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Cover photograph – "Little Ricky" - juvenile dolphin, San Salvador, Bahamas (courtesy of Sandra Voegeli, 2003)

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COMPARISON OF CALCAREOUS GREEN ALGAE COMMUNITY STRUCTURE AND CARBONATE PRODUCTION OF GRAHAM'S HARBOUR, RICE BAY AND SNOW BAY: SAN SALVADOR ISLAND, BAHAMAS

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ABSTRACT

Several genera of calcareous green algae (Chlorophyta, Bryopsidales) are a significant component of tropical near shore marine communities. Ongoing studies in San Salvador of *Halimeda* species have focused on their role in sediment production. These studies have not investigated if productivity of *Halimeda* species varies depending on whether the genus is solitary or part of an assemblage of other calcareous green algae (*Penicillus, Rhipocephalus, Udotea*). Shore parallel and shore perpendicular transect data for Graham's Harbour, Rice Bay and Snow Bay have included counts of the number and types of species present, and the number of segments (*Halimeda*) or width/circumference of crown (*Penicillus, Rhipocephalus, Udotea*), per each individual algal thallus collected. Graham's Harbour (GH) is a large (2 km x 3 km) sheltered lagoon at the north end of San Salvador, Rice Bay (RB) is an open windward lagoon (1 km x1 km) located in the northeast part of the island, and Snow Bay (SB) is a small (l km x 2 km), higher energy, inner shelf lagoon on the SSE side of the island. Along each transect, three ($0.25m^2$) quadrats were counted every fifteen meters by two divers and all species were collected from a fourth quadrat. A total of 405 quadrats were either counted or collected during two field seasons (July 2000, and December 2001). Standard ecological parameters (absolute and relative densities and coefficient of community similarity) have been determined for all calcareous green algal assemblages within these study sites. In addition, an *in situ* growth rate was calculated for *Halimeda incrassata* at GH and SB. It was determined that *H. incrassata* grows at a rate consistent with a complete turnover every 46.7 days in GH and every 19.8 days at SB. This gives a figure of 7.8 crops/yr for GH and 18.4 crops/yr for SB. In addition, at Snow Bay *Halimeda opuntia* buildups occur. These are small-elongated cushion-like structures (maximum size 5.4m L x 3.1m W and 1.0m thick). The incipient *Halimeda* mounds roughly follow the thickest and densest part of a *Thalassia* meadow. These data will be useful for developing an experimental design for addressing the ability of *Halimeda* to compete with other calcareous algal species. These data will also suggest which other calcareous algae species also make significant contribution to sediment production and should be targeted for further study. Our studies suggest that very different rates of calcium carbonate production are found in different microhabitats of a region. The results of the present study suggest that in San Salvador significant peaks in production associated with short term phenomena may contribute significantly to carbonate production.

INTRODUCTION

The benthic marine macroalgae (Bryopsidales) belonging to the genera *Halimeda, Penicillus, Udotea,* and *Rhipocephalus* (Division

Chlorophyta) are all calcifying and thus have both biological and geological importance. *Halimeda* tend to predominate in these algal communities. Dense patches of *Halimeda* have been documented at depths greater than 20 m in lagoons and on the slope break of various reef areas of the Pacific and the Atlantic (Goreau and Graham, 1967; Drew and Able, 1985, 1988; Hillis, 1985, 1986a,b,c, 1991; Colin *et al.*, 1986; Roberts *et al.*, 1987 a,b, 1988; Orme and Salama, 1988; Hine *et al.*, 1988; Liddell *et al.*, 1988; Ginsburg *et al.*, 1991; Freile *et al.*, 1995). Additionally, *Halimeda* bioherms are prominent features in Australia (Davies and Marshall, 1985; Drew and Able, 1985; Phipps *et al.*, 1985; Roberts *et al.*, 1987a,b; Marshall and Davies, 1988; Orme and Salama, 1988; Searle and Flood, 1988). Terms used to describe these algal habitats include 'meadow' (Orme *et al.*, 1978; Drew and Able, 1985; Freile *et al.*, 1995), 'mounds', 'banks' (Orme, 1985; Phipps *et al.*, 1985) and 'bioherm' (Davies and Marshall, 1985; Roberts *et al.*, 1987 a,b, 1988; Hine *et al.*, 1988). The primary types of *Halimeda* found in these environments are the rhipsalian or upright species. Hudson (1985) documented a high energy *Halimeda opuntia* sand accumulation resembling a "loosely interlocking series of connected plates that coalesce to form compact clumps and large cushion-like mats, some of which exceed 3 m in diameter" in the Marquesas Keys, FL at a depth of less than 2 m.

