

Spatial and temporal variation of *Marginopora vertebralis* on seagrass in Papua New Guinea during a six week period

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ABSTRACT: A seagrass flat, located on the south coast of Papua New Guinea, supports a large *Marginopora vertebralis* Quoy and Gaimard population and is subject to periodic subaerial exposure. Seagrass from 25 cm by 25 cm areas at seven stations along a transect on this flat was sampled for living *Marginopora* during six successive weekly intervals. The size-frequency distribution of *Marginopora* and the total seagrass area for each sample were computed. There is no correlation between seagrass area and *Marginopora* density, although there is a maximum number of *Marginopora* that can inhabit a given area of seagrass. There is no simple relationship between the size-frequency distribution of *Marginopora* and subaerial exposure, nor is there any systematic change in the distribution across the seagrass bed. Spatial variability is greater than temporal variability for *Marginopora* when the size scale is on the order of tens of meters and the time scale is on the order of weeks.

INTRODUCTION

Foraminifera are found in a wide variety of environments. One particularly extreme case was reported by Smith (1968) who found large numbers of *Marginopora vertebralis* Quoy and Gaimard, a common shallow water tropical foraminifer, in a seagrass flat in Suva Harbor, Fiji. This seagrass flat frequently was exposed subaerially and was also subject to drastic salinity variations caused by rainfall and fresh water run off. Fisher (1966) reported *Marginopora* populations from the New Hebrides and from Heron Island, Australia, that were subjected to repeated subaerial exposure. A seagrass bed that supports a large *Marginopora* population lies just off the north-western corner of Motupore Island, about 20 km southeast of Port Moresby, Papua New Guinea. This bed is subaerially exposed during times of extreme tides. These extreme tides are periodic, occurring fortnightly at the times of new and full moons. *Marginopora* is the dominant foraminifer in this seagrass bed (Haig 1978/79). Casual observations suggested their size-frequency distribution varied in some manner related with the periodicity of subaerial exposure. In a previous paper (Severin 1983), I presented a preliminary analysis (combining all stations for each sampling time) of size-frequency data for *Marginopora vertebralis* found on the seagrass flat. This paper presents a station by station analysis of the data and relates these data to the tidally-governed exposure of the seagrass flat.

STUDY AREA

The studied seagrass flat lies directly off the north-west corner of Motupore Island, a small island off the south coast of Papua New Guinea (text-fig. 1). It is bounded on its southern side by the island proper, to the west by coral reefs, and to the north by a rather sharp break in the bottom slope. To the east it grades into a sandy area that forms the harbor of the Motupore Island Research Center. In the north-south direction the seagrass flat extends approximately 120 m from the island to the slope break at an average depth of 0.5 to 1.0 m. The east-west extent is harder to quantify as the boundaries are less distinct, but a good estimate is 300–400 m.

The average tidal range at Motupore Island is approximately 1.5 m, but can vary from as little as 0.6 m to as much as 2.2 m (text-fig. 2; USDC-NOAA 1983). The seagrass flat is exposed whenever the lowest tide is approximately 0.7 m. During these extreme tides, only the most seaward parts of the seagrass flat remain completely submerged.

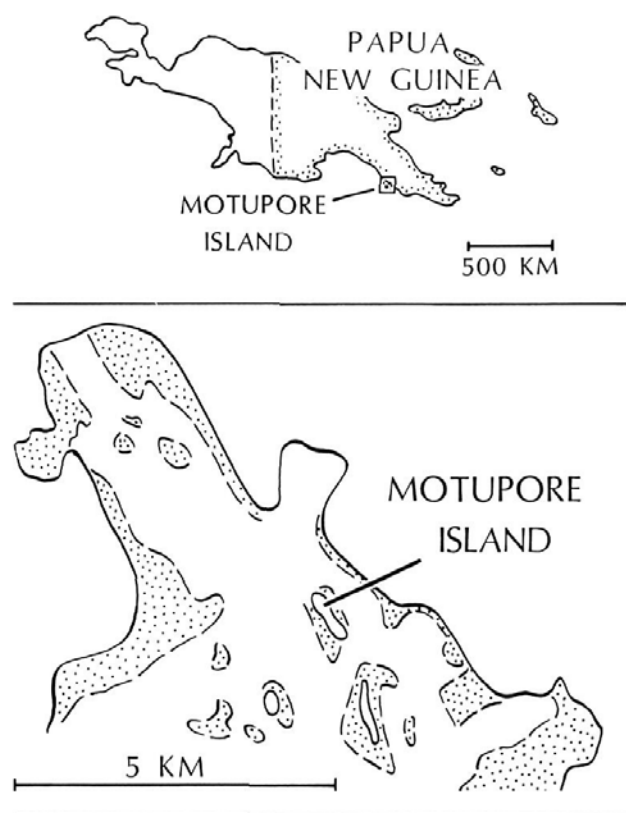
The substrate in the seagrass flat is a medium-grained calcareous sand. It is hummocky, most of the hummocks having a height of about 0.1 m. The hummocks probably are formed by callianassids common to the area. The seagrasses are noticeably more abundant in the areas between the hummocks, perhaps because these areas are subject to less bioturbation than the hummocks. The 'inter-hummock' areas were the last areas to become subaerially exposed during extreme tides.

