ECOLOGICAL CONTROLS ON STROMATOLITE DEVELOPMENT IN A MODERN REEF ENVIRONMENT: A TEST OF THE ECOLOGICAL REFUGE PARADIGM

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ABSTRACT: Paleontological and neontological studies suggest that stromatolite development may be limited to environments where ecological processes such as colonization (recruitment), growth, competition, and predation (herbivory) are low. We quantitatively tested this "ecological refuge paradigm" at a unique stromatolite-reef complex at Stocking Island, Bahamas where three contiguous zones grade in dominance from stromatolites in the back reef to a macroalgal turf in the reef flat to reef building corals and coralline algae and reef fishes in the fore reef. At two independent transects along this gradient, we quantified the distribution and abundance of the dominant organisms and measured the rates of the above-listed ecological processes and determined survival and growth of stromatolite, turf, and coralline algae transplanted to each of the three zones. We also measured both the sediment dynamics and temperature profiles along this gradient to determine if these may be controlling the ecological processes.

Stromatolites dominate the back reef zone where species diversity (especially among eukaryotes) and associated ecological pressures were low. Measured rates of colonization from calcified (i.e., coralline) and noncalcified macroalgae and filamentous turf algae were lowest in the back reef (i.e., <5% substrate colonization/y) and highest in the fore reef (95% substrate colonization/y). This suggests that competition for space was lowest in the stromatolite zone. Growth and survival rates of transplanted coralline algae were low in both the back reef (3 mm/y and 20-40% annual survival rates) and reef flat (< 2 mm/y, 0% surviving) and highest in the fore reef (about 10 mm/y, 80% surviving). Foraging activity from all fishes was lowest in the back reef (total 0.4 bites/m²/h) and reef flat (0 bites/m²/h) and highest in fore reef (900 - 2200 bites/m²/h, mostly from omnivorous wrasses). Herbivory from all potential sources was below detectable levels in the stromatolite zone and was highest in the fore reef.

The ecological refuge found in the back reef stromatolite zone resulted primarily from periodic sediment inundation. Most eukaryotic reef-dwelling organisms cannot persist under as much as 700 mm of sediment for periods up to 100 days. Although the reef flat suffered both desiccation and thermal stress (averaging more than 5°C greater daily temperature fluctuation than the fore reef), natural and transplanted eukaryotic turf algae thrived there.

Although transplanted stromatolites survived best in the back reef (about 80% of the original transplant surviving/y), they also persisted in the fore reef (about 40% surviving per year). Therefore, *Schizothrix*-dominated stromatolites can persist in fore reef environments but because of the presence of other organisms and associated ecological pressures, their laminated microbial-produced structure is lost or obscured. While the sediment and the organisms necessary for stromatolite formation exist in this and probably in other modern reef environments, their reef-building contribution will be low except in unusual habitats where abiotic stresses maintain an ecological refuge.

INTRODUCTION

For over three billion years, stromatolites were the only reef builders on Earth (Awramik 1990; Kauffmann and Fagerstrom 1993). Their global dominance began to decline during the later Proterozoic and was significantly diminished by the Vendian as macroscopic organisms radiated and became abundant (Riding 1991; Grotzinger et al. 1995). During the Early Cambrian radiation, a variety of calcifying metazoans and metaphytes created a new generation of reef-builders that fundamentally changed the nature of reef ecosystems and bioherms (Kauffmann and Fagerstrom 1993), and stromatolites were rare or absent (e.g., Awramik and Riding 1988). As summarized by Kauffmann and Fagerstrom (1993), the "ecologically simple" stromatolitic reefs were replaced by "complexly structured reef ecosystems, characterized by high species and community diversity" and these eukaryotic reefs "are continuously represented in strata spanning the last 650 million years." In other words, Phanerozoic reefs differ fundamentally from their Proterozoic ancestors.

Stromatolite reef resurgences have occurred periodically throughout the Phanerozoic but primarily following mass extinctions (e.g., Copper 1988; Donovan 1989; Schubert and Bottjer 1992). Because of this, stromatolites have been called "disaster-forms" (Schubert and Bottjer 1992). Others have pointed out that some stromatolite resurgences do not correspond with mass extinctions, but resulted from the "localized eradication of benthic marine communities" (Soja 1994). Regardless, the geological record clearly suggests a fundamental incompatibility between prokaryotic, cyanobacteria-dominated stromatolites and eukaryotic metaphytes and metazoan reefs. Thus the geological inference drawn from this is that stromatolites develop "in a relatively ecologically relaxed habitat...(Schubert and Bottjer 1992)."

The discovery of modern stromatolites in hypersaline regions of Shark Bay, Australia provided an opportunity to study living stromatolites and consider their ecological controls. However, ecological pressures are low under the harsh hypersaline conditions of Shark Bay and this, along with other discoveries of stromatolites in extreme environments such as

Figure 1. Photos of Stocking Island, Bahamas stromatolite-coral reef complex. Inset photos to right show representative photos of each zone. The upper right photograph shows major reef builders, *Millepora complanata* and *Neogoniolithon strictum*. Note sediment stakes in back reef. Scale across the reef zones is given in Figure 2.
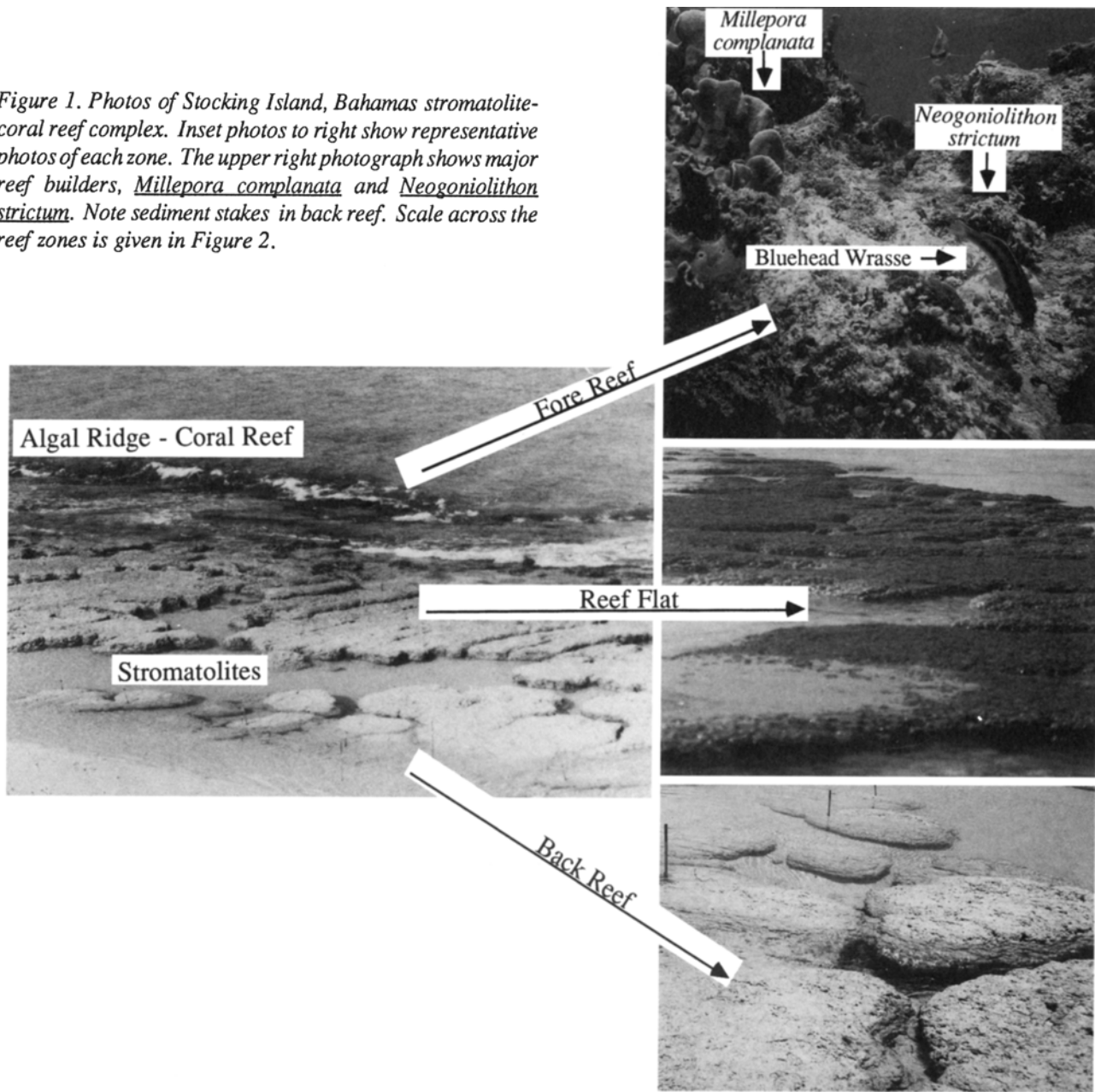
Antarctic lakes (Parker et al. 1981) and thermal springs (Ward et al. 1989), lead to the conclusion that stromatolites may only be able to persist today in refugia where ecological pressures from other organisms are low (Awramik and Riding 1988). This we call "*The Ecological Refuge Paradigm*".

The *ecological refuge paradigm* for modern stromatolite development is based on several neontological observations. For example, Garrett (1970) observed that living stromatolites at Andros Island were destroyed by the activity of grazing snails. Others have suggested that anything that disrupts the microfabric of stromatolites including competition from other reef-dwelling and reef-forming organisms will prevent stromatolite development (Monty 1973; Awramik 1990; Golubic 1991). Those and other neontological studies are based on observations and qualitative correlations. Lacking are experiments designed to quantify the ecological processes

said to eliminate stromatolites. That is, past studies have not measured rates of colonization, productivity, competition, and herbivory in stromatolite habitats and compared them to identical measurements on adjacent modern reef habitats.

The question of why stromatolites no longer commonly build reefs in tropical marine environments cannot be addressed by studying hypersaline, arctic lacustrine or hot-spring stromatolite environments (Awramik 1990). The modern intertidal and subtidal stromatolites of the Exuma region of the Bahamas are unique and offer an exceptional opportunity because they exist in normal marine salinities and in close proximity to modern eukaryote-dominated reefs (Dill et al. 1986; Reid and Browne 1991; Reid et al. 1995). Further, the specific reef system on Stocking Island that we studied had a uniquely contiguous gradient of habitats from reef-dominated to stromatolite-dominated build ups (Reid et al. 1995;

Macintyre et al. 1996; Steneck et al. 1997). Unlike most modern stromatolites that are found in environments of "elevated salinity or alkalinity, periodic desiccation, elevated temperatures, precipitation of mineral matter during growth, and strong currents or wave action (Awramik 1990)," the intertidal and subtidal stromatolites of Stocking Island are different because they do not fit this profile. They live in an environment of normal marine salinity and tropical temperatures with relatively low wave action and currents (Reid et al. 1995).

