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AT SALT RIVER SUBMARINE CANYON,
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Scleractinian Coral Recruitment Patterns at Salt River Submarine Canyon, St. Croix, U.S. Virgin Islands

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Abstract. Scleractinian coral recruitment patterns were studied at depths of 9, 18, 27 and 37 m on the east and west walls of Salt River submarine canyon, St. Croix, U.S. Virgin Islands, by censusing coral juveniles which settled on experimental settling plates placed on the reef for 3–26 months as well as coral juveniles within quadrats on the reef. The most common species in the juvenile population within quadrats were *Agaricia agaricites*, *Porites astreoides*, *Madracis decactis*, *Stephanocoenia michelinii*, and *A. lamarcki*. The only species settling on settling plates were *Agaricia* spp., *Madracis decactis*, *Porites* spp., *Stephanocoenia michelinii* and *Favia fragum*. A total of 271 corals settled on 342 plates, with 51% of the juveniles on the east wall and 49% on the west wall. Of these 34% settled on horizontal surfaces and 66% on vertical surfaces. Based on results from quadrats, *Agaricia agaricites* and *Porites astreoides* had high recruitment rates relative to their abundance on the reef. In contrast, *Agaricia lamarcki*, *Montastraea annularis*, *M. cavernosa* and *Siderastrea siderea* had high amounts of cover compared to their abundance as juveniles within quadrats. The mean number of juveniles per m² within quadrats ranged from 3 to 42. In general, there was a decrease in the mean number of juveniles and the number of species with depth. Total number of juveniles on settling plates was highest at 18 m on both walls. The largest number within quadrats was at 18 m on the east wall, followed by 9 m and 18 m on the west wall. High rates of coral recruitment tended to be associated with low algal biomass and relatively high grazing pressure by urchins and fishes.

Introduction

Scleractinian coral community structure on Caribbean coral reefs is a response to physical factors such as light, water circulation, and sedimentation, and to biological factors such as competition, predation, and grazing. The

distribution and relative abundance of hard corals reflect patterns of larval recruitment (Connell 1973; Birkeland 1977; Bak and Engel 1979; Birkeland et al. 1981; Rylaarsdam 1983), asexual reproduction or fragmentation (e.g., Highsmith 1982), mortality (Connell 1973; Bak and Engel 1979; Bak and Luckhurst 1980), regenerative capabilities (Bak et al. 1977; Bak 1983), and aggressive interactions between coral species (Lang 1970; Lang 1973; Bak et al. 1982).

Several studies of Caribbean coral reefs document changes in coral species composition with depth (e.g., Porter 1972; Goreau and Goreau 1973). However, there are few published studies on coral recruitment at different depths (see Birkeland 1977; Bak and Engel 1979; Birkeland et al. 1981). Birkeland (1977), working at 9, 20, and 34 m, noted an inverse relationship between number of coral recruits and biomass of algae (and other fouling organisms) on Caribbean and Pacific reefs off Panama. In Curacao and Bonaire, Bak and Engel (1979) studied recruitment and survival of juveniles from 3 to 37 m. They noted some species with few juveniles but high rates of survival, others with lower survival but higher recruitment rates, and, finally, some species which produce few juveniles and appear to depend more on fragmentation than sexual reproduction for their success.

Successful coral recruitment and survival depend on the complex interaction between competition for space and disturbance by grazers such as parrotfishes, surgeonfishes, and sea urchins. Grazing and browsing by fishes and urchins play a major role in determining both algal and coral community structure. Corals more readily settle when grazing by sea urchins and fish is intense enough to prevent filamentous, non-coralline algae from monopolizing available space (Dart 1972; Sammarco 1975; Brock 1979). Intense grazing by *Diadema antillarum* Philippi decreases colonization by coral larvae while low grazing pressure increases coral recruitment (Sammarco 1975, 1980). This urchin can feed directly on live coral (Bak and van Eys 1975; Gladfelter et al. 1979). When grazing pressure from *Diadema* is too high, juveniles are killed by abrasion or removed entirely. When grazing is absent or minimal, coral mortality is high be-

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cause of space competition with algae (Sammarco 1980).

Algal biomass increases when herbivores are excluded (e.g., Ogden et al. 1973; Sammarco et al. 1974; Mathieson et al. 1975). Herbivorous fishes are mostly found in the Scaridae (parrotfish), Acanthuridae (surgeonfish) and Pomacentridae (damselfish) families (Randall 1967; Ogden and Lobel 1978). Parrotfishes are able to crush and grind algal-covered dead coral. Surgeonfishes are browsers which swim in large schools feeding on algae without ingesting calcium carbonate. Territorial behavior of damselfishes limits grazing and browsing by other herbivorous fishes (Vine 1974; Brawley and Adey 1977) and inhibits successful coral settlement, as corals can not settle and survive on substrate heavily covered by non-coraline algae.

Our objective was to describe the distribution of hard corals (Scleractinians and the hydrozoan *Millepora* spp.) in Salt River submarine canyon, St. Croix, U.S. Virgin Islands, over a depth range from 9 m to 37 m and to determine the relationship between this distribution and the distribution of juvenile corals which settled on the reef and on experimental settling surfaces. We hypothesized that coral community structure (e.g., species composition, live coral cover) and the number and species of juvenile corals settling on experimental surfaces and within reef quadrats would change with depth or location in the canyon. Aspects of the relationship of coral recruitment to algal biomass and grazing intensity were also examined.