Six of the eight seagrasses commonly found in Papua New Guinea (Johnstone 1978, 1979) were seen on the seagrass flat. These included *Cymodocea rotundata*, *C. serrulata*, *Halodule uninervis*, *Enhalus acoroides*, *Halophila ovalis*, and *Thalassia hemprichii*. With the exception of *H. ovalis*, all were inhabited at some time by *Marginopora*. All seagrasses were distributed fairly evenly across the seagrass flat, with the exception of *E. acoroides* which was more abundant in the areas more distant from shore.

METHODS

A north-northwest trending transect of seven stations, at a spacing of 20 m, was marked with stakes across the seagrass flat. The stations were labeled from one to seven, Station 1 being nearest to shore. The stations were sampled at approximately weekly intervals (text-fig. 2) on 11 July, 20 July, 25 July, 2 August, 9 August, and 17 August 1983 (Times One to Six respectively). Samples were taken during low tide by collecting all living seagrass from an arbitrarily selected 25 cm by 25 cm area near the stake. Care was taken not to resample the same area on successive weeks.

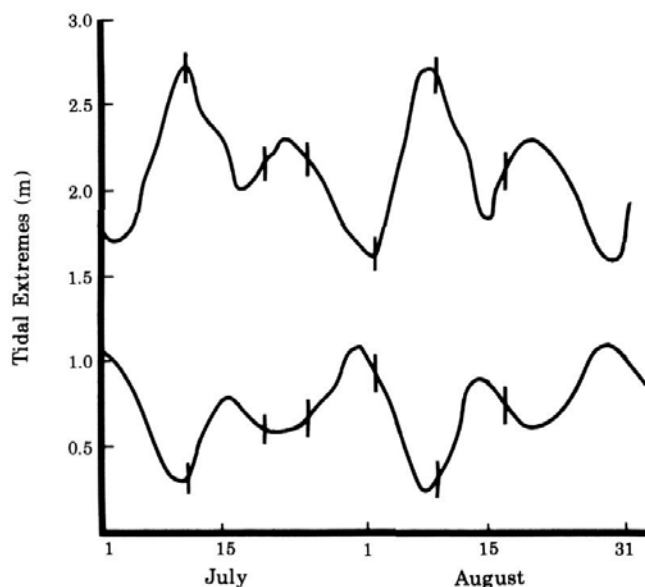
During periods of extreme tides, where the low tide was less than or equal to about 0.7 m, all stations with the exception of Station 7 were subaerially exposed. Samples at Times One and Five were taken when the seagrass bed was completely



TEXT-FIGURE 1
Sketch map of sampling location.

exposed, samples at Times Two and Three when the seagrass bed was partially exposed, and samples at Times Four and Six when the seagrass bed was completely submerged. Station 7 never was covered by less than about 0.25 m of water.

In the laboratory each piece of seagrass was measured to the nearest 2 mm in length and width and the size and number of living *Marginopora* for each station were recorded. During



TEXT-FIGURE 2
Level of highest and lowest daily tide at Port Moresby, Papua New Guinea. Vertical lines are placed at sampling times. Data calculated from USDC-NOAA (1983). (From Severin 1983)

transport to the laboratory some *Marginopora* became detached; these were included in the analysis.

SUMMARY OF PRELIMINARY RESULTS

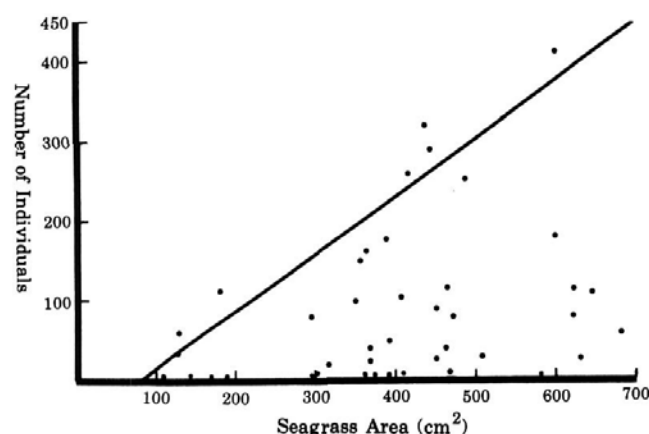
The following is a brief summary of Severin (1983) wherein I combined all stations for comparisons among the six sampling periods.