We tested the ecological refuge paradigm by quantifying the distribution and abundance of stromatolites and other reef organisms relative to measured ecological pressures and by conducting manipulative experiments along a contiguous gradient from a stromatolite reef to a modern reef community on Stocking Island in the Bahamas (Fig. 1). For this, we transplanted stromatolites to reef habitats and filamentous eukaryotic filamentous turf algae and crustose coralline algae from the reef to the stromatolite habitat. Our specific questions were, do the Stocking Island stromatolites only develop where ecological pressures such as colonization rates, competition, and herbivory from eukaryotes are low? That is, are these stromatolites confined to an ecological refuge? If they are, what environmental factors contribute to the low ecological pressures (i.e., what creates the ecological refuge)? Our approach differs from past studies because we used standardized methods to quantify ecological processes along a contiguous gradient and we employed manipulative experiments to determine how rates of colonization, survival, growth, and other ecological processes change along this gradient.

STUDY SITES

Experiments were conducted on Stocking Island which lies about two km northeast of Georgetown, Great Exuma Island, Bahamas. This stromatolite reef and its associated algal ridge and coral assemblages are well described in a series of papers (Reid and Brown 1991; Reid et al. 1996; Macintyre et al. 1996; Steneck et al. 1997). Placement of experiments and sampling locations are given in figure 2. Other environmental details are provided where appropriate below.

The stromatolite-algal ridge complex at Stocking Island was studied most intestively from May 1992 to June 1993. Detailed studies on its biology and ecology were done along transects from shore to beyond the seaward edge of the algal ridge (i.e., in the pinnacle zone). Two replicate transects about 100 m apart (often identified as T1 and T2) were identically sampled and contained most of our experimental manipulations. Sediment stakes and sediment traps were only deployed at T1. Both transects had zones similar to those diagrammed in figure 2.

Comparisions between stromatolite reefs and adjacent reef assemblages were conducted at 5 sites along about 120 km of the Exuma Island chain. Specific sites are identified in Results and full site descriptions are given by Reid et al. (1995).

METHODS

Patterns of Distribution and Abundance

To quantify the dominant organisms on the upper reef surfaces, quadrat sampling was used. Quadrats were 25 cm X
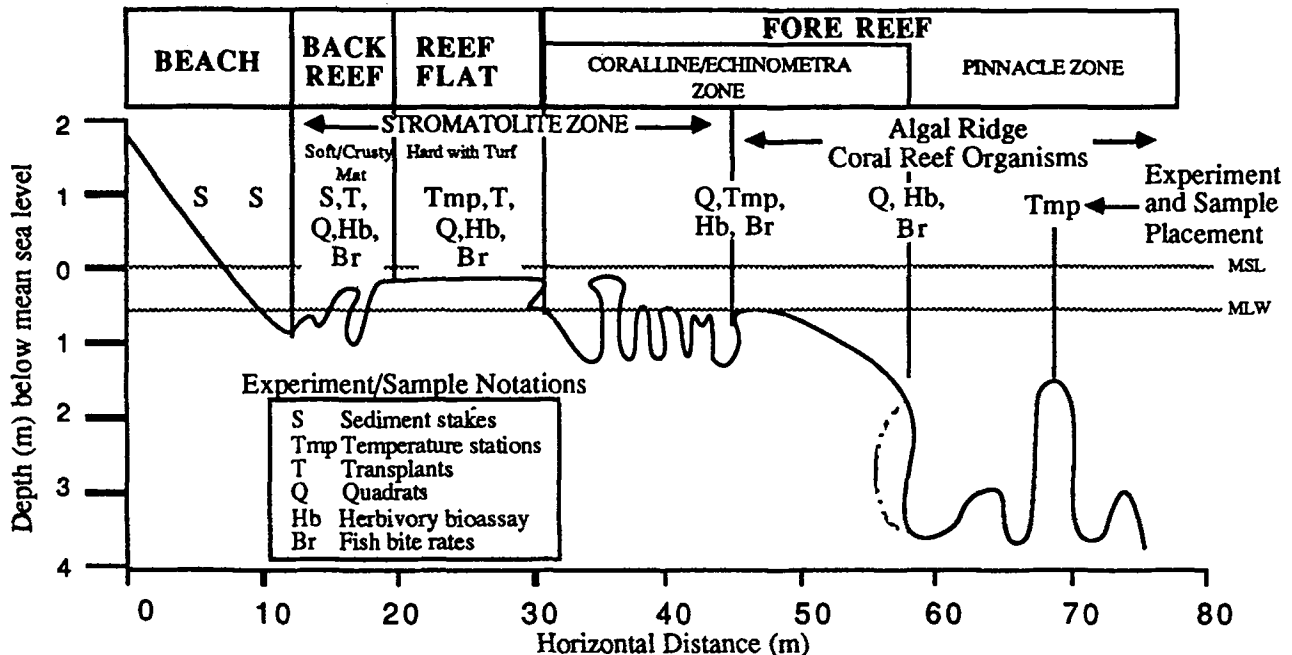

Figure 2. Diagrammatic cross section of the Stocking Island stromatolite-algal ridge-coral reef complex (after Steneck et al. 1997). Back reef, reef flat and fore reef zones are illustrated in Figure 1.

25 cm (i.e., one sixteenth of a meter square). They were haphazardly tossed and viewed for visual estimated percent cover. The advantages of this technique are discussed in Dethier et al. (1993).

Chain transects were used to quantify organisms on all reef surfaces. For this, a 10 m polypropylene line was stretched along the reef parallel to the seaward edge. Under or next to the 10 m line, a chain with 2 cm links was draped on the reef surface. A tally was made of each organism under each link. All three dimensional surfaces that could be reached by the researcher (thus limited by the width of spaces in which arms and hands can reach) were quantified. Reef complexity is obtained from these data by calculating the surface length of reef surface under each linear meter of the reef. The resulting "spatial index" is represented as m of reef/m linear. This technique and the spatial index are fully described in Rogers et al. (1983).

Biomass was determined by collecting three, 3.9 cm^2 substrate samples (each 1 mm deep) that were fixed in 5% formaline for 24 h and decalcified with 10% acetic acid solution for 7-10 d. Once decalcified, samples were kept in suspension, poured onto preweighed filter paper, oven dried to constant weight and reweighed. Ten control samples with only decalcifying solution, were filtered through preweighed filters and weighed. Control samples added negligible weight (i.e., 0.3 g/ m^2).

Abiotic Environment

Physical description of the Stocking Island Stromatolite-reef complex is given elsewhere (Reid and Brown 1991; Reid et al. 1996; Steneck et al. 1997). Water temperature sensors to illustrate thermal stress were placed at four locations from the fore reef pinnacle zone to the back reef (Fig. 2). Recording temperature sensors were Casio underwater temperature recording watches. These recorded temperature for up to 30d and were calibrated to an accuracy of 0.1°C. They were placed within white PVC housings that were open with screening at both ends to allow water flow. Temperatures were taken simultaneously in each zone at hourly or daily (at noon) intervals 25 days from 10 May to 4 June 1993.

Sedimentation rates were measured using sediment traps drilled into the reef at three locations within each of the three zones (methods and results were reported in Steneck et al. 1997). Sediment levels were monitored using fixed sediment stakes driven into hard substratum at five stations in each of the three zones. Sediment levels were monitored over the entire year from June 1992 until June 1993.

Biotic Environment: Ecological Processes of Survival, Colonization, Growth, Competition, and Herbivory

To determine patterns of survival, colonization, competition, growth, and herbivory, for the major reef-dwelling organisms

at the Stocking Island reef-complex, a series of transplant manipulations were performed. These involved setting stromatolites from the back reef, turfs from the reef flat and the coralline *Neogoniolithon strictum* from the fore reef into a nontoxic underwater epoxy (Splash Zone Compound, Koppers Co.). The stromatolites were chiseled from the back reef and their base surrounded with underwater epoxy that was fixed to the reef with 20 d nail spikes and copper wire. For the turf and coralline transplants, three pieces were embedded into the epoxy in standard plastic petri dishes (8 cm diameter) that were bolted to PVC pipes placed at three separate locations in each of the back reef, reef flat, and fore reef zones in both transects. Transplants back to the zones from which the stromatolites, turfs, or corallines were taken served as a transplant control for the technique. To determine survival and growth of the species in each of the three zones, photographs and in situ measurements were taken in May-June 1992, January 1993, and finally June 1993. These sampling periods resulted in experiment durations of 219 and 126 days respectively (total 345 days, i.e., since the first May-June sampling period). If 25 percent or greater of a transplant was dead at the time of a sampling period, the entire transplant was replaced. Only lateral growth rates of the coralline was measured so rates of substrate occupancy could be assessed. For that, the maximum growth away from the transplanted crust was measured on each of the three coralline plants embedded in the epoxy putty (illustrated in Results). Growth rate measurements were taken in January 1993 and May 1993 from coralline transplants initiated in June 1992. Average growth rates of each transplant is thus based on three measurements and from these values the average growth rates were determined. The epoxy around the transplants served as settlement and colonization substrata in each of the zones in which they were transplanted.

Herbivory was assessed by measuring the population density and body size of all mobile benthic invertebrates in quadrats. Quadrats were 25 X 25 cm and were haphazardly tossed at each of the five stations where sediment stakes were driven in each of the three zones (Fig. 2). Qualitative nocturnal observations for herbivores were also made.

