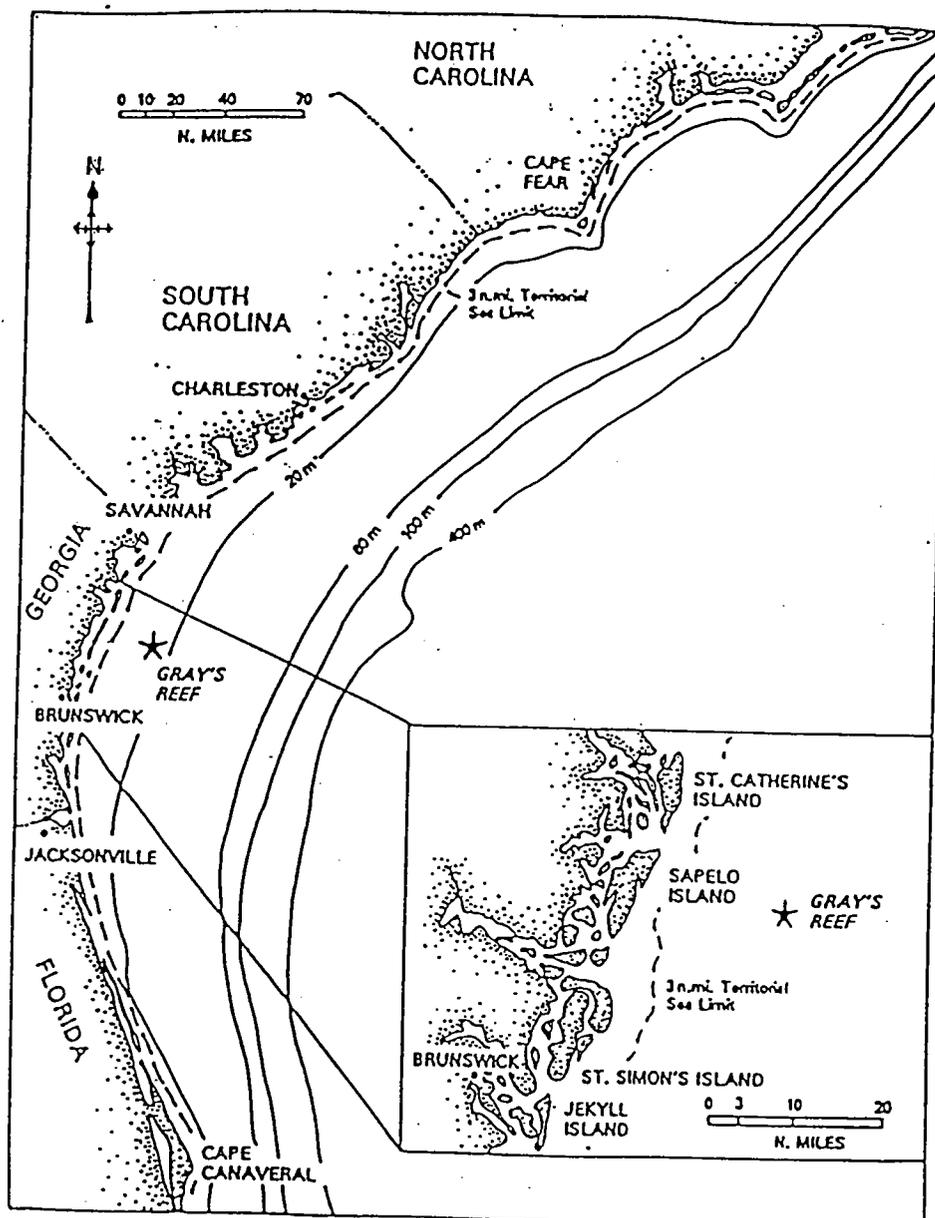
Figure 1. Map of the South Atlantic Bight showing specific location of Gray's Reef National Marine Sanctuary.