Salt River submarine canyon cuts across the island shelf about halfway along the northern coast of St. Croix. Starting in about 5 m of water near shore, the canyon extends seaward approximately 350 m to a depth of 90 m (Hubbard et al. 1981). At the study sites near the mouth of the canyon, there are some conspicuous differences between the east and west walls. The west wall has more overhangs, outcroppings, small caves, and distinct sand channels. The slope of both walls is vertical in several locations.

Research was done at depths of 9 m, 18 m, 27 m and 37 m on both walls near the mouth of the canyon. The canyon floor drops precipitously from about 40 m to abyssal depths here. The west wall slopes from 7.5–9 m to a depth of about 40 m at the study area. On the east side, there is a more gradual slope from 9 m to about 15 m where the wall abruptly drops to approximately 46 m. The 9 m study site on the west wall therefore occurs where the steep slope begins, while the 9 m site on the east wall is an area with little structural relief.

Because this research required several hours of deep diving, it would not have been possible without the use of NOAA's underwater habitat (Hydrolab). The Hydrolab is stationed at a depth of about 15 m near the head of Salt River canyon. Most of the field work was accomplished during two 7 day missions in the Hydrolab, the first in March 1981 and the second in June 1982. Additional research was done with conventional surface diving before and after the missions.

Materials and Methods

Reef Structure

Linear transects provide information on percent cover by reef organisms and non-living substrate as well as relative abundance of different coral species. Eight linear transects were established along depth contours at 9 m, 18 m, 27 m and 37 m along the east and west canyon walls for a total of 64 transects.

The transect method is a modification of methods described previously (e.g., Loya and Slobodkin 1971; Porter 1972; Adey et al. 1981) and is described in detail in Rogers et al. 1983. A 10 meter line is stretched over the surface of the reef. Subsequently, a chain is placed under the line along the bottom contours. The observer records the number of chain links covering live and dead coral, and other reef components, attempting to measure all surfaces under the chain.

As an indication of topographical complexity, a "spatial index" is calculated as the ratio of the number of meters of chain to the number of meters of line. The lowest possible index is 1.

Coral Recruitment

Settling Plates. To study recruitment of juvenile corals, we placed slabs of *Acropora palmata* (cross-sections of branches cut with a rock saw, roughly 120 cm² on a side) at depths of 9, 18, 27, and 37 m on both walls. Plates were oriented horizontally and vertically to test for possible effects of variations in light and sedimentation. The plates, in groups of 3, were bolted to small plastic bases which were secured to the substrate with nails. Forty-eight plates (24 vertical and 24 horizontal) were placed at each of the 8 study depths during the first Hydrolab mission in March 1981. Every 3 months thereafter, until the second mission in June 1982, 1 horizontal and 1 vertical plate were collected from each depth and examined with a dissecting microscope for juvenile corals. Orientation (top, bottom, vertical side, edge) and size of each coral were recorded. When possible, corals were identified to species. During the second Hydrolab mission, 24 plates were collected from each depth. All remaining plates were collected in May 1983.

Quadrats. Approximately 20 one-m² quadrats were examined at each of the study depths near the transect sites. All juvenile corals were identified with a juvenile defined as a coral with a maximum diameter less than or equal to 40 mm. This size probably represents corals 3 years old and younger (see Bak and Engel 1979). When small corals were clearly the product of fragmentation of older colonies they were omitted.

Algal Biomass

Algal biomass was estimated by scraping an approximately 25 cm² area from the top and bottom surfaces of horizontal settling plates and from each side of vertical plates. All plates from the first 4 collections were sampled, while 5 horizontal and 5 vertical plates were sampled from each depth after the fifth collection. Samples were placed in vials with 5% formalin in seawater. A 10% HCl solution was added to decalcify any carbonate sediments and calcareous algae scraped off the plates. After removal of conspicuous non-algal material, samples were filtered through pre-weighed Whatman #2 filters which had been rinsed with 250 ml of distilled water and carefully dried in an oven and desiccator. Then, 100 ml of distilled water was passed through the filter to remove salts. Filters were weighed again after drying in an oven and desiccator, and the weight of the algae was recorded.

Grazing Organisms

The abundance of the sea urchin *Diadema antillarum* at each study depth on the east and west walls was estimated by swimming along the depth contour and recording the total number of sea urchins observed within 1 or 2 meters on either side of each coral transect line (see above). Areas surveyed at each depth ranged from 160 m² to 320 m².

The relative abundance of fishes from each study depth on the two walls was estimated with the technique of Thompson and Schmidt (1977) (see also Jones and Thompson 1978). Each of 4 observers did two 50 minute surveys per depth for a total of 8 surveys per depth on each wall. For each survey, a diver swam along the depth contour recording all fish species seen in five 10 minute intervals, noting only the interval during which each species was first encountered. Species seen in the first interval received a score of 5, those in the second interval a score of 4, and so on. Individual species scores from all 8 surveys at each depth were totalled. Here we report only on the results for the three major herbivorous families, the Scaridae, Acanthuridae, and Pomacentridae.