STUDY AREA

Populations of calcareous green algae were measured in three shallow lagoons at San Salvador Island, Bahamas (Figure 1). San Salvador lies approximately 23°57' N to 24°10' N and 74°23' W to 74°30' W. This is a tropical marine dry climate characterized by seasonal wet and dry regimes. Rainfall is less than 1000 mm/yr and temperatures average 23° C in the dry season and 32° C in the wet (Sealey, 1992).

Graham's Harbour (GH) is a shallow (<6 m) windward lagoon 2 x 3 km in area, in the northern part of San Salvador. It is a high-energy area protected by cays, dunes, and a barrier reef complex (Colby and Boardman, 1989). Rice Bay (RB) is a small (1 km x 1 km), shallow (4m, max), open high-energy sandy lagoon in the NE corner of the island (Stuby *et al.*, 2001). Snow Bay (SB) is a shallow (<3 m) lagoon in the windward southeastern margin of San Salvador (Figure 1). It is a high-energy inner shelf lagoon 1 x 2 km in area rimmed by a barrier reef complex (Andersen and Boardman, 1989).

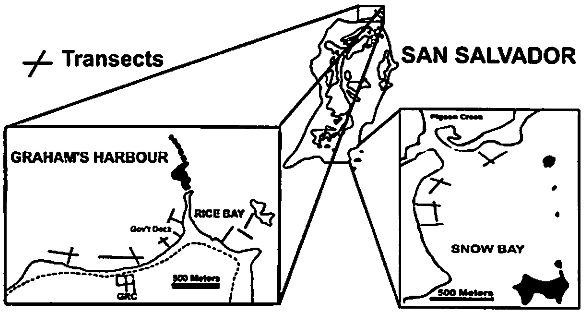


Figure 1. Map of San Salvador showing the study sites; Graham's Harbour, Rice Bay and Snow Bay as well as the location of transects .

METHODS

Density Counts and Diversity of Calcareous Algae

Several transects, both parallel and perpendicular to the shore, were established at Graham's Harbour, Rice Bay and Snow Bay (Figure 1). Each transect consisted of up to 12 stations, 15 or 30 meters apart. In addition, other randomly sampled quadrats were counted as well. Density counts were made using a 0.5 m x 0.5 m frame, producing a 0.25 m^2 quadrat. The stations on a transect were surveyed in the following manner: the algae within the frame at a station marker were counted then the frame was shifted one unit length to the right and left of the station marker and densities were again counted. Two divers counted three quadrats for each station and a fourth quadrat was harvested for laboratory work. A total of 213 thalli of *Halimeda* from Snow Bay and 256 from Graham's Harbour during July 2000, and December 2001. The number of segments was counted. The *H. opuntia* from Snow Bay was measured as a percentage cover of the substrate. The width of the capitula or fan was measured for *Penicillus*, *Rhipocephalus* and *Udotea*. In July 2000 and December 2001, 59 *Penicillus*, 6 *Rhipocephalus*, and 32 *Udotea* were measured from Snow Bay and 252 *Penicillus*, 21 *Rhipocephalus*, 84 *Udotea* from Graham's Harbour. A total of 405 quadrat counts were conducted at Graham's Harbour, Rice Bay and Snow Bay during 2 field seasons, July 2000, and December 2001. In total 207 quadrats were counted at GH, and 121 at SB. At Rice Bay 77 quadrats counts were made in July 2000 only. Within each quadrat, the genera *Halimeda, Penicillus, Udotea* and *Rhipocephalus* were counted. Select species were identified when possible. Littler and Littler (2000) is a good first order reference book for identification of the algae. Absolute and relative densities as well as 3 coefficients and indices of community similarity (Jaccard, Morisita and percent similarity) were calculated for genera and species encountered in quadrats sampled in GB, RB and SB using standard methods employed for traditional vegetation analysis (Brower *et al.*, 1998).