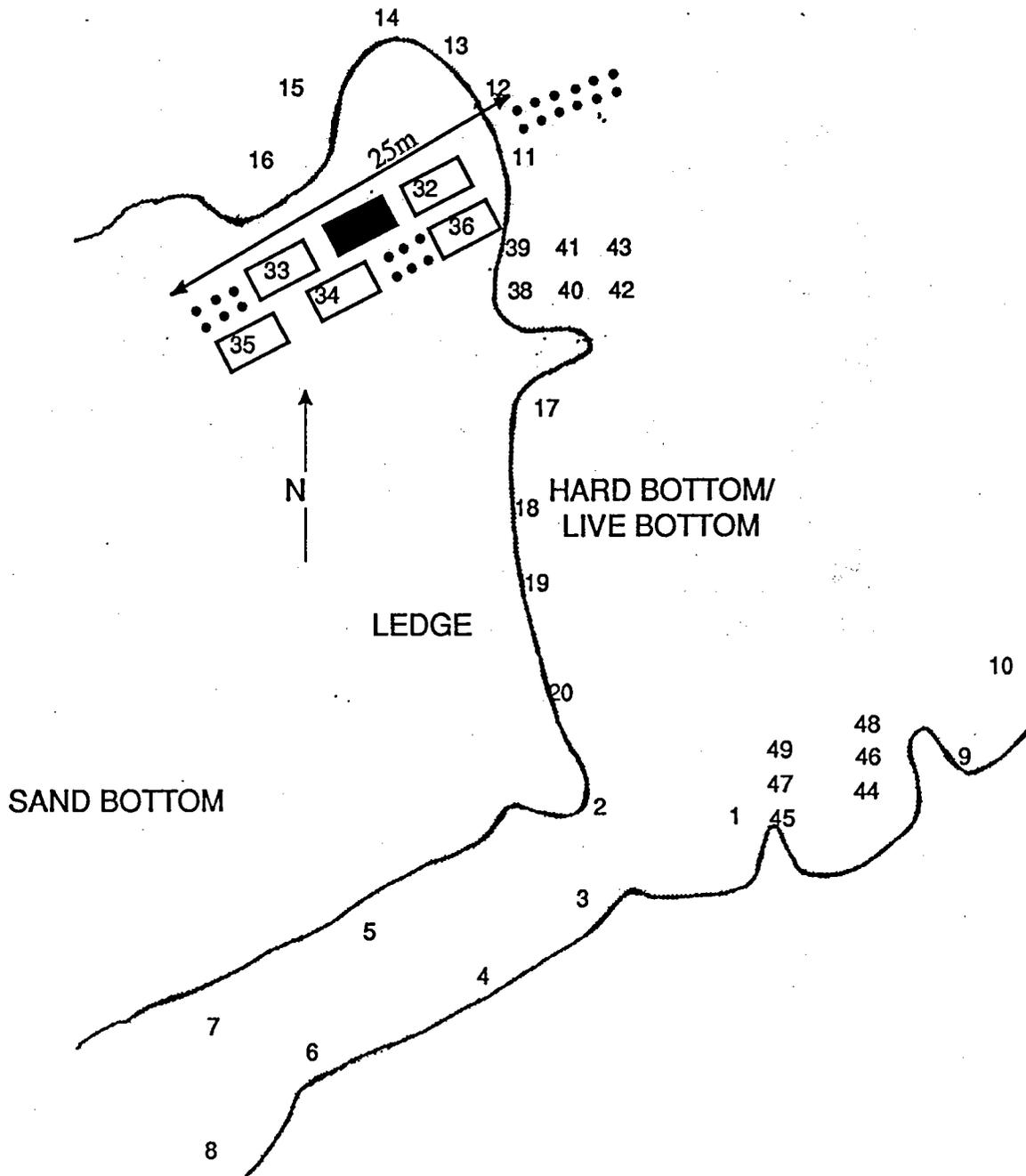
Figure 2. Study site map showing the different habitats and locations of the rocks. Block 33 and 32 indicate the uncovered platforms. The black block indicates stand 31 which was missing after the first sample. Block 34-36 indicate the covered platforms. The black dots indicate where the loose rocks were placed. The numbers throughout the map indicate the permanent monitoring stations at Gray's Reef National Marine Sanctuary.