Statistical Analyses

When analysis of variance (ANOVA) indicated that a significant difference in means existed, the Student-Newman-Keuls test was used to determine which means differed significantly (Sokal and Rohlf 1969). A confidence level of $P < 0.05$ was used for all statistical tests, and all percentage data were transformed (arcsine) prior to statistical analyses (Sokal and Rohlf 1969).

Results

Reef Structure

Coral transect results (Table 1) indicate that the highest mean percent cover of live coral on both the east and west walls occurred at 18 m. Percent live coral ranged from 6 ± 6 (SD) to 24 ± 8 (SD) on the east wall, and from 5 ± 4 (SD) to 24 ± 6 (SD) on the west wall. The low percent live coral cover at 37 m was correlated with a high cover by sponges.

Mean percent of dead coral was highest at 9 m on both walls. Percent dead coral ranged from 50 ± 12 (SD)

Table 1. Percent live and dead coral, total number of species, and spatial indices within transects on the east and west walls of Salt River canyon

Location	Live	Dead	Total no. of species	Spatial Index
9 m West Wall	19 ± 7 a*	69 ± 8 g	17	1.4 ± 0.2
18 m West Wall	24 ± 6 a	62 ± 7 g	17	1.9 ± 0.6
27 m West Wall	21 ± 5 a	50 ± 12 h	12	1.6 ± 0.3
37 m West Wall	5 ± 4 b	61 ± 15 g	4	1.3 ± 0.2
9 m East Wall	13 ± 7 d	77 ± 11 e	13	1.2 ± 0.1
18 m East Wall	24 ± 8 c	57 ± 10 f	18	1.7 ± 0.3
27 m East Wall	14 ± 9 d	56 ± 12 f	15	1.6 ± 0.3
37 m East Wall	6 ± 6 d	51 ± 10 f	10	1.5 ± 0.2

* Mean values designated by the same letter do not differ significantly (ANOVA). a significantly higher than b; c significantly higher than d; e significantly higher than f; g significantly higher than h

to 69 ± 8 (SD) on the west wall and from 51 ± 10 (SD) to 77 ± 11 (SD) on the east wall.

The spatial index was highest at 18 m for both walls of the canyon. The lowest spatial index was found at 9 m on the east wall. Number of coral species was significantly lower at 37 m on both walls (Table 1).

Twenty-six hard corals were found within transects (Table 2). *Agaricia lamarcki* was the most abundant species at 27 m and 37 m on both walls. At 9 and 18 m, the dominant corals were *Agaricia agaricites*, *Madracis decactis* and *Montastraea cavernosa*.

Table 2. Relative abundance (percent cover) of hard corals on the east and west walls of Salt River canyon

	East Wall				West Wall			
	9 m	18 m	27 m	37 m	9 m	18 m	27 m	37 m
<i>Stephanocoenia michelinii</i> *		1.6	3.4	1.5	13.3	4.0	7.0	3.9
<i>Madracis decactis</i> *		12.0	10.4	14.4	3.3	30.9	6.0	15.4
<i>Acropora cervicornis</i>	4.6							
<i>Agaricia agaricites</i> *	3.0	14.2	19.5	3.8	17.8	18.5	6.4	
<i>Agaricia lamarcki</i> *		11.9	43.3	48.4		12.7	53.4	79.9
<i>Agaricia fragilis</i> *				15.7		1.0	0.4	
<i>Helioseris cucullata</i>		0.6	1.2		0.5	3.3		
<i>Siderastrea siderea</i> *	9.0	5.6	5.4	9.2	10.4	6.0	8.5	1.0
<i>Porites astreoides</i> *	6.6	7.6	2.9		7.2	5.6	1.8	
<i>Porites porites</i>					1.1			
<i>Favia fragum</i>								
<i>Diploria labyrinthiformis</i>		4.9			1.1			
<i>Diploria strigosa</i>	9.2	2.3			0.4			
<i>Colpophyllia natans</i>		2.8			5.0	5.5	0.7	
<i>Colpophyllia breviserialis</i>		0.1			4.8	0.3		
<i>Montastraea annularis</i> *	6.9	10.7	5.9		10.6	4.3	6.0	
<i>Montastraea cavernosa</i> *	47.6	12.7	4.0	1.5	12.1	4.5	8.9	
<i>Meandrina meandrites</i> *	3.3	3.6	1.0	1.3	7.4	0.4	0.4	
<i>Dichocoenia stokesi</i>	3.0	2.6	0.5			2.0		
<i>Mussa angulosa</i>		0.2	0.4					
<i>Scolymia</i> sp.	0.2		0.5	2.1	0.1		0.3	
<i>Isophyllia sinuosa</i>	0.2							
<i>Mycetophyllia ferrox</i>		2.9	0.6					
<i>Mycetophyllia aliciae</i>				1.9				
<i>Eusmilia fastigiata</i>					0.2	0.2		
<i>Millepora</i> spp.	6.4	3.4	1.2		4.7	0.8		

* Denotes species which contribute 5% or more of the live coral cover in one or more sets of transects