The total area of collected seagrass was calculated to test for a correlation between the amount of seagrass and the number of *Marginopora* collected. A least squares regression on the total number of *Marginopora* versus the total seagrass collected at each station (text-fig. 3) shows them to be uncorrelated, with an r^2 value of 0.07. Text-figure 3 includes a straight line bounding the top of the plot. This line was obtained from a least squares regression using arbitrarily selected uppermost points on the plot and has an equation of

$$n = -54.8 + .72a$$

where n = the number of *Marginopora* and a = the area of seagrass in cm^2 . The r^2 value, 0.88, is of little statistical meaning because of the manner in which the points were selected. However, the line may represent the maximum number of *Marginopora* that could inhabit a given amount of seagrass. The x-axis intercept, no *Marginopora* and 76 cm^2 of seagrass, gives an estimate of the minimum amount of seagrass necessary for habitation by *Marginopora*. The blades in the seagrass flat average about 1 cm in width by 6–8 cm in length; thus, about 8–10 seagrass blades in a 25 cm by 25 cm area are necessary for the seagrass to become inhabited by *Marginopora*.

Text-figure 4 contains histograms of the size-frequency distributions of *Marginopora* for the combined seven stations



TEXT-FIGURE 3

Plot of total number of *Marginopora* vs. seagrass area. The line is the regression,

$$n = -54.8 + .72a,$$

(n = the number of *Marginopora*, a = the area of seagrass in cm^2) done on the uppermost points in the plot. Stations and sampling times not combined. (From Severin 1983)

at each of the sampling times. A Kruskal-Wallis test for difference in median size between all sampling times gives a chi-square value of 261.9 (corrected for ties) with 5 degrees of freedom. This corresponds to $p < 10^{-8}$; thus, at least one of the sampling times has a different median size than the others.

A multiple comparison, using Mann-Whitney tests, was performed to test for differences in median size between successive sampling times (table 1). For an overall significance level of 0.01, the p value of significance for the individual test of interest must be less than 0.002. While the median size of individuals is the same at Times Four and Five, there is a significant difference (at the 0.01 level) between all other successive times with the exception of Times Five and Six, which just fail significance. They would, however, be significantly different if an overall significance level of 0.05 were chosen.

To summarize, the median size of *Marginopora* at Time One is larger than that at Time Two, which is in turn larger than that at Time Three. The median size then increases from Time Three to Time Four, remains the same through Time Five, and decreases at Time Six (table 1).

There is no simple relationship between the median size of *Marginopora* (analyzing all stations combined) and extreme tides and the resulting subaerial exposure. If the size-frequency distribution of *Marginopora* were governed solely by the degree of subaerial exposure, then similar median sizes would be expected at times of similar subaerial exposure. This is not the case for the analysis of combined stations. Instead of similar median sizes for Sampling Times Two and Three, times when the seagrass flat was semi-exposed, the medians differ at almost any level of significance. The medians of Sampling Times One and Five, when the seagrass bed was completely exposed, should likewise be similar. In-

stead, a median test shows the median of Sampling Time One to be greater than the median of Sampling Time Five ($p < 10^{-9}$). Sampling Times Four and Six, when the seagrass bed was always submerged, should also have similar median sizes, but a median test shows the median of Sampling Time Four to be greater than that of Sampling Time Six ($p = 0.0038$). Finally, Sampling Times Four and Five, completely submerged and completely exposed respectively, are the most similar sampling times of all.

RESULTS OF ANALYSIS OF INDIVIDUAL STATIONS

I: Individual Stations Through Time

Station 1

Marginopora were not abundant for the first four sampling periods, then increased in abundance for the final two periods (table 2). Visual inspection of table 2 indicates that there is a significant difference in the size of the *Marginopora* population when considering all times; this is confirmed by a Kruskal-Wallis test ($p = 0.08$, table 3). Examination of successive sampling times, however, does not give any clear indication of exactly when the significant change in *Marginopora* median size occurs. Because the comparisons between successive sampling times are five-way multiple comparisons, the p values for the individual tests must be five times smaller than the overall desired p value. Thus, when considering Times Five and Six, with the lowest multiple comparison value of $p = 0.06$, we find an overall p value of about 0.3, hardly significant by any standard. Further comparisons between non-successive times may indicate a trend in median *Marginopora* size through the sampling times. However, because of the relatively small *Marginopora* population at Station 1 the effort is probably not warranted.