To compare fish grazing at Stocking Island with that reported elsewhere, bite rates were measured by marking five areas of 1 m^2 each, on each of the three zones (Fig. 2) along the two reef transects (i.e., a total of 30 observation stations). At each station, the square meter was watched for a period of five minutes and the number of bites from all species of fish was recorded. Bite-rate determinations for all herbivorous fish species were analyzed by functional groups of excavating, denuding, and nondenuding grazers (after Steneck 1988). Usually one or two such observations were made for each station each day (methods of Steneck 1994; Steneck and Dethier 1994). Additional visual bite-rate determinations were made to assess herbivory in the west Exuma Sound region and at coral reefs in the vicinity of the stromatolites.
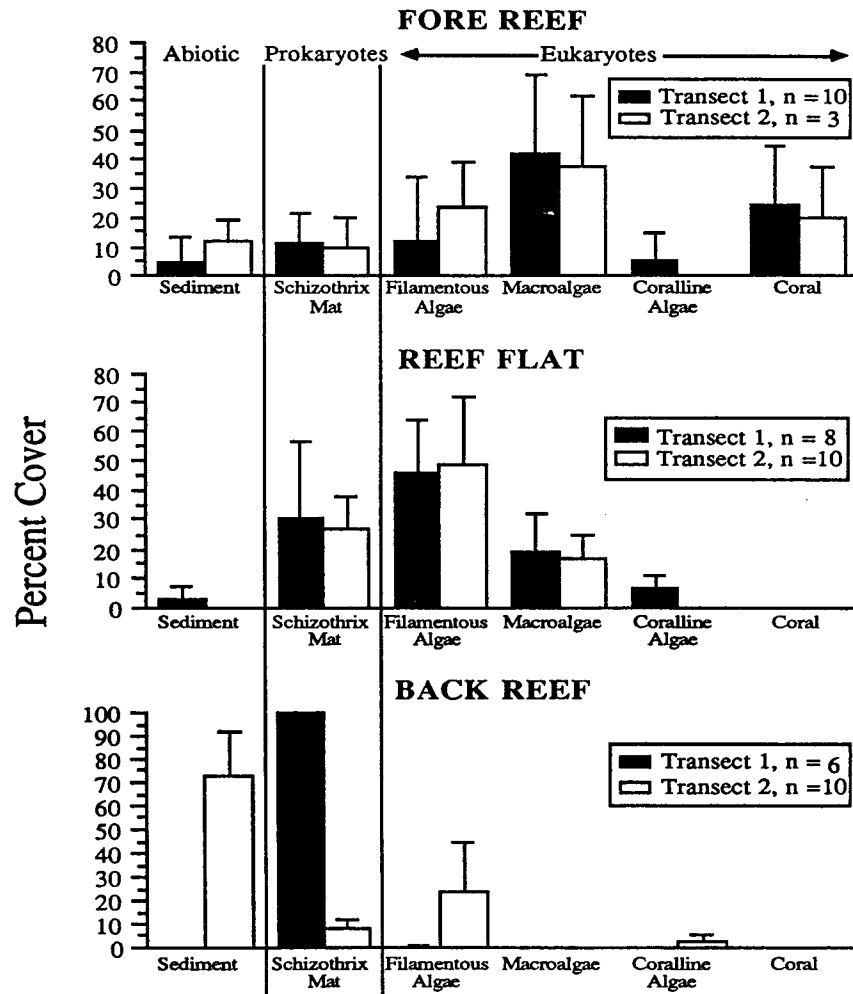
Figure 3. Dominant reef components on upper surfaces from fore reef to back reef on the two reef transects determined by quadrat sampling. Variance is given as one standard deviation. Sample size, "n" is number of quadrats.

RESULTS

Patterns of Distribution and Abundance of Dominant Organisms

Quadrat sampling indicated that the cyanobacteria, *Schizothrix* complex (Pinckney et al. 1995) dominates the back reef (Fig. 3). Dominance shifts to eukaryotic filamentous turf algae on the reef flat and to macroalgae in the fore reef (Figs. 1 and 3). Overall diversity increased from the back reef to the fore reef, Fig. 3, Table 1). The fore reef also had several species of reef-building corals and hydroids such as *Millepora complanata*, *Porites astreoides*, and *Colpophyllia natans*. Although *Schizothrix* mats, turf algae, and coralline algae were found in all zones (Fig. 3, Table 1) their relative abundances changed dramatically among zones. Further microhabitats such as small tidepools harbored otherwise stress-susceptible species such as coralline algae.

Chain transect sampling was employed in the same zones (but not the exact same areas as the quadrats) to determine the relative composition of all macroscopic, surface-dwelling organisms (not just those on upper surfaces). With chain

transects, more reef area was sampled and at a higher taxonomic resolution than the quadrat sampling (Fig. 3) but with similar results (Table 2).

The back reef was dominated by the stromatolite-forming cyanobacteria complex dominated by *Schizothrix* sp. Stromatolite development was better developed and *Schizothrix* dominance was greater in the back reef of transect one than in transect two. Coincident with lower *Schizothrix* abundance on transect two was the somewhat higher eukaryotic filamentous turf algal abundance (Table 2). Because sediment-binding *Schizothrix* was less abundant at T-2, free sediment was more abundant (Fig. 3).

The reef flat was dominated by turf algae comprised of chlorophytes, *Cladophora* and *Ernodesmis verticillata* and the diminutive articulated coralline rhodophyte, *Jania capillacea* along with several other small macrophytes. The fore reef was dominated by a micro-turf characteristic of coral reef turfs (i.e., *Herposiphonia*, *Lophosiphonia*, *Taeneoma* and associated cyanobacteria such as *Oscillatoria* sp) (Adey and Steneck 1985; Carpenter 1986), along with larger filamentous (*Cladophora* sp) and other macroalgae (i.e.,

Table 1. Major identifiable eukaryote components on upper surfaces from quadrat data for Transect 1. Each taxonomic group is listed from most to least abundant (percent cover). Reef building corals and coralline algae were kept separate. The proportion of these and other functional groupings are given in Fig. 3. A complete listing of microscopic and prokaryote species is given in Pinckney et al. 1995.

Zone Data	Taxonomic Group	Taxa	% Cover
Fore Reef	Coral (Scleractinians and Hydrozoans)	*Millepora complanata*	19.0
Transect 1		*Porites astreoides*	2.5
n = 10 quadrats		*Colpophyllia natans*	3.0
	Green algae (Chlorophyta)	*Ernodesmus verticillata*	25.6
		Cladophoropsis macromeres	21.5
		Dasycladus vermicularis	3.5
		Caulerpa spp	2.0
		Anadyonome stellata	1.0
	Brown algae (Phaeophyta)	*Dictyota divaricata*	4.5
		Dictyosphaeria cavernosa	1.0
	Red algae (Rhodophyta)	*Neogoniolithon strictum*	5.0
		Dasya baillouviana	2.0
		Paragoniolithon typica	1.0

Zone Data	Taxonomic Group	Taxa	% Cover
Fore Reef	Coral (Scleractinian and Hydrozoan)	*Millepora complanata*	13.3
Transect 2		*Porites astreoides*	6.7
n = 3 quadrats	Green algae (Chlorophyta)	*Ernodesmus verticillata*	3.3
	Brown algae (Phaeophyta)	*Dictyota divaricata*	3.3
		Lobophora variegata	1.7
	Red algae (Rhodophyta)	*Laurencia obtusa*	18.3

Zone Data	Taxonomic Group	Taxa	% Cover
Reef Flat	Green algae (Chlorophyta)	*Cladophoropsis macromeres*	55.6
Transect 1		*Ernodesmus verticillata*	25.0
n = 8 quadrats	Brown algae (Phaeophyta)	*Dictyosphaeria cavernosa*	5.0
	Red algae (Rhodophyta)	*Fosliella sp.*	10.0
		Colpomenia sinuosa	1.5

Zone Data	Taxonomic Group	Taxa	% Cover
Reef Flat	Green algae (Chlorophyta)	*Cladophoropsis macromeres*	35.0
Transect 2		*Ernodesmus verticillata*	20.0
n = 10 quadrats			

Zone Data	Taxonomic Group	Taxa	% Cover
Back Reef	Green algae (Chlorophyta)	*Battophora oerstedii*	0.1
Transect 1		*Cladophoropsis macromeres*	0.5
n - 10 quadrats	Diatoms (Chrysophyta)	Diatoms spp.	2.5

Zone Data	Taxonomic Group	Taxa	% Cover
Back Reef	Green algae (Chlorophyta)	*Cladophoropsis macromeres*	17.5
Transect 2		*Ernodesmus verticillata*	1.2
n = 6 quadrats	Brown algae (Phaeophyta)	*Dictyosphaeria cavernosa*	1.7

Dictyota dichotoma and *Laurencia obtusa*) (Table 2). In places, large heads of the delicately branched coralline *Neogoniolithon strictum* were conspicuous.

The entire Stocking Island stromatolite-algal ridge and reef complex has relatively low spatial heterogeneity. Chain transects analyzed to determine the average spatial index value (described in methods above) indicated the back reef and reef flat averaged between 1.2 and 1.4 m/m (± 0.6 SD). The fore reef lip was only slightly higher with an average of 1.6 m/m (± 0.9). Overall, however, this entire reef complex is architecturally simple since other reefs typically have average values as high as 4 (Steneck 1994).

Species diversity of eukaryotes was lowest in the back reef (3-7 spp), slightly higher in the reef flat (6-7 spp), higher still in the fore reef (8-12) and highest on the seaward edge of the fore reef zone (14 spp). Thus a biodiversity gradient was evident from the stromatolites in the back reef and the diverse reef-like seaward edge (Fig. 1). Dominant reef organisms change dramatically along the short gradient from the back reef to the

fore reef at the Stocking Island stromatolite-reef complex (Fig. 1). Most striking is the shift from prokaryote, low diversity-dominated back reef habitats to the much more diverse, eukaryote-dominated fore reef (Fig. 4).

Overall biomass of both prokaryotic and eukaryotic algae did not change significantly along the gradient from the back reef (145.9 (± 157.7) g/m²), reef flat (192.3 (± 95.9) g/m²) to the fore reef (295.9 (± 121.4) g/m²) on transect 1 (p=0.395, ANOVA) or on transect 2 (p=0.203, ANOVA) (back reef (53.5 (± 67.1) g/m²), reef flat (75.6 (± 68.4) g/m²) and fore reef (228.9 (± 173.0) g/m²). Therefore, changes in dominance between prokaryotes in the back reef and the eukaryotes in the reef flat and fore reef represent a constant biomass replacement between the two groups.

Physical Environment of the Stocking Island Stromatolite-Reef Complex

From fore reef to back reef, the physical environment changes dramatically. Moderate to low wave action on the fore reef is

Table 2. The percent of categories recorded with chain transects. Ten linear meters of chains were surveyed for each transect in each zone. The number of link intercepts under each meter segment of a stretched 10 m line was recorded (this resulted in over 400 link intercepts for each transect per zone) and reported here as averages. Variance is given as standard deviation (SD). Note that the stromatolite-building cyanobacteria is delimited.