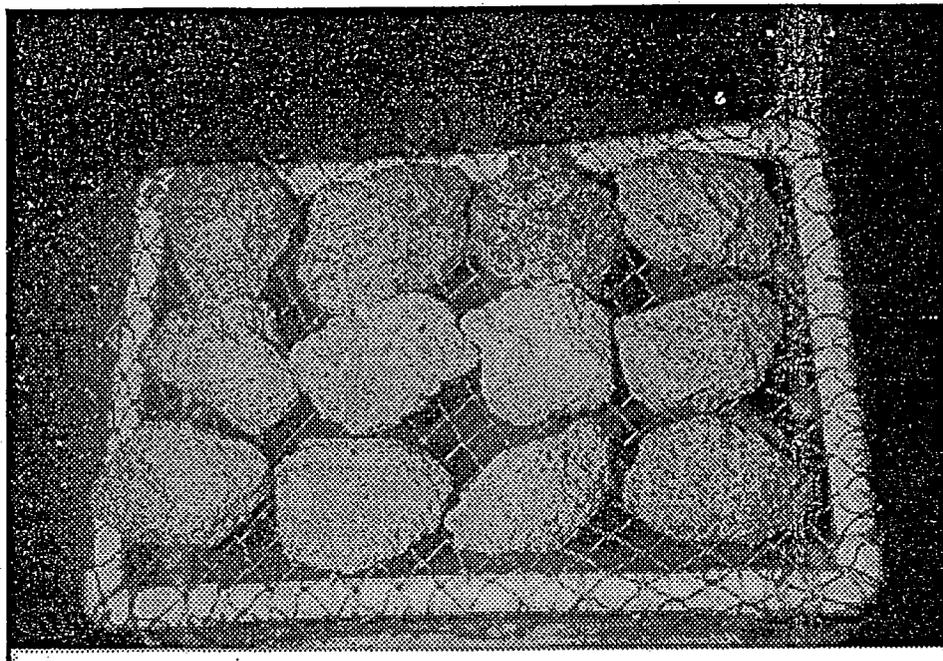
Figure 3. Picture of the PVC pipe platform underwater when first deployed in June 1996. This is the uncovered treatment.

Figure 4. Picture of the PVC covered platform when first deployed in June 1996. This is the raised covered treatment. The diver is securing the mesh cover with tie wraps around the PVC platform.
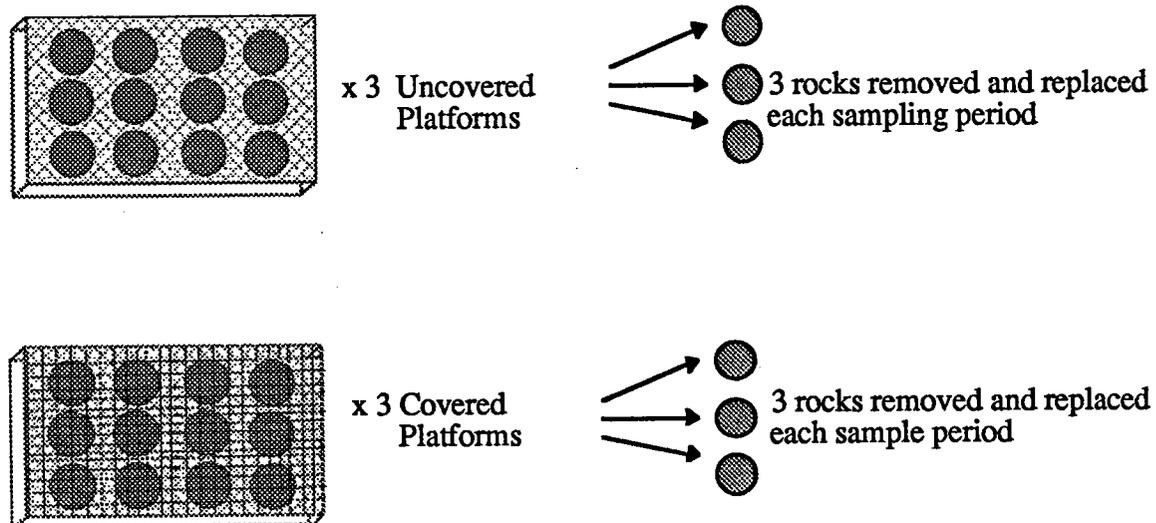
Figure 5. Schematic experimental design for the predator effect test. The PCV pipe platform dimensions were 1.6 m in length, 1.4 m in width, and 0.8 m in height. The covered platforms had a mesh cover with 2cm^2 openings.