Dyeing Experiment

Selected areas within the lagoons were established and the algae were dyed *in situ* using Alizarin Red S stain (Sigma® Alizarin Sodium Sulfonate) dissolved in seawater (Wefer, 1980; Hudson, 1985; Multer, 1988; Payri, 1988; Freile and Hillis, 1997). Glass, plastic or Plexiglas® aquaria (Figure 2) were inverted over algal patches containing at least 15 thalli or plants. The aquaria were banked up with surrounding sediment and weighted with lead weights to prevent accidental overturning by currents. A volume of 240 cc of approximately 25,000 ppm Alizarin Red S stain was introduced through a syringe and hose. This gave a final concentration of 300 ppm in the aquaria. This concentration was one or two orders of magnitude greater than the concentrations used by Wefer (1980) or Payri (1988) and was determined after previous attempts (Freile and Hillis, 1997) at lesser concentrations failed to give observable results. Several aquaria were placed at different parts of the lagoons during several different days.

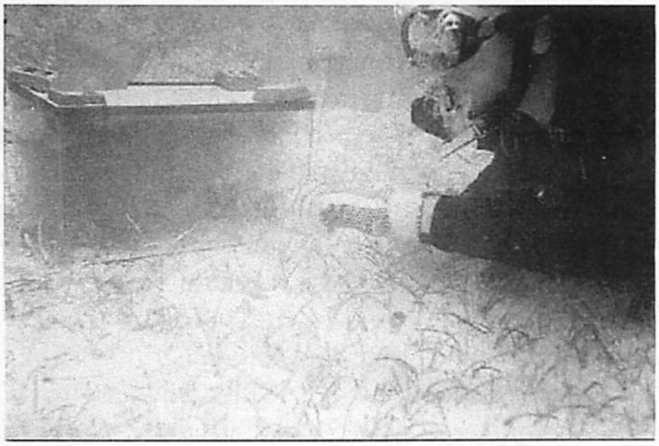


Figure 2. In situ *dyeing experiment. A glass aquarium is inverted over a patch of 15 or more thalli and Alazarin Red S dye is introduced through a syringe and tube. The aquarium is weighted down with lead weights and marked with flags.*

A total of 108 algal thalli were dyed (56 at GH and 52 at SB, the dying experiment at Rice Bay was unsuccessful). The algae at Graham's Harbour were sampled at intervals of 2, 4, 5, 8, 10, 11, 14, and 17 days, and the Snow Bay algae were sampled at 2, 6, 7, and 9-day intervals. The algae were harvested by removing the entire thallus and holdfast, were air-dried, and then stored for further analysis. Once in the laboratory, the algae were soaked in a mixture (1:1) of distilled water and Clorox® for 3 minutes to remove organic matter, washed with distilled water, and then allowed to air-dry. Dyed old segments and new-growth segments were clearly observable. All segments were counted. Growth rate was measured as the proportion of new segments per total segments (Wefer, 1980; Multer, 1988; Freile and Hillis, 1997).