Species/Group	BACK REEF Transect 1 Ave.	SD	Transect 2 AVE	SD	REEF FLAT Transect 1 Ave	SD	Transect 2 Ave	SD	FORE REEF Transect 1 Ave	SD	Transect 2 Ave	SD	SEAWARD Transect 1 Ave	SD
Bare							6.0	10.7					5.8	7.5
Sand	14.4	13.4	41.0	11.8	5.8	4.7	18.1	14.3					0.0	0.0
Schizothrix sp.	82.5	9.0	32.7	12.6	1.4	2.2								
Diatoms	1.2	1.6	1.6	2.6			0.2	0.3						
Micro-turf			0.1	0.2					37.5	7.9	31.4	5.1	28.8	13.1
Cladophora sp.	1.4	2.2	23.2	10.5	42.6	8.1	47.8	14.4	13.5	7.1	25.5	10.0		
Cladophoropsis macromeres													20.3	11.7
Filamentous turf													1.5	0.0
Spyridia filamentosa											1.8	1.6		
Wrangelia penicillata											8.8	4.4		
Anadyomene stellata													2.7	3.1
Dictyota dichotoma			1.0	1.4			2.5	3.2	33.7	16.1	2.4	1.5	5.3	5.1
Ernodesmis verticillata					16.1	8.8	4.3	2.6	6.0	5.2				
Padina pavonica					1.2	1.3	0.7	0.8						
Batophora oerstedii	0.6	1.0												
Bryothamnion triquetrum			0.2	0.5										
Caulerpa spp.													0.2	0.0
Dasycladus vermicularis			0.1	0.2							5.3	4.2		
Dictyospheria cavernosa											0.2	0.3		
Gracilaria cylindrica									1.9	1.7	0.7	1.0		
Hypnea musciformis					0.8	1.3								
Laurencia obtusa							0.3	0.4			19.1	9.5	5.0	4.1
Jania capillacea					30.8	5.2	20.1	9.5			2.2	1.9		
Pneophyllum farinosa					1.2	1.9								
Neogoniolithon strictum													5.7	2.8
Unbr. coralline													6.2	7.1
Peyssonnelia sp.													4.0	3.4
Col. tunicate													1.2	0.0
Millepora alcicornis									1.0	1.6			2.8	0.0
Millepora complanata									5.6	7.1			7.2	5.9
Porites asteroids									1.0	1.6	1.8	2.2	2.5	2.7
Siderastrea radians			0.1	0.2							0.7	1.0		
Total # Eukaryote Species	**3**		**7**		**6**		**7**		**8**		**12**		**14**	

Dominant Reef Components
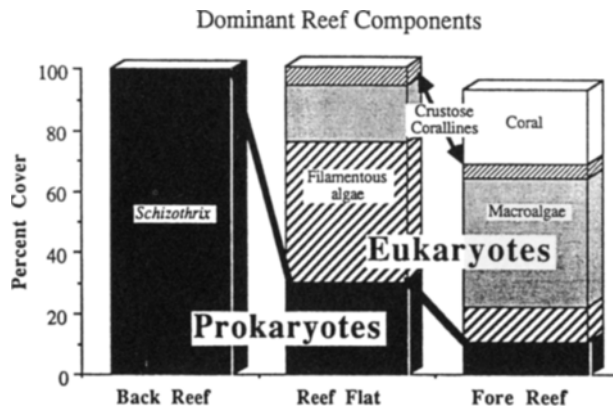
dampened at high tide and is nonexistent at low tide in the back reef (Fig. 1, Steneck et al. 1997). The emergent reef flat undergoes the most extreme temperature fluctuations, the fore reef pinnacle the least. From 10 May to 4 June 1993 temperature comparisons were made betwen the fore reef and the three other zones (locations in Fig. 2). The greatest thermal deviations from the fore reef were recorded on the reef flat (-2.8 to +3.1°C), next the back reef (-0.8 to +2.8) and the least in the fore reef pinnacle zone (-0.8 to +0.4°C). While the ambient water mass fluctuated from 18 to 26°C during this period, the most rapid thermal shock occured during diurnal spring tides when elevated temperatures during daytime low tides were more than 3 degrees warmer and nighttime low

Figure 4. Changes in biotic dominance along the back reef to the fore gradient. Data are from quadrats and placed into functional group categories (similar results were obtained using the chain data). Note that the modern reef components of coral, corallines, and eukaryotic algae are virtually absent in the prokaryote-dominated back reef.
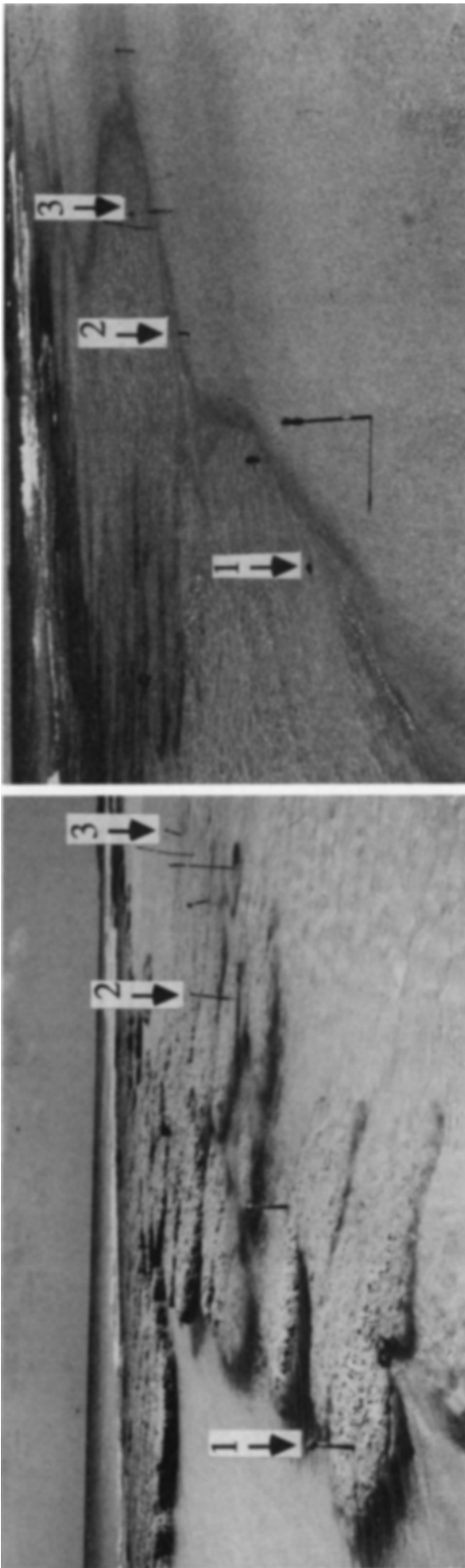
Figure 5. Photographs of fixed sediment stakes taken in back reef and beach environment. June 1992 (left) August 1992 (right). Three representative stakes are identified by arrows 1-3 are all nearly buried. One stake between number 2 and 3 is buried. Note that the stake to the right of number 1 on the right photo was installed after the June 1992 photo.

tides were nearly 3 degrees cooler than temperatures recorded in the fore reef zone. Desiccation stress is likely to correspond with the sharply elevated warm daytime temperatures recorded on the reef flat.

Sediment resuspension and gross sedimentation rates were high over the entire stromatolite-reef complex (see Steneck et al. 1997). While gross sedimentation was measured to be about 200 mm/d in the fore reef, reef flat and back reef sites (Steneck et al. 1997), the only measurable accumulation of sediment over a year of observations was in the back reef. There, the greatest sediment stress resulted from migrating sand waves over the back reef (Fig. 5). Repeated measures of fixed sediment stakes revealed periodic inundation to sediment depths exceeding 500 mm for periods of up to 100 d (Fig. 6). Sediment that accumulated on the back reef (measured at 5 stakes, Figs. 5 and 6), probably resulted from shoreward migrating intertidal sand waves.

Biotic Environment: Ecological Processes of Survival, Colonization, Growth, Competition, and Herbivory

Transplant survival.-- A simple way to determine if stromatolites can live in reef habitats and if reef-dwellers can live in stromatolite zones is through reciprocal transplantation. For this, dominant organisms from the fore reef (coralline, *Neogoniolithon strictum*), reef flat (algal turf) and back reef (soft mats of *Schizothrix*-dominated stromatolites) were transplanted into all three zones (Fig. 7).

Coralline and stromatolite-*Schizothrix* transplants had the greatest survival rates in the zone from which they had been originally taken (Fig. 8). Thus corallines thrived in the fore reef, *Schizothrix* in the back reef. Turf algae did as well in the fore reef as it did in the reef-flat from which it was taken. The results during the first half of the experiment (from June 1992 to January 1993) corresponded well with those recorded during the second half (from January 1993 to May 1993) (Fig. 8). Corallines were particularly susceptible to desiccation and died within a day of being transplanted to the reef flat (Figs. 7 and 8).

Survival of all reef components was greatest in the fore reef. Even a fair proportion of the transplanted stromatolites survived there (Figs. 7 and 8). The primary cause for stromatolite decline in the fore reefs was the stromatolite erosion from wave action. This was evident as the soft *Schizothrix*-dominated mats that form the stromatolites were being transplanted to the fore reef, we observed fine carbonate sand drifting away. The erosion stopped when a lithified horizon of the stromatolite was reached. The soft *Schizothrix* mat of the back reef (Fig. 1) did most poorly in the reef flat (Fig. 8) presumably due to desiccation-killed *Schizothrix*.