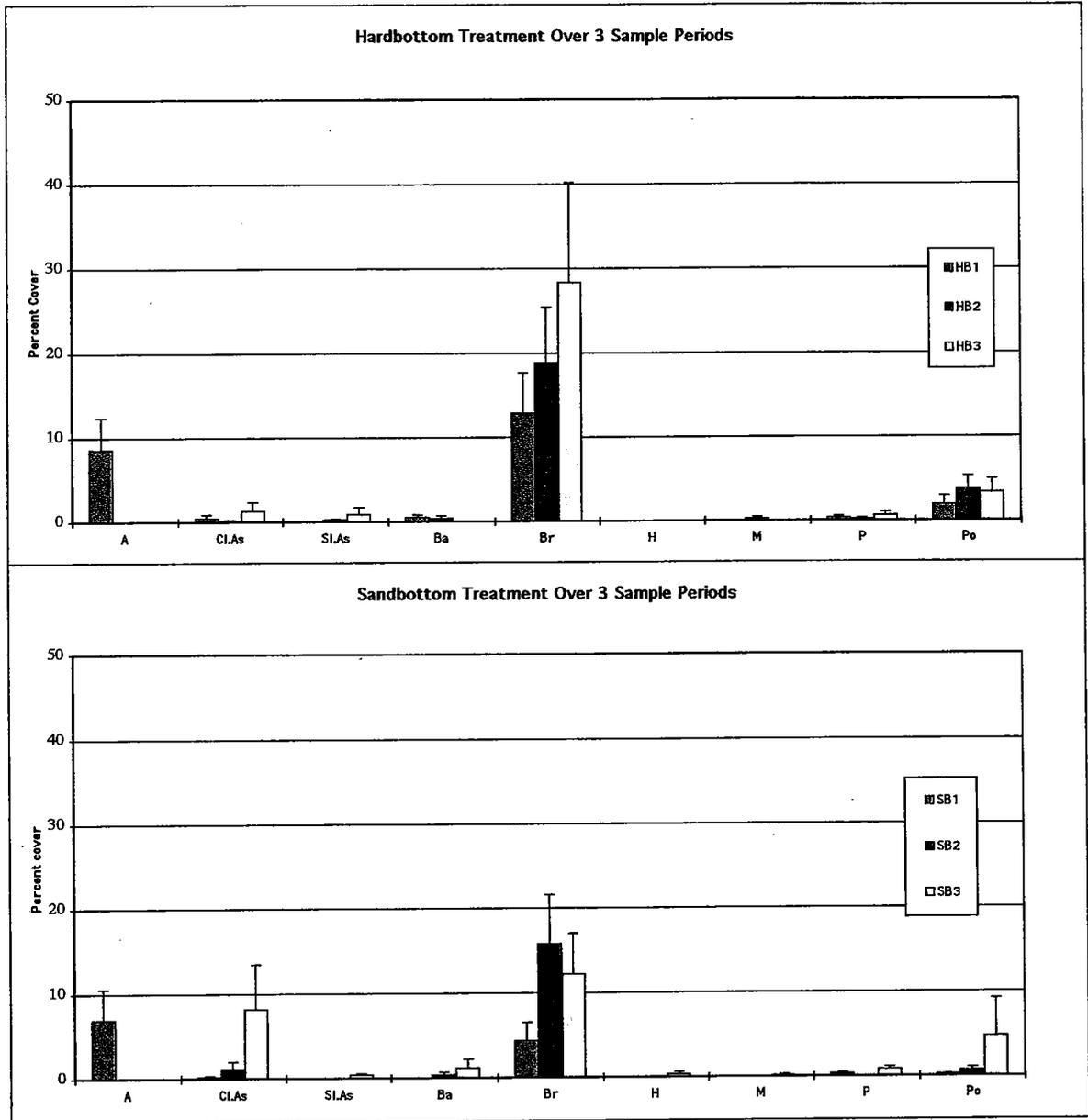
Figure 6. Mean percent cover for rocks on HB (hard bottom) and SB (sand bottom) habitat over three sample periods for the major taxonomic groups colonized.