Table 3. Distribution and orientation of coral juveniles on settling plates, east and west walls of Salt River canyon

	9 m		18 m		27 m		37 m		Totals	
	East	West	East	West	East	West	East	West	East	West
Total no. of juveniles	16	38	54	48	36	34	32	13	138	133
Vertical (no., %)	9 (56)	21 (55)	41 (76)	20 (42)	31 (86)	24 (71)	22 (69)	10 (77)	103	75
Horizontal (no., %)	7 (44)	17 (45)	13 (24)	28 (58)	5 (14)	10 (29)	10 (31)	3 (23)	35	58
Top		1 (3)	1 (2)	1 (2)	3 (8)	1 (3)	2 (6)	1 (8)	6	4
Bottom	7 (44)	16 (42)	12 (22)	27 (56)	2 (6)	9 (26)	8 (25)	2 (15)	29	54
Total no. of <i>Agaricia</i> spp. juveniles	9	26	32	17	21	19	2	2	64	64
Vertical (no., %)	4 (44)	14 (54)	27 (84)	11 (65)	20 (95)	17 (89)	1 (50)	1 (50)	52	43
Horizontal (no., %)	5 (56)	12 (46)	5 (16)	6 (35)	1 (5)	2 (11)	1 (50)	1 (50)	12	21
Top		1 (4)	1 (3)		1 (5)		1 (50)	1 (50)	3	2
Bottom	5 (56)	11 (42)	4 (13)	6 (35)		2 (11)			9	19

Table 4. Coral juveniles within quadrats on the east and west walls of Salt River canyon

Location	Total no. of juveniles	Area surveyed (m ²)	No. of juveniles per m ²	Range in juveniles per m ²	Total no. of species
East Wall					
9 m	257	20	13 b*	4–34	15
18 m	792	19	42 a	15–80	16
27 m	369	20	18 b	1–58	15
37 m	106	20	5 b	0–18	10
All depths	1524	79	19	0–80	
West Wall					
9 m	668	20	33 c	10–68	24
18 m	553	19.75	28 c	8–64	15
27 m	152	19.75	8 d	1–25	10
37 m	58	19	3 d	0–10	6
All depths	1431	78.50	18	0–68	

* Mean values designated with the same letter do not differ significantly. a is significantly larger than b; c is significantly larger than d

Coral Recruitment

Settling plates. A total of 271 juvenile corals were observed on 342 settling plates during the 26 month study. Of the corals which were identifiable to species (189), 68% were *Agaricia* spp., 20% *Madracis decactis*, 11% *Porites* spp., 2% *Favia fragum*, and 1% *Stephanocoenia michelinii*. Fifty-one percent of the corals settled on the east wall plates and 49% on west wall plates. Thirty-eight percent of all juveniles settled at 18 m (Table 3).

Of all the juveniles, 34% settled on horizontal surfaces and 66% on vertical surfaces (includes 37% on sides of vertical plates and 29% on edges). Of all corals which settled on horizontal surfaces, 89% settled on the bottom of the plates and 11% on the top.

Orientation of coral juveniles changed with depth on both walls, with similar numbers of corals settling on horizontal bottom surfaces as on vertical surfaces in shallower water, and an increasing percentage of corals settling on vertical surfaces at deeper depths. This shift in orientation was evident at 18 m on the east wall but not

until 27 m on the west wall. Orientation of *Agaricia* juveniles (Table 3) followed this same pattern, showing the shift to vertical surfaces from horizontal undersurfaces with increasing depth and a difference in orientation between the east and west walls at 18 m.

Coral juveniles ranged in size from 1 mm to 31 mm in greatest dimension. Corals present on plates after 26 months included not only the largest juvenile measured, but many only 1–2 mm across. A minimum growth rate of 1.2 mm/month can be calculated based on the size of the largest juvenile found, an *Agaricia agaricites*.

Quadrats. A total of 1,524 juvenile corals were observed in quadrats on the east wall and 1,431 on the west wall (Table 4). Omitting the results from 9 m on the east wall, we find a decrease in the number of coral juveniles with depth, the number of juveniles per m², and the number of species. The number of juveniles per quadrat ranged from 0 to 80. On the east wall, the mean number of juveniles per m² was significantly higher at 18 m than at all other depths. On the west wall, the juvenile density at 9 m and 18 m was significantly higher than at 27 m and 37 m.

Of all the juveniles that were observed, 47% were *Agaricia agaricites*, 27% *Porites* spp., 13% *Madracis decactis*, 3% *Agaricia lamarcki*, and 2% *Montastraea cavernosa*. A total of 29 species were present as juveniles, with the distribution of the species changing markedly with depth (Table 5). *Madracis decactis* was more abundant at 37 m on both walls than *Agaricia agaricites*.

Algal Biomass

Mean algal biomass (Table 6) was significantly higher at 9 m on the east wall (25 ± 20 g/m²) and significantly lower at 9 m on the west wall (5 ± 4 g/m²) than at all other depths (ANOVA, following log transformations). Algal biomass on the upper surfaces of horizontal settling plates was higher than on lower (bottom) surfaces (*t* test, $P < 0.05$). Biomass on vertical surfaces did not differ from biomass on bottom surfaces, but it was significantly lower than on top surfaces of horizontal plates.