Transplant results suggest that sediment stress contributed to the low survival rate of both turf and coralline algae (Fig. 9) in the back reef. One coralline alga, *Neogoniolithon strictum* is
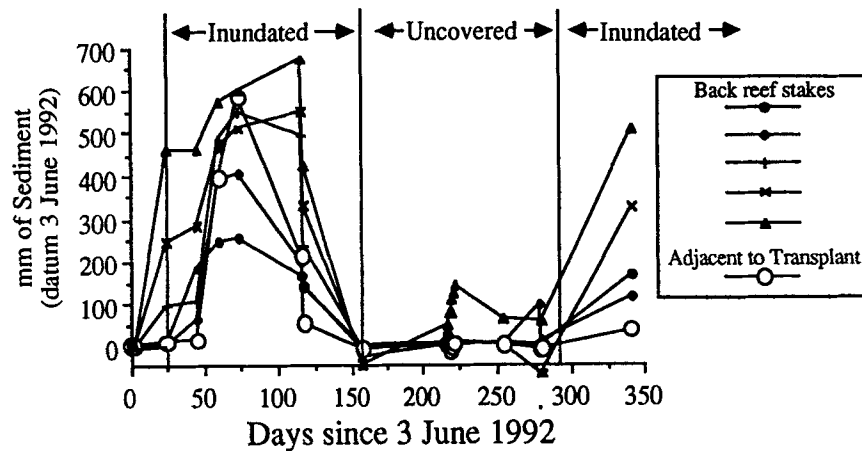
Figure 6. Annual pattern of sediment inundation measured at 6 fixed stakes in the back reef (Fig. 5). Five of the stakes run parallel with the landward edge of the back reef and one is adjacent to the back reef transplant station (open circle and is near stake #1 in Fig. 5). Similar fixed states on the reef flat and fore reef measured no accumulation of sediment over the year of observation.

uniquely capable of tolerating sediment inundation and is able to persist and grow as an unbranched crust (Steneck et al. 1997). No other reef-dwelling coralline is known to have this tolerance to sediment stress (Steneck et al. 1997). Desiccation was the primary stress in the reef flat (Fig. 9) although the rapid rate of temperature change there could contribute to thermal stress as well. The fore reef was by far, the most physically benign environment of the three zones studied (Fig. 9).

Colonization, competition, and growth.-- Colonization of underwater epoxy substrata was dominated by filamentous and crustose coralline algae in the fore reef and *Schizothrix* mat in the back reef (Fig. 10). Macroalgae other than corallines were most abundant in the fore reef. There, the noncoralline crustose alga, *Peyssonellia* sp. and the corticated macroalgae *Laurncia obtusa* were most abundant. Only the sediment-dwelling dasyclad, *Batophora oerstedii* colonized the back reef (Fig. 10) which is a zone where it is commonly found (Tables 1 and 2).

Competition for primary substrate corresponds directly with the colonization rates of hard substratum. Thus, in the back reef, where the percent of uncolonized epoxy putty is greatest (Fig. 11), competitive pressures are probably least. Both the back reef and reef flat had low rates of colonization compared to the fore reef but those low rates were probably due to sediment inundation (Fig. 6) and desiccation respectively. Over half the colonizers in the fore reef were metaphytes (turf, *Laurencia, Peyssonellia* and crustose corallines; Fig. 12) but there were also some metazoans such as *Millepora* in the fore reef and barnacles on the reef flat. Had the experiment continued for more than a year, the recruited *Millepora* would probably have over grown several of the transplants. The observed colonization rates on epoxy putty in the fore reef reflect the organisms that dominate that zone (Tables 1 and 2).

The barnacles that colonized the reef flat did so after the surveys were completed and thus were not recorded in either the quadrat (Table 1) or chain transect samples (Table 2).

Only the transplanted coralline, *Neogoniolithon strictum*, could be reliably measured at all three zones over the year of this study. By far, the fastest lateral rates of growth were in the fore reef, followed by the back reef which had about one third the rate measured on the fore reef (Fig. 13). The lowest rates were recorded on the reef flat. There, only transplants covered by water in small tide pools were used so these transplants probably suffered thermal stress (i.e., 5.9°C temperature deviation from the fore reef zone; discussed above). All three zones had significantly different growth rates (p <0.05, ANOVA).

Herbivory.-- Herbivores thought to have the greatest influence on community structure on reefs include those capable of grazing deeply calcium carbonate substrates (Steneck 1988; Steneck and Dethier 1994) such as parrotfish (Lewis 1986), sea urchins (Carpenter 1986), and limpet and chiton molluscs (Littler et al. 1995).

No herbivorous invertebrates were found in either the back reef or reef flat zones (20 quadrats in each zone). Evening observations for grazing gastropods such as *Cerithium* sp. failed to find any although hermit crabs of unknown trophic habit were observed inside cerithid shells. Herbivorous molluscs were found at very low densities on the fore reef. Two small (6 mm shell length) key hole limpets, *Fissurella angusta*, and one chiton (2 mm length) were found in 15 quadrats sampled on the two reef transects.

The most abundant herbivore was the small black regular echinoid, *Echinometra lucunter* which burrows into the ridge and feeds mostly on drift algae (Abbott et al. 1974). This
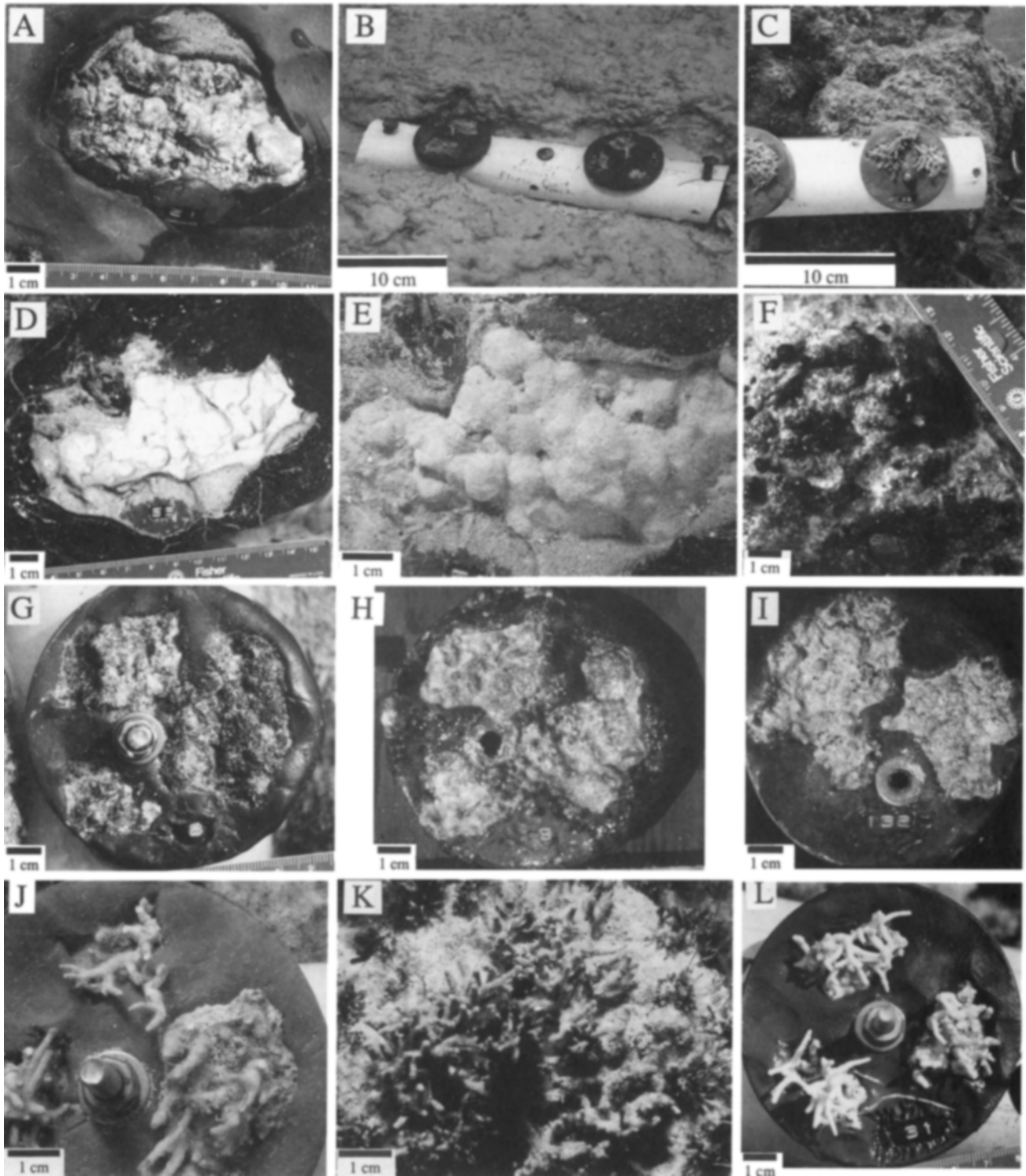
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Figure 7. Reciprocal transplant design (A-C) and representative results (D-L). Scales are in the lower left corner of each photograph. Transplants photographed soon after being transplanted are identified as t = 0, the duration of all others are given to the nearest month since t = 0. A. Transplanted stromatolite from back reef to reef flat (t = 0). B. White PVC transplant support holding petri dish filled with underwater epoxy putty into which turf (left) and coralline (right) algae were transplanted to back reef (t = 0). C. Coralline algal transplanted to the fore reef (t = 0). D. Transplanted stromatolite from back reef back to back reef 6 mo later (E) shows no change and devoid of other organisms. F. Is stromatolite transplant (A, above) from back reef to reef flat (t = 6 mo). Note that it has been so overgrown by turf algae that it obscures the original transplant. G. Turf algae transplanted from the reef flat (t = 0) back to reef flat (H; t = 6 months). I. Another turf transplant from the reef flat to the back reef (t = 6 mo). J. Coralline, Neogoniolithon strictum transplanted from the fore reef (t = 0) to the fore reef (K, 6 mo). L. Another coralline tranplanted from the fore reef to the reef flat (two days later) but bleached white and died within 24 h due to desiccation stress.

urchin was largely confined to its burrow. Because graze marks on corallines are easy to identify (Steneck 1983), the absence of such marks in the fore reef zone, suggests that these urchins are relatively unimportant as grazers in this system. Within the *Echinometra* zone (see Fig. 2) we recorded population densities averaging 55 urchins/m² (±23, SD; n=7) at T2.

Herbivory from parrotfishes (i.e., *Sparisoma* spp. and *Scarus* spp.) is one of the most important bioerosive processes impacting coral reefs. Parrotfish influence macroalgal community structure (Lewis 1986; Steneck 1988; Steneck and Dethier 1994). They also have the greatest per-bite bioerosive impact on carbonate substrata (Steneck 1986, 1988). Grazing rates of scraping herbivorous fish were greatest on the fore reef

and virtually nonexistent in the back reef and reef flat zones (Fig. 14, Table 3). In the fore reef only two species were observed grazing over a total observation period of over 5 hours (i.e., 47 and 14 five minute observations at transect one and two, respectively). Although the highest rates were recorded for the fore reef, they were more than an order of magnitude less than similar methods have yielded on the well developed coral reefs of St. Croix and Jamaica (Fig. 14).