Station 2

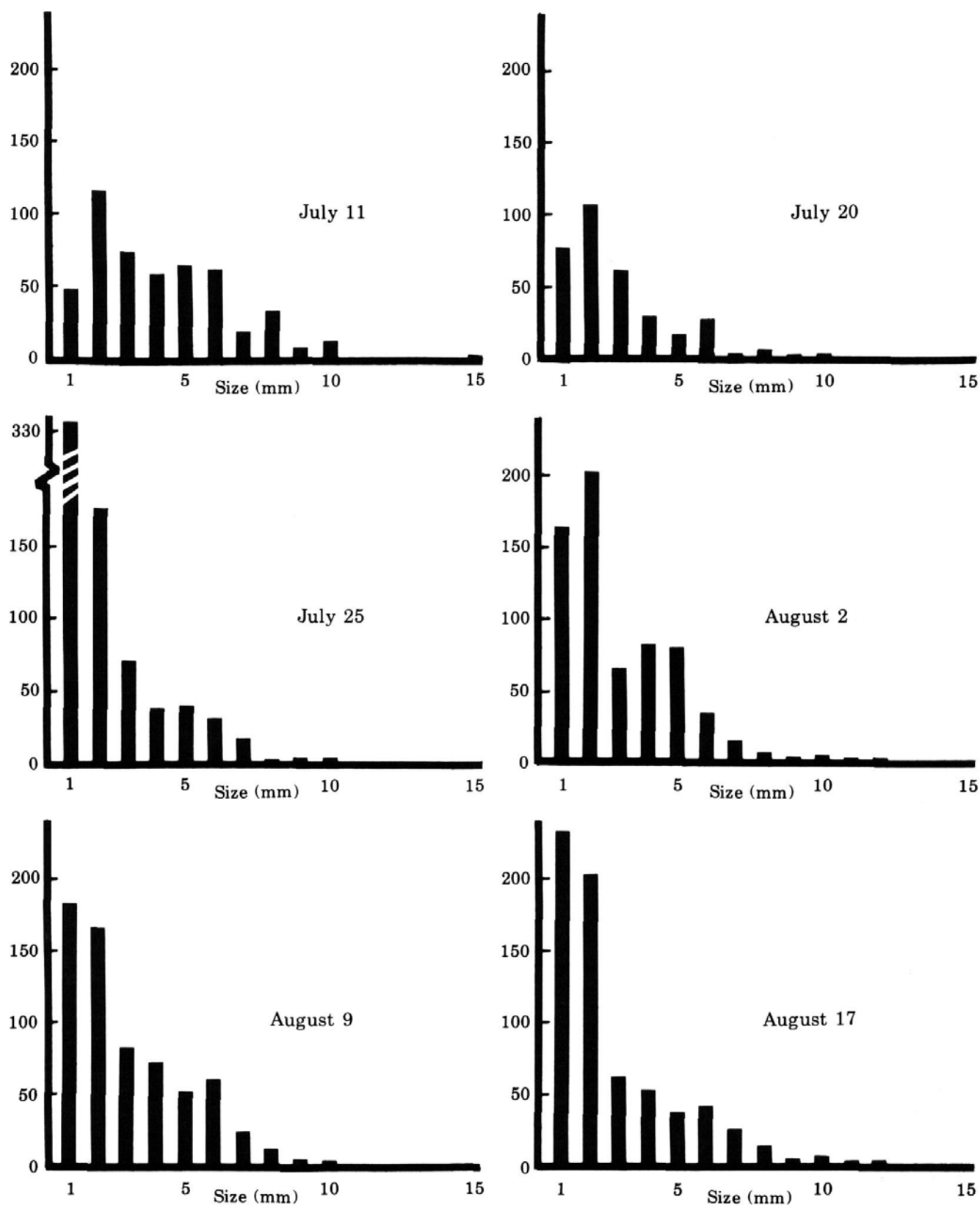
Small *Marginopora* were very abundant at Station 2 during Sampling Times Three and Six (table 4), and a Kruskal-Wallis test confirms the visual observation that there is an overall difference in median *Marginopora* size when considering all sampling times (table 5). Examination of successive sampling times shows significant changes between Times Two and Three, where median *Marginopora* size decreased, Times Three and Four, where median *Marginopora* size increased, and Times Four and Five, where median size again decreased (table 5).

Station 3

In spite of the relatively large abundance of small *Marginopora* at Sampling Times Three and Five (table 6), there is no overall difference in median *Marginopora* size when considering all sampling times ($p = 0.22$, table 7). Median *Marginopora* size remains the same through Times One to Five, then increases at Time Six. This increase is significant when considering only Times Five and Six, but comparison among all successive sampling times gives a difference only at a p level of about 0.20.

Station 4

Over half of the individuals found at Station 4 during Times Three and Four were one mm in diameter, while only a third



TEXT-FIGURE 4

Size-frequency histograms of *Marginopora*. All stations combined for each sampling time. (From Severin, 1983)

of the individuals found at Time Five, the time with highest abundance of *Marginopora* were in this size class (table 8). This may be partly responsible for the difference in median *Marginopora* size when considering all times (table 9). Median *Marginopora* size decreased from Time Two to Time Three, remained constant through Time Four, and increased at Time Five (table 9).

Station 5

The abundance of *Marginopora* at Station 5 was the largest of all stations examined. At all times the majority of the individuals were in the one and two millimeter size class (table 10). It also showed the greatest variability in median *Marginopora* size. Not only was there an overall difference of median *Marginopora* size when comparing all sampling times, only Times Five and Six show similarity (at the 0.05 level) when comparing successive sampling times (table 11).