Table 5. Distribution of hard coral species as juveniles: percent of total number of juveniles within quadrats

	East Wall				West Wall			
	9 m	18 m	27 m	37 m	9 m	18 m	27 m	37 m
<i>Stephanocoenia michelinii</i>	0.8	2.3	13.3	18.3	10.9	4.7	10.5	8.6
<i>Madracis decactis</i>	4.7	10.6	8.1	41.3	1.6	23.3	25.0	69.0
<i>Madracis mirabilis</i>					0.1			
<i>Acropora palmata</i>					0.1			
<i>Acropora cervicornis</i>	2.7				0.1			
<i>Agaricia agaricites</i>	27.6	60.2	42.8	17.3	53.9	45.6	42.1	3.4
<i>Agaricia lamarcki</i>		3.0	6.5	9.6	0.1	5.0	5.3	15.5
<i>Helioseris cucullata</i>		3.3	1.0		1.6	4.7	0.7	1.7
<i>Siderastrea siderea</i>	3.9	1.5	3.3	2.8	1.3	0.9	3.9	1.7
<i>Porites astreoides</i>	26.8	12.0	10.3		21.3	9.8	5.3	
<i>Porites porites</i>					0.1		0.7	
<i>Favia fragum</i>	0.4							
<i>Diploria labyrinthiformis</i>		0.1						
<i>Diploria strigosa</i>	5.8				0.4		0.7	
<i>Manicina areolata</i>					0.1			
<i>Colpophyllia natans</i>		0.3	1.6		0.3	0.4		
<i>Montastraea annularis</i>		2.5	0.5		2.3	1.6		
<i>Montastraea cavernosa</i>	8.5	1.1	3.3	1.0	1.3	0.5	2.0	
<i>Meandrina meandrites</i>	1.6	0.3	0.8	1.9		0.2	0.7	
<i>Dichocoenia stokesi</i>	3.1		0.8			0.4		
<i>Dendrogyra cylindrus</i>					0.1			
Unidentified mussid	0.8	0.3	0.3		1.2			
<i>Mussa angulosa</i>	1.6	0.3	2.4	1.9		2.5	2.6	
<i>Scolymia</i> spp.	0.4	1.1	4.6	5.8				
<i>Isophyllastrea rigida</i>	0.4				0.1			
<i>Mycetophyllia lamarckiana</i>					0.1			
<i>Mycetophyllia ferox</i>		0.6			0.7			
<i>Mycetophyllia aliciae</i>					0.1			
<i>Mycetophyllia</i> spp.					0.7	0.2		
<i>Eusmilia fastigiata</i>		0.1	0.3		0.1			
<i>Millepora</i> spp.	11.3	0.3			0.3	0.2		

Table 6. Algal biomass (g/m²) from settling plates on the east and west walls of Salt River canyon

	9 m East	18 m East	27 m East	37 m East	9 m West	18 m West	27 m West	37 m West
All samples combined	25 ± 20 (34)	11 ± 7 (36)	9 ± 8 (36)	9 ± 8 (36)	5 ± 4 (41)	8 ± 8 (36)	8 ± 5 (34)	9 ± 8 (34)

Table 7. Abundance of herbivorous fishes on east and west walls of Salt River canyon

	Location	
	East Wall	West Wall
Acanthuridae, Scaridae,	9 m 45.8	9 m 49.6
Pomacentridae	18 m 40.8	18 m 44.5
(total scores)	27 m 40.0	27 m 40.1
	37 m 32.3	37 m 23.8

Table 8. Density of *Diadema antillarum* on the east and west walls of Salt River canyon

Location	No. of urchins	Area surveyed	No./m ²
9 m West	422	160	2.6
18 m West	78	180	0.4
27 m West	2	240	0.0
37 m West	0	240	0.0
9 m East	29	320	0.1
18 m East	57	200	0.3
27 m East	0	240	0.0
37 m East	0	240	0.0

Grazing Organisms

The technique used for fish surveys does not provide absolute abundances for the different species. In spite of this limitation, a comparison of total combined scores for the herbivorous species in the Acanthuridae, Scaridae, and Pomacentridae from 9 m to 37 m suggests a decrease in the abundance of herbivorous fishes for both the east and west walls with increasing depth (Table 7).

The abundance of *Diadema antillarum* also decreased with depth on both walls (Table 8). The highest density (3/m²) was found on the west wall at 9 m.

Discussion

Certain coral recruitment patterns appear consistent for all reefs studied to date. However, there are definite dif-

ferences between Atlantic and Pacific reefs and among reefs within the same region.

Relative Distribution of Species Present as Juveniles

As in previous studies of Atlantic reefs (Birkeland 1977; Bak and Engel 1979; Rylaarsdam 1983), *Agaricia agaricites* juveniles were more abundant overall than those of all other species, comprising 47% of the juveniles within quadrats and 68% of the juveniles which settled on settling plates. This species comprised 60% of all juveniles observed on a Curacao reef (Bak and Engel 1979) and 84% of the coral larvae which settled on *Acropora palmata* fragments after hurricane damage to St. Croix reefs (Rogers et al. 1982). *Agaricia agaricites* had more juveniles than would be expected based on its abundance in the adult population. *Porites astreoides* also had high recruitment rates relative to its coverage on the reef.