Bite rates from other herbivores and from other fishes show virtually all fish activity is confined to the fore reef zone (Table 3). Other stromatolite-reef comparisons were made along the Exuma archipelago (locations described in Reid et al. 1995) with similar results. The stromatolites at Adderly Channel, Iguana Key, Bock Cay, Little Darby, South Halls Pond, White
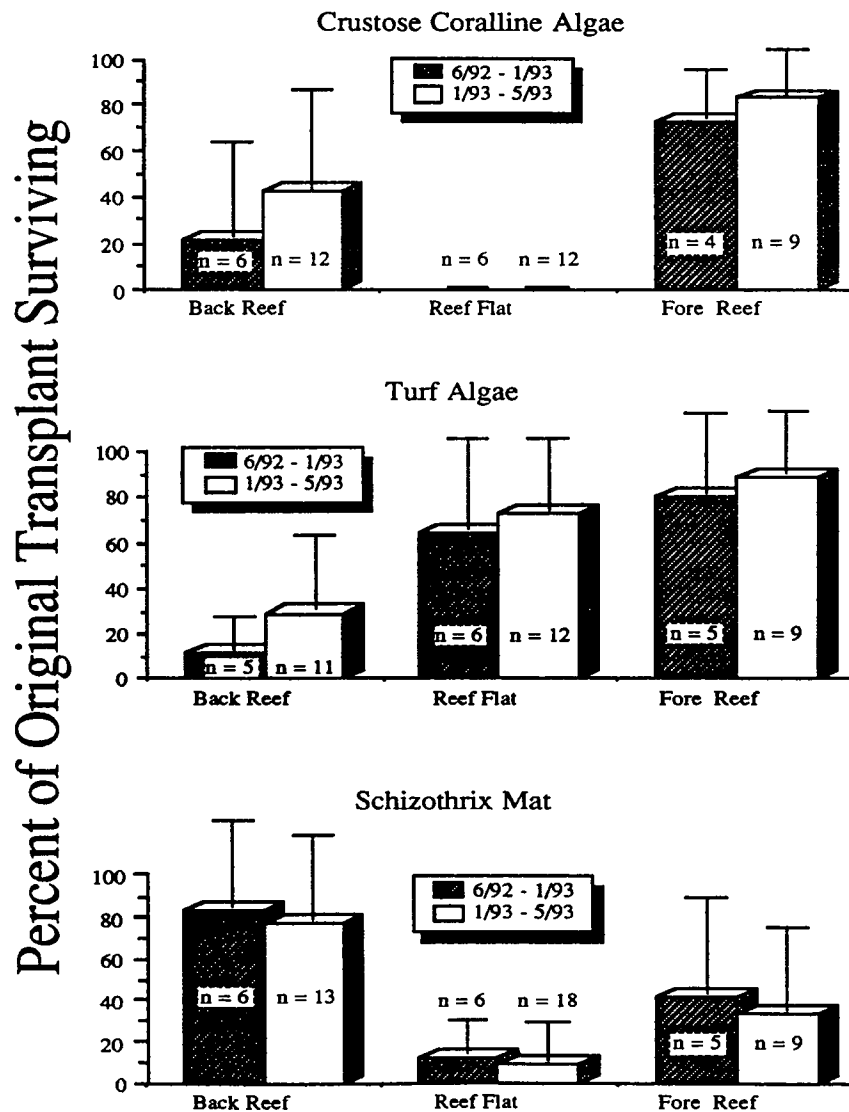

Figure 8. Survival rates of transplanted components of the reef community. The percent of the original transplant surviving for crustose coralline algae (top), turf algae (middle), and Schizothrix mats of the back reef stromatolites (bottom). Data combine results from transplants on transect 1 and 2 and show results from the period between June 1992 and January 1993 and from January 1993 and May 1993. All transplants that suffered significant mortality during the first period were replaced in January 1993. Number within the bar is the number of transplants recorded. Each bar represents the percent surviving an approximately six month period.
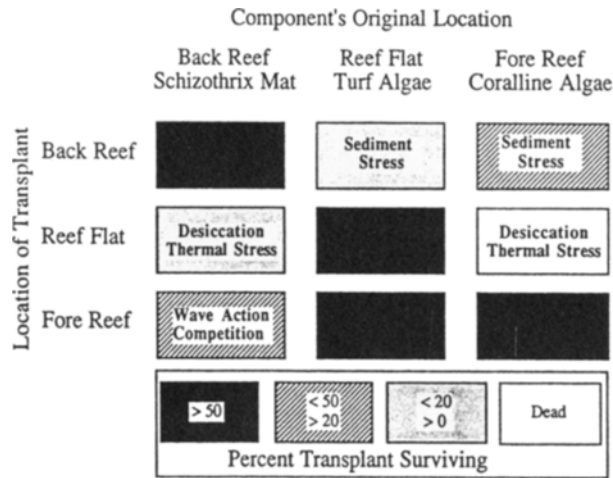
Figure 9. Summary results of transplant experiment indicating the percent of the transplant surviving (Fig. 8) and the observed cause of mortality written inside each box.

Bay Cay, and South Warderick Wells all had lower levels of herbivory than was recorded for the nearest coral reef system. Thus all known stromatolites in the Bahamas live in an environment of relatively low rates of herbivory from fishes.

An additional way to assay herbivory without human presence, is the *Thalassia* bioassay technique (Hay 1984). Using this technique, we observed the highest rates of herbivory in the fore reef habitats (Fig. 15).

SUMMARY AND CONCLUSIONS

It is probably not a coincidence that stromatolite formation in normal marine sea water is common only along the western side of Exuma Sound in the Bahamas (Reid et al. 1996). In all likelihood, the same regional ocean chemistry that creates ooid shoals and 'whitings' is necessary for stromatolite formation and lithification. This could explain why
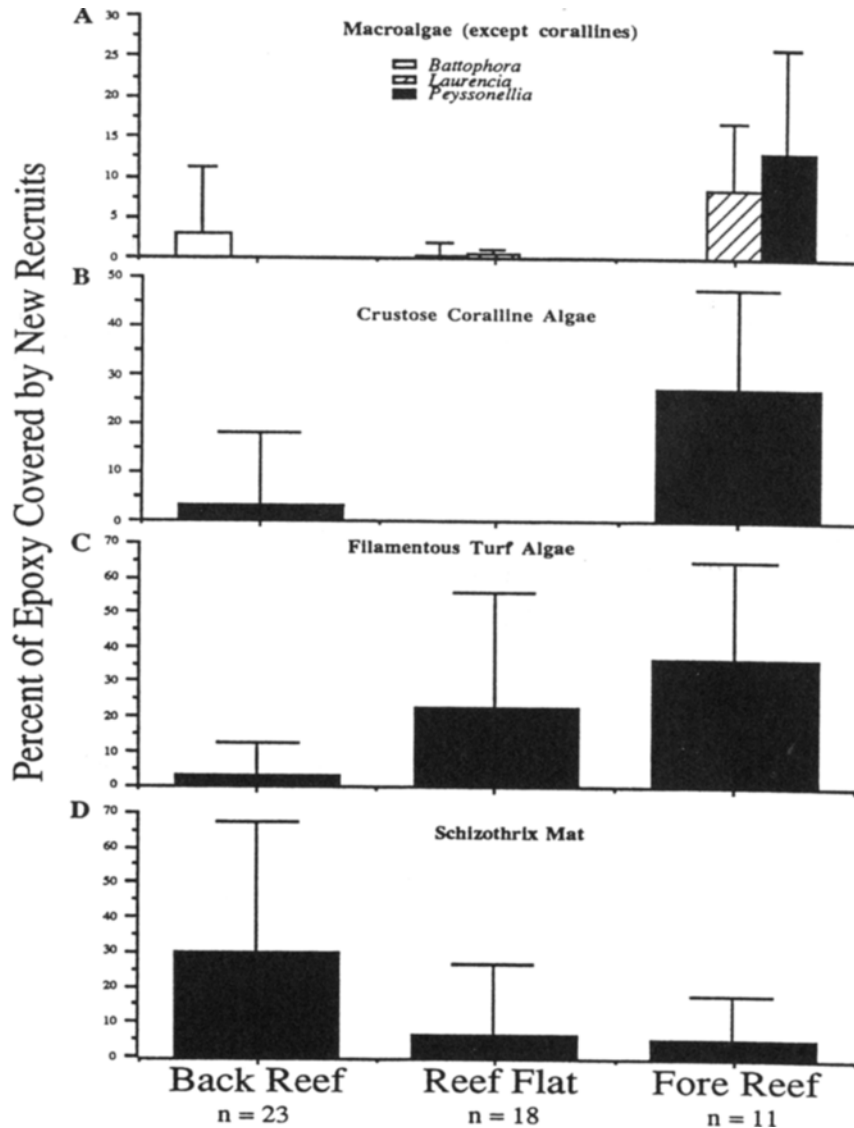

Figure 10. Colonization experiment. Percent of epoxy putty colonized A. Macroalgae, B. Crustose coralline algae (primarily Neogoniolithon strictum), C. Filamentous turf algae, Schizothrix mat. Sample sizes, n = number of epoxy substrata surveyed.
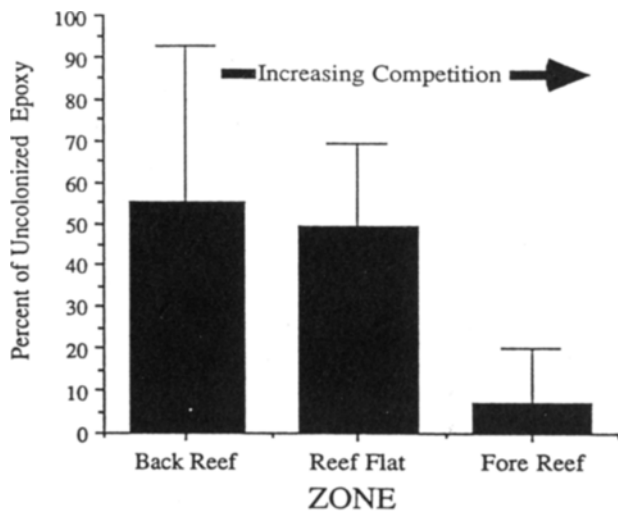
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Figure 11. Percent of uncolonized substratum as an inverse indication of competition for space. Note that Schizothrix colonization was greatest (Fig. 10) where the overall colonization rates were lowest. Data from colonization experiment therefore identical sample sizes as Fig. 10.

stromatolites are not commonly found in other physiologically stressed *ecological refuge* habitats throughout the Caribbean even though cyanobacterial mats form on those areas (e.g., on the back reef at Discovery Bay, Jamaica). Thus, the ecological question of what controls stromatolite formation presupposes we are only considering stromatolite-reef complexes under the same stromatolite-producing ocean chemistry necessary for modern (e.g., Whittle et al. 1993) and ancient (e.g., Awramik and Riding 1988) stromatolite development. Specifically, in our study, we examined gradients and habitats of reef and stromatolites that are close enough to one another to essentially be in the same water mass. Our question then became, given the ocean chemistry found in the Exumas, what