Station 6

In some respects Station 6 is very similar to Station 1. *Marginopora* were moderately abundant during five of the six sampling times, but only five individuals occur at Time Two (table 12). This may account for the difference in median *Marginopora* size found when considering all sampling times, but similarity from one sampling period to the next (table 13).

Station 7

Marginopora were not abundant enough at Station 7 to be statistically analyzed (table 14).

II: Comparison Among Stations Through Time

Comparison among stations at the same sampling period is complicated by the lack of individuals at Station 7 during

some sampling times. Because of this, Kruskal-Wallis tests for overall differences, i.e. differences among all stations simultaneously, were performed omitting Station 7 where warranted. Similarly, because of the low abundance of *Marginopora* at Station 1, Kruskal-Wallis tests were performed using only Stations 2 through 6. Notice that, when comparing different numbers of stations, the multiplier used in multiple comparisons changes.

Time One

At Time One there was a large difference among all stations whether Stations 1 and 7 were included or omitted (table 15). In spite of the fact that the overall difference became smaller with the omission of Stations 1 and 7, multiple comparisons show Stations 1 and 2 and Stations 6 and 7 to have *Marginopora* of similar median size (table 15).

Time Two

At Time Two there were no individuals at Station 7 (table 14). Examination of Stations 1 through 6 and Stations 2 through 6 show differences in overall median *Marginopora* size (table 16). Most of the difference occurs between Stations 2 and 3 and Stations 4 and 5 which are different at the 0.10 level (table 16).

Time Three

At Time Three there were no individuals at Station 7 (table 14), but the rest of the stations show a significant difference in median *Marginopora* size when compared simultaneously (table 17). However, only one pair of adjacent stations show

TABLE 1
Results of five way multiple comparison using Mann-Whitney test.

Sampling time	Median size	Probability of equal median size
1 vs. 2	1 > 2	<10 ⁻¹⁰
2 vs. 3	2 > 3	<10 ⁻¹⁰
3 vs. 4	3 < 4	<10 ⁻¹⁰
4 vs. 5	4 = 5	0.4602
5 vs. 6	5 > 6	0.0059

TABLE 2
Abundance of *Marginopora* at Station 1.

	Size (in mm)															Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Jul 11					1	1										2
Jul 21	3					1										4
Jul 25		1	1													2
Aug 2	1	1														2
Aug 9	18	4	1		2		1	1								27
Aug 17	5	12	1				1									19

TABLE 3
Comparisons for Station 1 through time. A Kruskal-Wallis test was used for overall differences, Mann-Whitney tests were used for comparison between successive sampling times.

Sampling time	Median size	Probability of equal median size
Overall	equal	0.0812
1 vs. 2	1 = 2	0.2113
2 vs. 3	2 = 3	0.3252
3 vs. 4	3 = 4	0.2207
4 vs. 5	4 = 5	0.8386
5 vs. 6	5 < 6	0.0615

a significant difference in median *Marginopora* size, Stations 5 and 6 (table 17).

Time Four

At Time Four there were no individuals at Station 7 (table 14). This time shows the most variability among the remaining stations, both when compared simultaneously and when comparing adjacent stations. Only Stations 3 and 4 are not different at the 0.05 level when considering Stations 1 through 6 ($p = 0.052$); they differ at the 0.042 level when omitting Station 1 from consideration (table 18).

Time Five

At Time Five all stations differ when considered simultaneously, whether or not Stations 1 and 7 are included (table 19). Stations 3 and 4 and Stations 5 and 6 differ when considered as adjacent stations (table 19).

Time Six

At Time Six all stations differ when considered simultaneously, whether or not Stations 1 and 7 are included (table 20). While Station 2 may have a slightly smaller mean *Marginopora* size than Station 3, depending on the level of significance selected, only Stations 5 and 6 have clearly different median *Marginopora* sizes (table 20).

DISCUSSION

I: Relationship Between *Marginopora* Abundance and Seagrass Area

The clearest result of this study is contained in text-figure 2. While it shows no correlation between the number of *Marginopora* and the area of seagrass collected, it suggests a maximum number that can inhabit any given area of seagrass, and also a minimum area of seagrass necessary to support

TABLE 4
Abundance of *Marginopora* at Station 2.

	Size (in mm)															Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Jul 11	11	7		2	5	10		12	5	5						57
Jul 21		1	2		3	2				1						9
Jul 25	96	38	8	7	15	6	5		1	2						178
Aug 2	3	2	1	3	11	2	1		2			1				26
Aug 9	46	31	1	3	2	3	1	1	1		1					90
Aug 17	145	100	13	11	6	11	16	4	9	3		1				319

TABLE 5
Comparisons for Station 2 through time. A Kruskal-Wallis test was used for overall differences, Mann-Whitney tests were used for comparison between successive sampling times.

Sampling time	Median size	Probability of equal median size
Overall	not equal	$<10^{-9}$
1 vs. 2	1 = 2	0.6503
2 vs. 3	2 > 3	0.0001
3 vs. 4	3 < 4	$<10^{-6}$
4 vs. 5	4 > 5	$<10^{-6}$
5 vs. 6	5 = 6	0.1516

TABLE 7
Comparisons for Station 3 through time. A Kruskal-Wallis test was used for overall differences, Mann-Whitney tests were used for comparison between successive sampling times.