Almost all species found within transects at Salt River were present as juveniles within quadrats, but the relative abundances varied greatly. (*Agaricia fragilis*, *Colpophyllia breviserialis* and *Isophyllia sinuosa* were not identified within quadrats, but their juveniles would be difficult to distinguish from those of closely related species when very small).

Some Pacific studies indicate that the most abundant corals produce the highest number of juveniles (Connell 1973; Grigg and Maragos 1974). In contrast, at Salt River, some coral species which were abundant within transects had very few juveniles (Tables 2, 5). For example, *Montastraea cavernosa* was the dominant species on the east wall at 9 m, comprising c. 48% of the live coral cover, but only 9% of the juveniles within quadrats at that depth were of this species. *Agaricia lamarcki* made up 80% of the live coral cover at 37 m on the west wall but comprised only 13% of the juveniles observed at this depth, although the relative abundance of the juveniles of this species increased with depth as in Bak and Engel's study (1979). *Montastraea annularis* and *Siderastrea siderea* also had high cover compared to their abundance in the juvenile population.

Bak and Engel (1979) describe different life history strategies for different coral species. *Montastraea annularis* is an example of a species with few juveniles but high rates of survival. Our work and that of Bak and Luckhurst (1980) suggest that *M. cavernosa* and possibly *Agaricia lamarcki* also fall into this category. *Agaricia agaricites* has higher recruitment rates but lower survival. Branching species like *Acropora palmata* and *A. cervicornis*, which are absent or rare at the relatively deep study sites at Salt River, appear to depend more on fragmentation than on sexual reproduction. It is logical that these species predominate in shallow reef zones where heavy swells and seas have the greatest impact.

At Salt River, the species with the greatest numbers of juveniles within quadrats were, in decreasing order, *Agaricia agaricites*, *Porites astreoides*, *Madracis decactis*, *Stephanocoenia michelinii*, and *Agaricia lamarcki*. On the

west wall, *Madracis decactis* was second in abundance and *Porites astreoides* third. On Curacao reefs, the most common juveniles were *A. agaricites*, *Helioseris cucullata*, *P. astreoides*, *Meandrina meandrites* and *A. lamarcki*. The only species of corals identified from settling plates, in decreasing abundance, were *Agaricia* spp., *Madracis decactis*, *Porites* spp., *Favia fragum* and *Stephanocoenia michelinii*. Both within quadrats and on settling plates, *M. decactis* was more abundant at 37 m than *Agaricia agaricites*.

The mean number of juveniles per m² (within quadrats) at Salt River canyon ranged from 3 to 42 over the depth gradient with an average of 19 for the east wall and 18 for the west wall. In contrast, Bak and Engel (1979) found about the same number of juveniles per quadrat over all depth zones between 3 and 37 m. Average number of juveniles per m² for all depths was c. 17. Connell (1973) found 15 recruits per m² on the shallow (sometimes exposed) outer reef crest at Heron Island.

Orientation of Juvenile Corals

In most cases in shallow water, coral juveniles settle on vertical and undersurfaces of settling plates, concrete blocks, and branches of dead coral (e.g., Birkeland 1977; Birkeland et al. 1981; Rogers et al. 1982). This "preference" could reflect lower siltation rates, lower algal biomass (Birkeland 1977), or lowered light intensities (Bak and Engel 1979) on these surfaces. Birkeland (1977) noted an inverse relationship between number of coral recruits and algal biomass on Caribbean and Pacific reefs off Panama and found that about 65% of the juveniles settling on concrete blocks at depths less than 20 m settled on vertical surfaces, while all of the juveniles in 34 m settled on upper, horizontal surfaces. Competition with faster-growing algae on horizontal surfaces exposed to higher light intensities may explain the scarcity of coral recruits on these surfaces in shallow water. Nutrients associated with upwelling off the Pacific coast of Panama accelerated the growth of algae which outcompeted the hermatypic corals on settling plates (Birkeland 1977). In Curacao, where algal biomass is lower, Bak and Engel (1979) reported only 2% of the juveniles settled on undersurfaces.

For reefs in Guam (Birkeland et al. 1981), Curacao and Bonaire (Bak and Engel 1979), and Panama (Birkeland 1977), orientation of the settlement surface shifted from mostly vertical to mostly horizontal with increasing depth. In contrast, in Salt River canyon, more juveniles were found on vertical settling plate surfaces in deeper water (Table 3). In shallower water, similar proportions of juveniles settled on bottom surfaces as on vertical surfaces. In all cases, the shifts in orientation probably reflect a response to lower light intensities in deeper water. The shift to vertical surfaces as opposed to upper horizontal surfaces may be a result of higher sedimentation rates at Salt River than at the other reefs. It is interesting that Bak and Engel (1979) found the highest sedimenta-

tion rates at the shallowest depths where most juveniles settled on vertical surfaces.