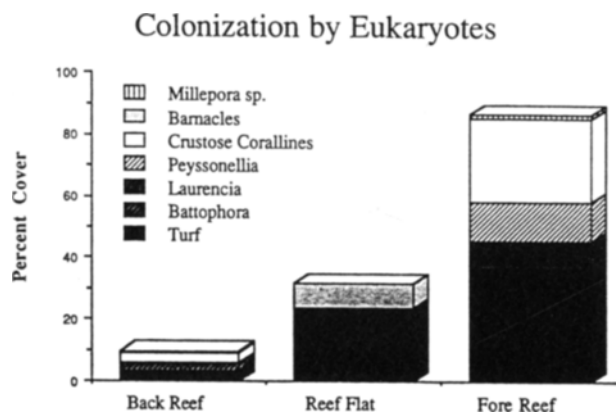## Colonization by Eukaryotes

Figure 12. Colonization rates by eukaryotes. Staked histogram showing average percent cover over a year of all metazoan and metaphyte groups that colonized the epoxy putty substrata. Note that eukaryotes were the dominant colonizers in the fore reef where primary space was most limited (Fig. 11). Among the colonizers are coral reef building Millepora and crustose coralline algae.
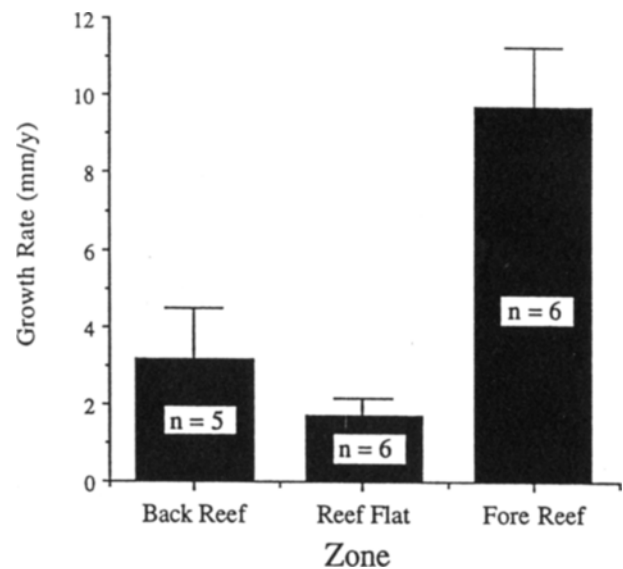

Figure 13. Lateral growth rate of the crustose coralline alga, Neogoniolithon strictum. Several measurements were taken for each of the three plants on each of the transplants (e.g., Fig. 7). Variance is expressed as +1 standard error. Sample sizes are given within each bar and represent the number of transplants that were measured. Corallines that died were omitted from the growth rate measurements.

are the ecological controls on stromatolites development in a modern reef environment?

The stromatolite-algal ridge-reef assemblages of Stocking Island provide an excellent laboratory in which to examine the patterns of distribution and abundance of stromatolites relative to the abundance of modern eukaryote reef-dwelling biota. The back reef environment is dominated by stromatolites composed of a near monoculture of Schizothrix and relatively few eukaryotes (Figs. 3, 4, and 16). The low-diversity back reef grades into a filamentous algal turf-stromatolite complex on the reef-flat and to a diverse eukaryote-dominated reef-assemblage of coral, coralline, macro- and turf algal assemblages on the fore reef (Tables 1 and 2, Fig. 16).

Several independent measures indicate the Stocking Island stromatolite complex is physiologically stressed and grades to a relatively benign fore reef (Fig. 16). Whereas the reef flat experiences desiccation and thermal stress as would be expected for an intertidal zone in the tropics, the sediment stress in the back reef is unique (Figs. 5, 6, and 16). Periodic and prolonged inundation of back reef substrates preclude the establishment of long-lived eukaryotes as evidenced in our transplant experiments (Figs. 8 and 9). The coralline algae, *Neogoniolithon strictum*, transplanted to that zone was found to be surprisingly hardy. This is because of coralline's natural ability to withstand environments having a low productivity potential (e.g., Vadas and Steneck 1988), but also because this species may be uniquely capable of shunting photosynthates
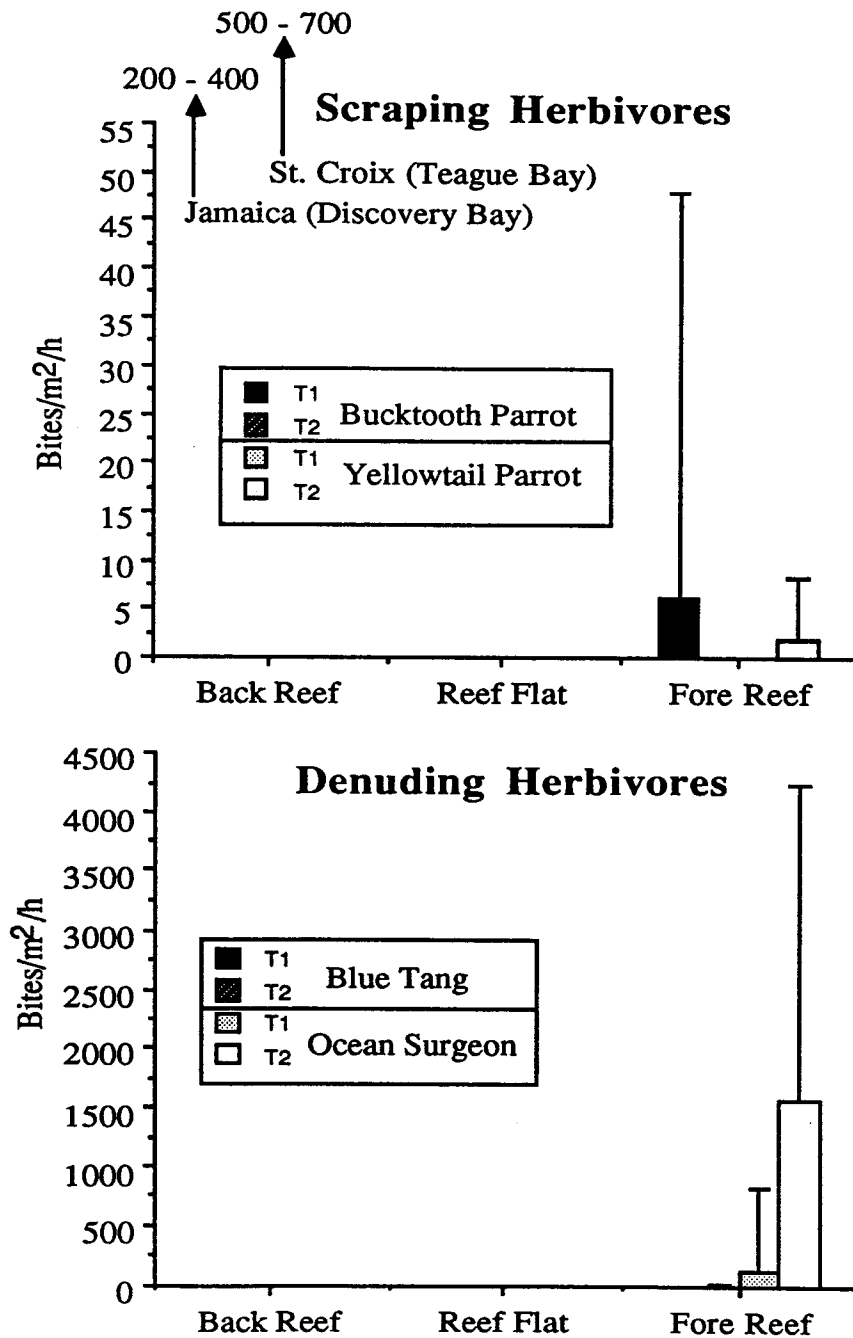
Figure 14. Grazing rates of scraping (scarid) and denuding (acanthurid) herbivorous fish at three zones (all results and sample sizes are given in Table 3). Comparison of the same technique used in St. Croix and Jamaica (from Steneck 1994) for scraping herbivores on coral reefs is indicated in the upper left corner of the top graph.

within its thallus to nourish its buried portions (Steneck et al. 1997).

Stromatolites dominate in refugia from ecological pressures. All measured ecological pressures increased toward the fore reef (Fig. 16). Rates of colonization (Figs. 10 and 12) and growth rates of coralline algae (Fig. 13), competition with them, other macroalgae and metazoans (Fig. 11) and rates of herbivory from both invertebrates (i.e., sea urchins) and

vertebrates (fishes, Figs. 14 and 15; Table 3) were greatest in the fore reef and lowest in the stromatolite-dominated back reef (Fig. 16).

Because herbivory has been singled out by many authors as a leading cause of the decline of ancient stromatolites (Garrett 1970; Awramik 1990; Riding 1991; Schubert and Bottjer 1992), fish grazing comparisons were done on five other subtidal stromatolite-reef complexes over an approximately

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Table 3. Fish bite rates per zone. Bite rate recorded at all the five sites in three reef zones (i.e., back reef, reef flat, and fore reef) at two transects (e.g., BR-1 and BR-2 are back reef samples from transects 1 and 2 respectively). Sample size ("n") indicates the number of 5 minute observation periods. All data were transformed to per hour rates for comparision with other studies (see text). Variance is expressed as one standard deviation ("SD"). Herbivore trophic groups are defined in Steneck (1988; see text).