Sampling time	Median size	Probability of equal median size
Overall	equal	0.2155
1 vs. 2	1 = 2	0.9342
2 vs. 3	2 = 3	0.5605
3 vs. 4	3 = 4	0.1071
4 vs. 5	4 = 5	0.1550
5 vs. 6	5 < 6	0.0411

TABLE 6
Abundance of *Marginopora* at Station 3.

	Size (mm)															Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Jul 11	16	2		2				4		3					1	28
Jul 21	3	3		1		1										8
Jul 25	28	19	6	2		1	2		1							59
Aug 2	6	8	3		3					1						21
Aug 9	55	22	25	3	3		3			1						112
Aug 17	7	22	4	3	1	1						1				39

an epiphytic *Marginopora* population. This may be due to some spatially dependent resource that *Marginopora* requires. *Marginopora* contain photosymbiotic algae that provide some of their nutrition (Smith and Wiebe 1977). However, other large foraminifera such as *Amphisorus hemprichii* and *Amphistegina lobifera* can supply only about 10% of their needs with their symbionts and provide the remaining amount by feeding on bacteria (McEnery and Lee 1981). Alternatively, *Marginopora* may not be limited by resources. This could happen if *Marginopora* population was limited by a predator that only foraged for *Marginopora* when they were present at some minimum density.

II: Temporal Variability in *Marginopora* Abundance

This study was initiated to test for a correlation between median *Marginopora* size and subaerial exposure. Thus, it

was expected that the following pairs of sampling times would have similar mean *Marginopora* sizes: Sampling Times Two and Three, when the seagrass flat was semi-exposed, Sampling Times One and Five, when the seagrass flat was completely exposed, and Sampling Times Four and Six, when the seagrass flat was completely submerged. As mentioned above, when all stations are combined the median *Marginopora* size does change through time, but not in a manner that is simply related to subaerial exposure (Severin 1983).

This is also the case when the stations are examined individually. Of the six stations, one through six, where *Marginopora* were abundant enough to be meaningfully examined, only Station 3 did not show any change when considering all six sampling times.

Analysis of Sampling Times Two and Three must be performed eliminating Station 1 from consideration due to the

TABLE 8
Abundance of *Marginopora* at Station 4.

	Size (in mm)															Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Jul 11	16		12	13	17	11		8		3						80
Jul 21	11	10	4	9	5	5		4	1							49
Jul 25	71	14	4	9	7	10										115
Aug 2	63	23	5	2	7		2			1	1					104
Aug 9	55	26	14	11	14	26	10	3								159
Aug 17	17	29	13	4	5	6	1	2		1						78

TABLE 9
Comparisons for Station 4 through time. A Kruskal-Wallis test was used for overall differences, Mann-Whitney tests were used for comparison between successive sampling times.

Sampling time	Median size	Probability of equal median size
Overall	not equal	$<10^{-8}$
1 vs. 2	1 > 2	0.0623
2 vs. 3	2 > 3	$<10^{-5}$
3 vs. 4	3 = 4	0.7016
4 vs. 5	4 < 5	$<10^{-6}$
5 vs. 6	5 = 6	0.6387

TABLE 11
Comparisons for Station 5 through time. A Kruskal-Wallis test was used for overall differences, Mann-Whitney tests were used for comparison between successive sampling times.

Sampling time	Median size	Probability of equal median size
Overall	not equal	$<10^{-8}$
1 vs. 2	1 > 2	$<10^{-10}$
2 vs. 3	2 > 3	$<10^{-7}$
3 vs. 4	3 < 4	$<10^{-10}$
4 vs. 5	4 < 5	0.0048
5 vs. 6	5 = 6	0.1475

TABLE 10
Abundance of *Marginopora* at Station 5.

	Size (in mm)															Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Jul 11	3	97	55	34	28	30	7	3								257
Jul 21	60	90	55	19	8	19	2	2								255
Jul 25	137	77	36	15	10	6	4		1							286
Aug 2	72	156	48	62	41	21	7	7								414
Aug 9	7	56	35	23	13	8	3	6								151
Aug 17	54	32	22	22	16	15	7	6	1	4						179

low number of individuals present. The median *Marginopora* size remains the same for Stations 3 and 6 while it decreases from Time Two to Time Three at Stations 2, 4, and 5. For all stations there is an increase in the number of individuals from Time Two to Time Three.

For analysis of Sampling Times Two and Five, Station 1 must be eliminated from consideration due to the low number of individuals present. As expected, the *Marginopora* had equal median sizes at Stations 3 ($p = 0.60$), 5 ($p = 0.25$), and 6 ($p = 0.32$). However, median *Marginopora* size decreased from Time One to Time Five at Station 2 ($p < 10^{-8}$) and at Station 4 ($p = 0.0019$).