Comparison of the East and West Walls

Comparison of the east and west walls at 9 m showed that the east wall had a lower number of juveniles both on settling plates and within quadrats than the 9 m west wall site, a lower mean percent of live coral, a higher percent of dead coral, a lower number of species, and a lower spatial index (Table 1). The 9 m east wall site, an area of low structural relief, may have higher sedimentation rates than the 9 m west wall site. Variations in the abundances of grazing organisms (Tables 7, 8) and the amount of algal biomass (Table 6) may explain some of the differences between the two canyon walls. Estimates of the abundance of *Diadema antillarum* indicated that the urchin was more abundant at 9 m on the west wall than anywhere else. Abundance of herbivorous fishes decreased with depth on both walls. Clavijo (1978) found a decrease in herbivorous fishes with increasing depth at Salt River as well. These fish and urchin data suggest decreased grazing intensity at greater depths, although we do not have data on the significance of grazing by "micro-grazers" such as amphipods. At 9 m on the west wall, low algal biomass and high grazing pressure are associated with a high rate of recruitment (both on settling plates and within quadrats). At 9 m on the east wall, high algal biomass and lower grazing pressure are associated with much lower recruitment.

On the east wall, 18 m appears optimal for coral recruitment and survival, while 9 m appears optimal on the west wall. For both walls, 18 m had the highest live coral cover, spatial indices, and number of juveniles on settling plates, and for the east wall only, the highest number of juveniles within quadrats. While the number of juveniles within quadrats was high at 18 m on the west wall, it was exceeded at 9 m. It is interesting to note the similarity between the 9 m west wall and the 18 m east wall sites. Both are slope-edge environments. In contrast, the 9 m east wall site has very low relief and no sloping topography.

Survival of coral recruits is partly a function of grazing pressure and of competition with algae. At deeper depths, grazing pressure decreases and corals may not be able to compete successfully with algae. However, lower light intensities at these depths can limit algal growth. Fish and urchins seem to show some selectivity in feeding upon algae (Ogden and Lobel 1978), but there is little information on avoidance of corals by urchins or fish. Brock (1979) noted that small parrotfishes (but not large ones) avoided coral colonies larger than 6 to 8 polyps. Birkeland (1977) found that scarid fish which scraped algae from plexiglass plates avoided corals as small as 2.5 mm. Bak and Engel (1979), however, found no evidence that fish avoided coral recruits off Curacao.

Sedimentation can also affect the competition between coral larvae and algae and the influence of grazers on this interaction (Sammarco 1980). At Salt River, the

higher number of coral juveniles within quadrats on the east wall at 18 m, 27 m and 37 m than on the west wall may partly be a function of higher sedimentation on the west wall (Rogers et al., unpublished data). The number of corals which settled on settling plates on the two walls was almost identical. Perhaps recruitment rates are similar for the two walls, but survival is somewhat lower on the west wall.

Conclusion

1) High rates of recruitment tended to be associated with low algal biomass and relatively high densities of urchins and fishes.

2) *Agaricia agaricites* and *Porites astreoides* had high recruitment rates relative to their abundance on the reef. In contrast, *A. lamarcki*, *M. annularis*, *M. cavernosa* and *S. siderea* had high amounts of cover compared to their abundance as juveniles.

3) The only species settling on plates, in decreasing abundance, were *Agaricia* spp., *Madracis decactis*, *Porites* spp., *Favia fragum* and *Stephanocoenia miche-linii*.

4) The species with the greatest numbers of juveniles within reef quadrats, in decreasing order, were *Agaricia agaricites*, *Porites astreoides*, *Madracis decactis*, *S. miche-linii* and *A. lamarcki*.

5) A total of 271 corals settled on settling plates during the 26 month study. Of these 34% settled on horizontal surfaces and 66% on vertical surfaces. Of all corals which settled on horizontal plates, 89% settled on the bottom and 11% on the top. Fifty-one percent of the corals settled on east wall plates and 49% on plates from the west wall. There was a trend towards settlement on vertical surfaces at deeper depths, while in shallower water similar numbers of corals settled on horizontal bottom surfaces as on vertical surfaces.

6) For both walls, 18 m had the highest live coral cover, spatial indices, and number of juveniles on settling plates, and for the east wall only, the highest number of juveniles within quadrats. While the number of juveniles within quadrats was high at 18 m on the west wall, it was exceeded at 9 m. Possibly at 18 m there is an optimal combination of light intensity, grazing pressure, and sedimentation rates which result in the most favorable conditions for coral settlement and growth.