| Species and Trophic Groups	Common Name	Bite Rates (bites/m^2/h)											
		BACK REEF				REEF FLAT				FORE REEF			
		n = 39		n = 30		n = 40		n = 24		n = 47		n = 14	
		BR-1	SD	BR-2	SD	RF-1	SD	RF-2	SD	FR-1	SD	FR-2	SD
SCRAPING HERBIVORES													
Sparisoma radians	Bucktooth Parrotfish	0	0	0	0	0	0	0	0	6	42	0	0
Sparisoma rubripinne	Yellowtail Parrotfish	0	0	0	0	0	0	0	0	0	0	2	6
DENUDING HERBIVORES													
Acanthurus coeruleus	Blue Tang	0	0	0	0	0	0	0	0	0	0	3	7
Acanthurus bahianus	Ocean Surgeon	0	0	0	0	0	0	0	0	245	987	1563	2670
NONDENUDING HERBIVORES													
Stegastes leucostictus	Beaugregory	0	0	0	0	0	0	0	0	64	265	0	0
Stegastes planifrons	Threespot Damsel	0	0	0	0	0	0	0	0	39	179	0	0
OMNIVORES													
Gramma loreto	Fairy Basslet	0	0	0	0	0	0	0	0	6	42	0	0
Paraclinus fasciatus	Banded Blenny	0.4	6	0	0	0	0	0	0	3	21	0	0
Malacoctenus triangulatus	Saddled Blenny	0	0	0	0	0	0	0	0	9	47	103	385
Serranus tabacarius	Tobaccofish	0	0	0	0	0	0	0	0	6	42	51	192
Halichoeres maculipinna	Clown Wrasse	0	0	0	0	0	0	0	0	3	21	0	0
Halichoeres bivittatus	Slippery Dick	0	0	0	0	0	0	0	0	34	128	2	6
Thalassoma bifasciatum	Bluehead Wrasse	0	0	0	0	0	0	0	0	499	1519	483	653
Total Bite Rate (all fish)		0.4		0		0		0		915		2207	
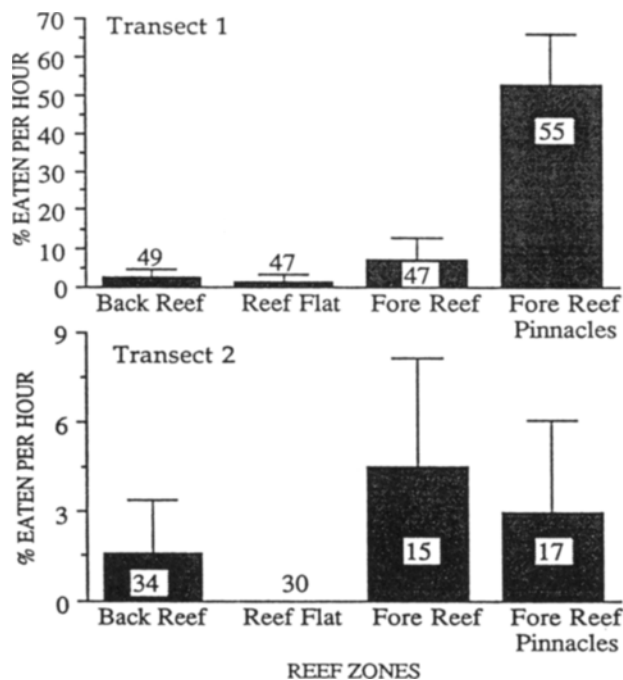
Figure 15. Thalassia bioassay technique for determining rates of herbivory. Number of observations are given with each bar. Variance is given as one standard deviation. Overall the highest grazing rates were on the fore reef.

120 km stretch of the Exuma archipelago (see Reid et al. 1996). Invariably, grazing rates were lower on stromatolite reefs than they were on their nearby coral counterparts (see text). While this supports the *ecological refuge paradigm*, it

doesn't explain why herbivory is so low. If important herbivores such as fish (Lewis 1986; Steneck 1988) were in the vicinity and there were no strong currents to interfere with their grazing, as was the case for the Lee Stocking Island stromatolites (Dill et al. 1991) but not the case for the Darby stromatolites (Reid et al. 1996), why then were grazing rates so uniformly low?

It is possible that calcium carbonate-saturation that characterizes the Bahamas and the Exuma region may be necessary for stromatolite development by both facilitating sediment-trapping cyanobacteria (Riding 1990) and also by interfering with herbivory. Recent research demonstrated that calcium carbonate can deter herbivorous fish (Pitlik and Paul 1997; Paul 1997; Hay 1997) that use acid for digestion (e.g., see Horn 1989) without increasing the algas toughness or resistance to disturbance (sensu Steneck 1988). The herbivorous fish most affected by calcium carbonate are the acanthurids such as blue tangs and ocean surgeons. While these were one of the most abundant herbivores in the forereef, they were virtually absent from the back reef (Table 3). However parrotfish, that regularly ingest calcium carbonate, were also rare in the back reef zone (Fig. 14 top). The unusually low rates of grazing from carbonate-scraping parrotfish in the fore reef (Fig. 14 top), suggests that low levels of herbivory alone may not explain for the lack of stromatolites in the fore reef.

Perhaps most important was the observation that stromatolites

transplanted to the fore reef persisted (Fig. 8). This was also true for the transplanted corallines and algal turfs. It indicates that the fore reef environment is not inhospitable to any of the groups found in this system and thus species diversity and competition for space is very high (Fig. 11).

While paleontologists debate whether stromatolites should be called "disaster forms" (sensu Schubert and Bottjer 1992) because they frequently build reefs following major marine extinction events or "survival forms" (sensu Soja 1994) because they obviously survive such events, all indications are that stromatolite reefs form where ecological pressures are low. Based on our research, we cannot reject the *Ecological Refuge Paradigm*. However the cyanobacteria that form stromatolites are common on modern reefs. Such reefs are

often dominated by relatively inconspicuous but highly productive turf algae (Adey and Steneck 1985; Carpenter 1986; Hatcher 1990) which often has a majority of its biomass comprised of cyanobacteria (Adey and Steneck 1985; Hatcher 1990). That the stromatolites we transplanted to the reef environment, did not die or disappear entirely, supports the idea that stromatolite-forming cyanobacteria simply became incorporated into eukaryotic bioherms throughout the Phanerozoic and because they are more eurytopic than most of their eykaryotic counterparts, they survive stresses and even mass extinctions that periodically eliminate the modern reef builders.

There is no smoking gun associated with episodes of stromatolite declines since their global dominance in the

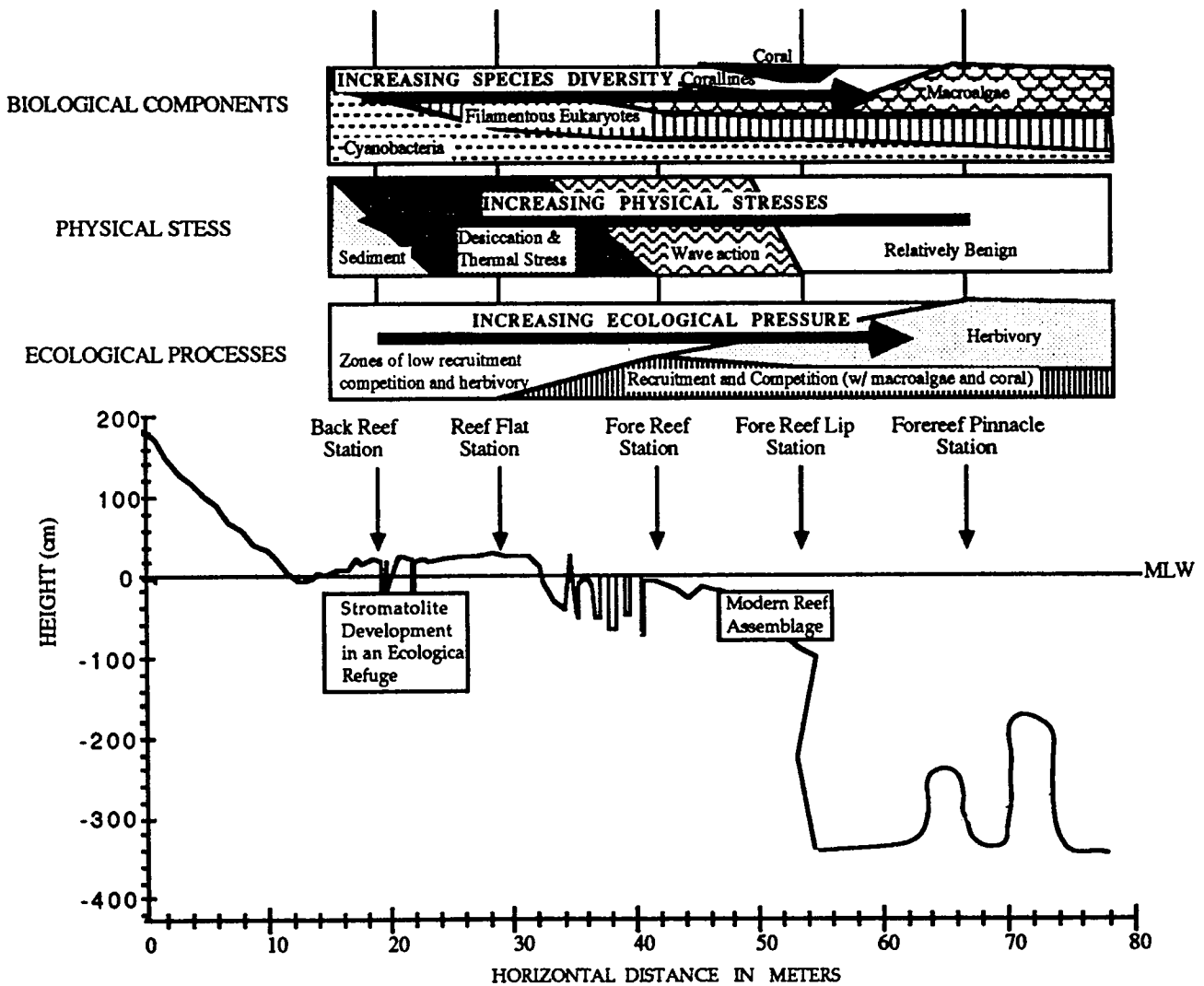## STOCKING ISLAND STROMATOLITE - REEF GRADIENT

Figure 16. Ecological factors controlling the distribution of stromatolites along the Stocking Island stromatolite-reef gradient. The back reef where stromatolites dominate the biota is an ecological refuge. There, species diversity (Tables 1 and 2) and functional group diversity (Fig. 4) are low, physical stresses especially from sediment (Figs. 5 and 6) are high, so that most other organisms cannot survive (Figs. 8 and 9) and other ecological pressures from reef dwellers are low because they cannot colonize (Fig. 10), they grow slowly (Fig. 13) and experience virtually no grazing (Fig. 14, 15, or other activity from fish; Table 3).

Proterozoic. This may be because the constituent organisms of stromatolite reefs are not extinct. At least as a functional group, sediment-binding cyanobacteria may have always been present and on occasions when, or in locations where, ecological pressures such as competition, colonization, consumption, or disruption become very low, these delicate, microbially-produced reefs show themselves. Today we only get glimpses of them in these relatively rare ecological refugia.

ACKNOWLEDGMENTS

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