For comparison between Sampling Times Four and Six Sta-

tion 1 was eliminated due to the low number of individuals present. As expected the median *Marginopora* size remained equal at Stations 3 ($p = 0.95$), 5 ($p = 0.63$), and 6 ($p = 0.14$). Median *Marginopora* size changed from Time Four to Time Six at Stations 2 and 4, decreasing at Station 2 ($p < 10^{-5}$) and increasing at Station 4 ($p < 10^{-5}$).

Thus, Stations 3 and 6 always had similar median *Marginopora* size at times of similar subaerial exposure. For Station 3 this is merely the result of no overall change in median *Marginopora* size throughout the entire sampling period (table 7). For Station 6 the case is slightly more complex as there is a change in median *Marginopora* size when considering all sampling times simultaneously, but no significant

TABLE 12
Abundance of *Marginopora* at Station 6.

	Size (mm)															Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Jul 11	2	7	1	6	4	1	8		3							32
Jul 21		2		1	1	1										5
Jul 25	4	28	15	6	8	8	6	2		1						78
Aug 2	19	13	9	14	18	13	6			2		1				95
Aug 9	2	26	6	30	15	22	9			1						111
Aug 17	3	6	10	12	11	8	3	3	1							57

TABLE 13
Comparisons for Station 6 through time. A Kruskal-Wallis test was used for overall differences, Mann-Whitney tests were used for comparison between successive sampling times.

Sampling time	Median size	Probability of equal median size
Overall	not equal	0.0570
1 vs. 2	1 = 2	0.4290
2 vs. 3	2 = 3	0.7978
3 vs. 4	3 = 4	0.6243
4 vs. 5	4 = 5	0.1104
5 vs. 6	5 = 6	0.7578

TABLE 15
Comparisons for Time One across stations. Kruskal-Wallis tests were used for multiple differences, Mann-Whitney tests were used for comparison between adjacent stations.

Station	Median size	Probability of equal median size
Overall	not equal	$< 10^{-7}$
1 to 6	not equal	$< 10^{-5}$
2 to 6	not equal	$< 10^{-5}$
1 vs. 2	1 = 2	0.8486
2 vs. 3	2 > 3	0.0135
3 vs. 4	3 < 4	0.0429
4 vs. 5	4 > 5	0.0018
5 vs. 6	5 < 6	0.0044
6 vs. 7	6 = 7	0.2600

TABLE 14
Abundance of *Marginopora* at Station 7.

	Size (mm)															Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Jul 11		3	6	2	10	8	4	5		1						39
Jul 21																0
Jul 25																0
Aug 2																0
Aug 9		2		2	2	1										7
Aug 17		1														1

TABLE 16

Comparisons for Time Two across stations. Kruskal-Wallis tests were used for multiple differences, Mann-Whitney tests were used for comparison between adjacent stations.

Station	Median size	Probability of equal median size
Overall	—	—
1 to 6	not equal	0.0008
2 to 6	not equal	0.0010
1 vs. 2	1 < 2	0.0839
2 vs. 3	2 > 3	0.0168
3 vs. 4	3 = 4	0.1572
4 vs. 5	4 > 5	0.0110
5 vs. 6	5 = 6	0.1108
6 vs. 7	—	—

TABLE 17

Comparisons for Time Three across stations. Kruskal-Wallis tests were used for multiple differences, Mann-Whitney tests were used for comparison between adjacent stations.

Station	Median size	Probability of equal median size
Overall	—	—
1 to 6	not equal	<10 ⁻⁸
2 to 6	not equal	<10 ⁻⁹
1 vs. 2	1 = 2	0.2633
2 vs. 3	2 = 3	0.8401
3 vs. 4	3 = 4	0.3815
4 vs. 5	4 = 5	0.2109
5 vs. 6	5 < 6	<10 ⁻¹⁰
6 vs. 7	—	—

TABLE 18

Comparisons for Time Four across stations. Kruskal-Wallis tests were used for multiple differences, Mann-Whitney tests were used for comparison between adjacent stations.

Station	Median size	Probability of equal median size
Overall	—	—
1 to 6	not equal	<10 ⁻⁸
2 to 6	not equal	<10 ⁻¹⁰
1 vs. 2	1 < 2	0.0585
2 vs. 3	2 > 3	0.0013
3 vs. 4	3 > 4	0.0104
4 vs. 5	4 < 5	<10 ⁻¹⁰
5 vs. 6	5 < 6	0.0002
6 vs. 7	—	—

change when comparing the specific times of interest (table 11). As such, there is nothing simple to be said about Station 6.

Stations 2, 4, and 5 were, with the exception of Station 5 at Times One and Five, different at times of similar subaerial exposure. Only, however, between Times Two and Three did

TABLE 19

Comparisons for Time Five across stations. Kruskal-Wallis tests were used for multiple differences, Mann-Whitney tests were used for comparison between adjacent stations.