(A=Algae, Cl.As=Colonial Ascidian, Sl.As.=Solitary Ascidian, Ba=Barnacle, Br=Bryozoan, H=Hydroids, M=Mollusks, P=Polycheate, Po=Porifera)
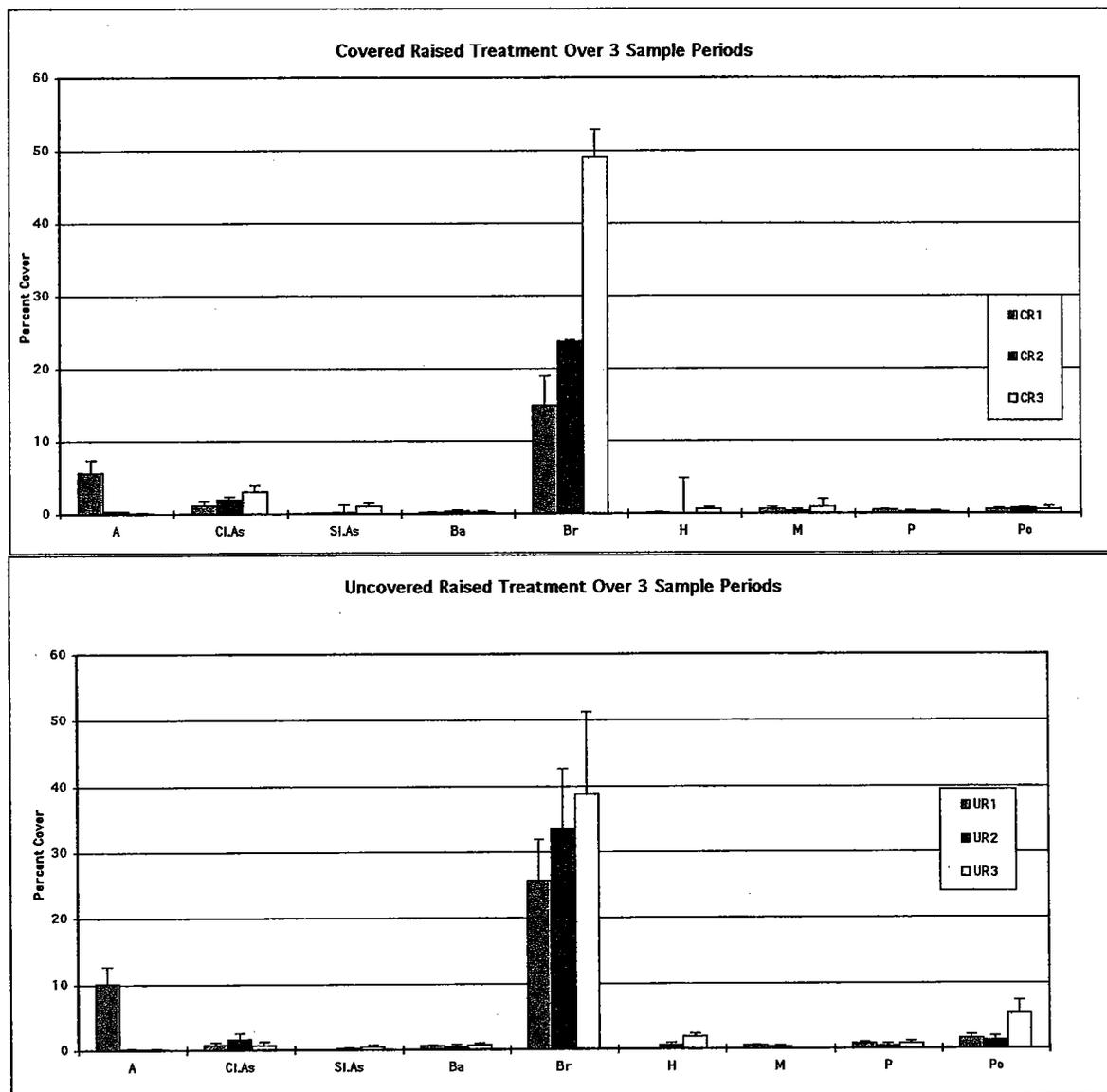
Figure 7. Mean percent cover for treatment CR (covered raised) and UR (uncovered raised) over three sample periods for the major taxonomic groups colonized.