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References

- Adey WH, Rogers C, Steneck R, Salesky N (1981) The south St. Croix reef. Report to the Dept. of Conservation and Cultural Affairs, Virgin Islands Government. West Indies Laboratory, Fairleigh Dickinson University
- Bak RPM (1983) Neoplasia, regeneration and growth in the reef-building coral *Acropora palmata*. *Mar Biol* 77:221-227
- Bak RPM, Brouns JJWM, Heys FML (1977) Regeneration and aspects of spatial competition in the scleractinian corals *Agaricia agaricites* and *Montastrea annularis*. *Proc 3rd Int Coral Reef Symp* 1:143-148
- Bak RPM, Engels MS (1979) Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. *Mar Biol* 54:341-352
- Bak RPM, Luckhurst BE (1980) Constancy and change in coral reef habitats along depth gradients in Curacao. *Oecologia (Berlin)* 47:145-155
- Bak RPM, Termaat RM, Dekker R (1982) Complexity of coral interactions: influence of time, location of interactions and epifauna. *Mar Biol* 69:215-222
- Bak RPM, van Eys G (1975) Predation of the sea urchin *Diadema antillarum* Philippi on living coral. *Oecologia (Berlin)* 20:111-115
- Birkeland C (1977) The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *Proc 3rd Int Coral Reef Symp* 1:15-21
- Birkeland C, Rowley D, Randall RH (1981) Coral recruitment patterns at Guam. *Proc 4th Int Coral Reef Symp* 2:339-344
- Brawley SH, Adey WH (1977) Territorial behavior of threespot damselfish (*Eupomacentrus planifrons*) increases reef algal biomass and productivity. *Env Biol Fish* 2:45-51
- Brock RE (1979) An experimental study on the effects of grazing by parrotfishes and role of refuges in benthic community structure. *Mar Biol* 51:381-388
- Clavijo IE (1978) Diel and depth variation in the population densities of herbivorous fishes on the walls in Salt River submarine canyon. Final Scientific Report, NOAA, Mission 78-3a
- Connell JH (1973) Population ecology of reef building corals. In: Jones OA, Endean R (eds) *Biology and geology of coral reefs, II. Biology 1*. Academic Press, New York London, pp 205-244
- Dart JK (1972) Echinoids, algal lawn and coral recolonization. *Nature (London)* 239:50-51
- Gladfelter EH, Gladfelter WB, Hubbard DK, Carpenter RC, Simpson GS (1979) Environmental studies of Buck Island Reef National Monument. St Croix, USVI, US National Park Service Report
- Goreau TF, Goreau NI (1973) The ecology of Jamaican coral reefs. II. Geomorphology, zonation, and sedimentary phases. *Bull Mar Sci* 23:399-464
- Grigg RW, Maragos JE (1974) Recolonization of hermatypic corals on submerged lava flows in Hawaii. *Ecology* 55:387-395
- Highsmith RC (1982) Reproduction by fragmentation in corals. *Mar Ecol Prog Ser* 7:207-226
- Hubbard DK, Sadd JL, Miller AI, Gill IP, Dill RF (1981) The production, transportation, and deposition of carbonate sediments on the insular shelf of St Croix, US Virgin Islands. Final Report for NOAA Sea Grant Number 04-8-MOI-135, Technical Report No MG-1
- Jones RS, Thompson MJ (1978) Comparison of Florida reef communities by the employment of a rapid visual technique. *Bull Mar Sci* 28:159-172
- Lang JS (1970) Interspecific aggression within the scleractinian reef corals. PhD thesis, Yale University
- Lang JS (1973) Interspecific aggression by scleractinian corals. II. Why the race is not only to the swift. *Bull Mar Sci* 23:260-279
- Loya Y, Slobodkin LB (1971) The coral reefs of Eilat, Red Sea. *Symp Zool Soc Lond* 28:117-139
- Mathieson AC, Fraclick RA, Burns R, Flahive W (1975) Phycological studies during Tektite II at St John, USVI. In: Results of the Tektite Program: coral reef invertebrates and plants. *Nat Hist Mus LA County, Sci Bull* 20:77-103
- Ogden JC, Lobel PS (1978) The role of herbivorous fishes and urchins in coral reef communities. *Env Biol Fish* 3:49-63
- Ogden JC, Brown RA, Salesky N (1973) Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indies patch reefs. *Science* 182:715-717
- Porter JW (1972) Patterns of species diversity in Caribbean reef corals. *Ecology* 53:745-748
- Randall JE (1967) Food habits of reef fishes of the West Indies. *Proc Int Conf Trop Ocean* 1965. University of Miami
- Rogers C, Gilnack M, Fitz III HC (1983) Monitoring of coral reefs with linear transects: a study of storm damage. *J Exp Mar Biol Ecol* 66:285-300
- Rogers C, Suchanek TH, Pecora F (1982) Effects of Hurricanes David and Frederic on shallow *Acropora palmata* reef communities: St Croix, US Virgin Islands. *Bull Mar Sci* 32:532-548
- Rylaarsdam KW (1983) Life histories and abundance patterns of colonial corals on Jamaican reefs. *Mar Ecol Prog Ser* 13:249-260
- Sammarco PW (1975) Grazing by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): density-dependent effects on coral and algal community structure. 11th Meeting, Assoc Island Mar Labs Carib. St Croix, USVI (abstr)
- Sammarco PW (1980) *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. *J Exp Mar Biol Ecol* 45:245-272
- Sammarco PW, Levington JS, Ogden JC (1974) Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): a preliminary study. *J Mar Res* 32:47-53
- Sokal RR, Rohlf FJ (1969) *Biometry*. Freeman, San Francisco
- Thompson MJ, Schmidt TW (1977) Validation of the species/time random count technique sampling fish assemblages at Dry Tortugas. *Proc 3rd Int Coral Reef Symp* 1:283-288
- Vine PF (1974) Effects of algal grazing and aggressive behavior of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral reef ecology. *Mar Biol* 24:131-136