Station	Median size	Probability of equal median size
Overall	not equal	<10 ⁻¹⁰
1 to 6	not equal	<10 ⁻¹⁰
2 to 6	not equal	<10 ⁻⁸
1 vs. 2	1 = 2	0.3159
2 vs. 3	2 = 3	0.3613
3 vs. 4	3 < 4	0.0001
4 vs. 5	4 < 5	0.0989
5 vs. 6	5 < 6	<10 ⁻⁵
6 vs. 7	6 = 7	0.7486

TABLE 20

Comparisons for Time Six across stations. Kruskal-Wallis tests were used for multiple differences, Mann-Whitney tests were used for comparison between adjacent stations.

Station	Median size	Probability of equal median size
Overall	not equal	<10 ⁻¹⁰
1 to 6	not equal	<10 ⁻⁸
2 to 6	not equal	<10 ⁻⁹
1 vs. 2	1 = 2	0.5744
2 vs. 3	2 < 3	0.0300
3 vs. 4	3 = 4	0.3278
4 vs. 5	4 = 5	0.3912
5 vs. 6	5 < 6	0.0001
6 vs. 7	6 = 7	0.1734

the three stations act similarly, with median *Marginopora* size decreasing at all three stations. At the other times of similar subaerial exposure the stations behaved independently.

For Station 1 and Station 7 a pattern may not be present simply because of a low abundance of individuals.

Overall, then, the conclusion must be that median *Marginopora* size does not respond systematically to bi-weekly subaerial exposure, although for some stations there seems to be a systematic variability through time. At the stations at the ends of the transect, Stations 1 and 7, *Marginopora* are not abundant enough to have any discernable pattern. This may be due to, at Station 1, too frequent subaerial exposure which effectively prevents *Marginopora* from inhabiting the seagrass. Similarly, at Station 7, some other environmental variable which causes the seagrass bed to stop, but not apparent in this study, may prevent *Marginopora* from living there. At the stations which are not at the edges of the seagrass bed there is either no change in median *Marginopora* size through time, or somewhat systematic changes that do not correspond to subaerial exposure.

A delay in reaction to subaerial exposure could produce a lag in size-frequency response that may not be visible over

the time period studied. A delayed response would certainly complicate the correlation of size-frequency changes and exposure.

Ross (1972) estimated the life span of *Marginopora* to be on the order of several years, with individuals reaching reproductive maturity when they are about one year old. If this is the case then the size-frequency distribution of *Marginopora* would not be expected to vary cyclically over fortnightly periods because of reproductive effects. Instead, the median size would be expected to increase as individuals grow. But this also was not observed in this study. The median *Marginopora* size both increased and decreased during the times sampled.

III: Spatial Variability in *Marginopora* Abundance

Whether Stations 1 and 7 were included in the analysis or not there was always a significant difference in median *Marginopora* size when considering all stations simultaneously. Furthermore, when considering only Stations 2 through 6, sixteen out of the twenty-four possible adjacent pairs showed differences in median *Marginopora* size, although this of course depends on the level of significance chosen. There was only one pair of stations, however, that showed a consistent trend over most sampling times: The median *Marginopora* size at Station 5 was smaller than that at Station 6 for all but Sampling Time Two. Among other stations, adjacent pairs had sometimes larger, sometimes smaller, and sometimes equal median *Marginopora* sizes. Thus it is not possible to construct some sort of environmental gradient across the seagrass bed that is responsible for controlling *Marginopora* size. Nonetheless, the variability of median *Marginopora* size is greater when considering space than when considering time.

The spatial variability in median *Marginopora* size could be the result of several causes. Buzas (1968) pointed out that the scale of observation controls, to some extent, whether or not a species distribution will appear to be aggregated or not. If *Marginopora* distribution is aggregated on the order of distances of 25 cm then the variability in median *Marginopora* size could be the result of sampling from "patches" of different *Marginopora* populations, and the spatial variability recorded in this study would merely be a sampling artifact. Movement of large numbers of *Marginopora* individuals during the times between sampling could also affect the observed size-frequency distribution. Ross (1972) measured movements about a centimeter per hour for individuals on hard substrates in the laboratory. This translates to crawling rates of one to two meters per week if the movement is continued. Thus, while it is unlikely that *Marginopora* could have moved from one station to the next between sampling periods (at least by crawling), there could have been enough motion to affect the size distribution of *Marginopora*.

CONCLUSIONS

Except for the apparent maximum number of *Marginopora* that may inhabit a given area of seagrass (text-fig. 2), there are no clear patterns that emerge from this study. The size-frequency distribution of *Marginopora* changes through time, but not in a pattern that can be explained by the fortnightly change in subaerial exposure. The size-frequency distribution

also changes across the seagrass bed, but not in a manner that can be correlated with obvious physical parameters such as distance from shore. Spatial variability in *Marginopora* populations may be the result of individual aggregations on the order of 25 cm, but may also result from the movement of individuals across the substrate.

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