(A=Algae, Cl.As=Colonial Ascidian, Sl.As.=Solitary Ascidian, Ba=Barnacle, Br=Bryozoan, H=Hydroids, M=Mollusks, P=Polycheate, Po=Porifera)
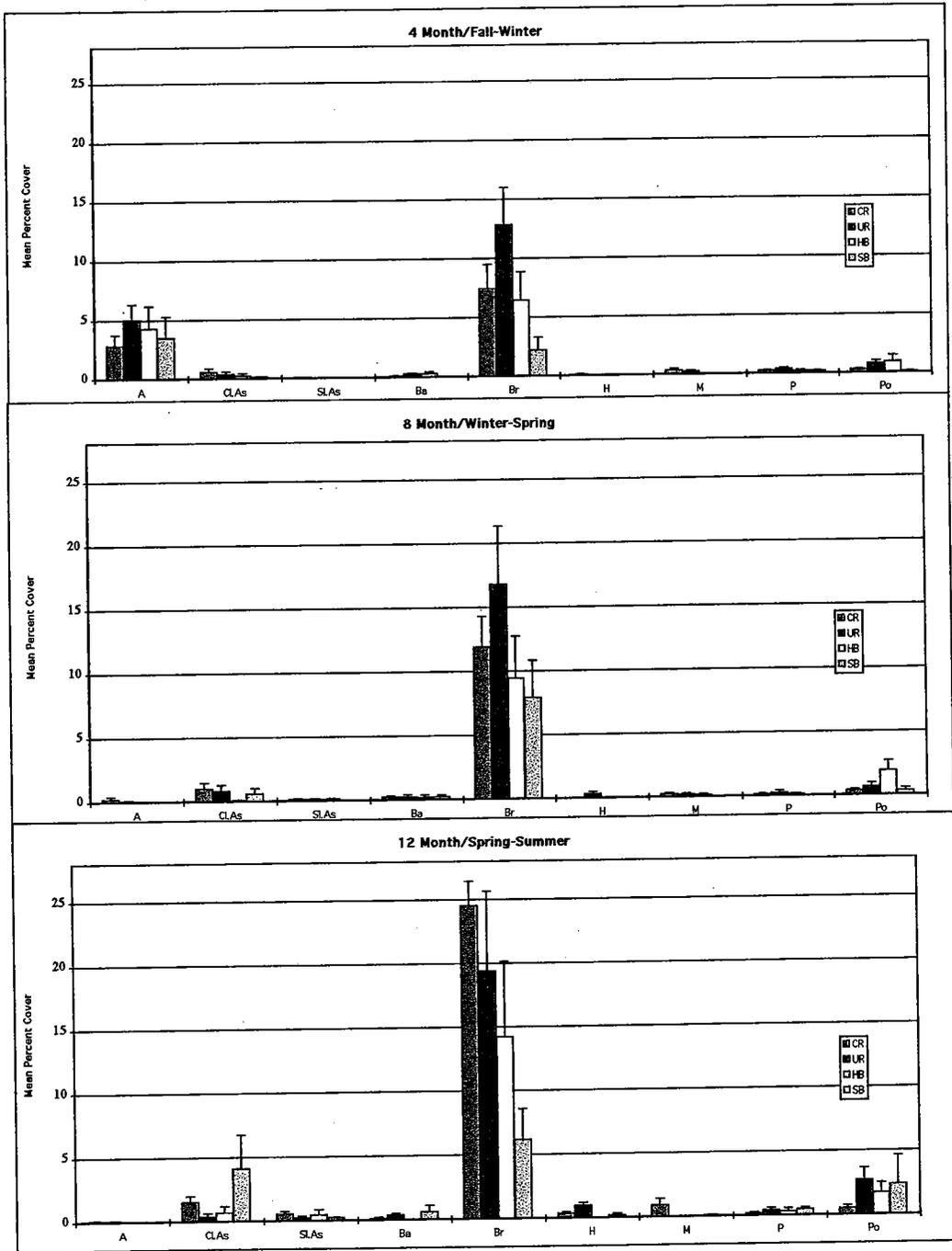
Figure 8. Mean percent cover for treatment CR (covered raised), UR (uncovered raised), HB (hard bottom), and SB (sand bottom) over three sample periods for the major taxonomic groups colonized. (A=Algae, Cl.As=Colonial Ascidian, Sl.As.=Solitary Ascidian, Ba=Barnacle, Br=Bryozoan, H=Hydroids, M=Mollusks, P=Polycheate, Po=Porifera)