RESULTS

Algal Density and Diversity of Calcareous Algae

Both Graham's Harbour and Snow Bay show a decrease in salinity from July to December of 1-3 ‰ (35.6‰ December vs. 38.0‰ July for GH and 35.5‰ December vs. 37.0‰ July for SB). Graham's Harbour appeared to maintain a relatively constant water temperature throughout

Species	Density July thalli/m²	Relative Density July	Density Dec. thalli/m²	Relative Density December
P. capitatus	6.18	0.11	15.2	0.24
P. dumetosus	2.32	0.04	8.35	0.13
Penicillus sp.	7.15	0.13	5.85	0.09
H. incrassata	32.14	0.57	25.75	0.42
H. monile	0.85	0.02	0.57	0.01
Halimeda sp.	0	0	0.27	0.004
U. cyathiformis	4.92	0.09	0	0
Udotea sp.	0.87	0.02	2.95	0.05
Rhipocephalus	1.84	0.03	3	0.05
Total *Penicillus*	15.66	0.28	29.4	0.47
Total *Halimeda*	32.99	0.59	26.58	0.43
Total *Udotea*	5.79	0.10	2.95	0.05
Total *Rhipocephalus*	1.84	0.03	3	0.05

Table 1. Algal absolute and relative density data for Graham's Harbour at the species and genus level.

Species	Density July thalli/m²	Relative Density July	Density Dec. thalli/m²	Relative Density December
P. capitatus	3.28	0.06	4.38	0.08
P. dumetosus	3.83	0.07	1.25	0.023
Penicillus sp.	4.61	0.089	1.2	0.02
H. incrassata	27.17	0.51	27.15	0.51
H. monile	10	0.19	6.99	0.13
H. opuntia	0	0	4.61	0.09
Halimeda sp.	0.39	0.01	4.82	0.09
U. cyathiformis	1.67	0.03	0	0
Udotea sp.	1.94	0.04	1.72	0.03
Rhipocephalus	0.78	0.01	1.25	0.02
Total *Penicillus*	11.72	0.22	6.82	0.13
Total *Halimeda*	37.56	0.70	44.42	0.82
Total *Udotea*	3.61	0.07	1.72	0.03
Total *Rhipocephalus*	0.78	0.01	1.25	0.02

Table 2. Algal absolute and relative density data for Snow Bay at the species and genus level.

the year, but Snow Bay was on average 3-4 °C cooler in December (22.3°C v. 26.7°C). Colorimetric nutrient (N,P) tests conducted at the sites were inconclusive.

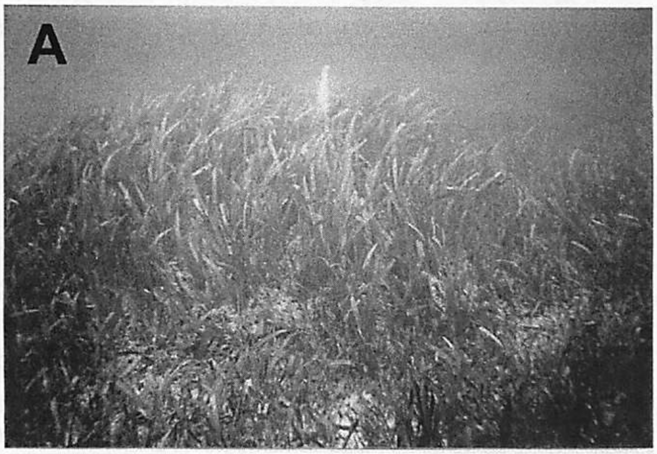
Three species of Halimeda, the sand-growing taxa H. incrassata and H. monile (Section Rhipsalis) and the sand-rock sprawler H. opuntia (Section Opuntiae) were counted. Other Halimeda species (H. scabra and H. simulans) were also noted. Halimeda incrassata predominated at most sites during both July and December. Absolute and relative density data for Graham's Harbour, Rice Bay and Snow Bay are illustrated in Tables 1, 2 and 3.

Species	Density July thalli/ m²	Relative Density July
P. capitatus	1.12	0.05
P. dumetosus	1.43	0.06
Penicillus sp.	4.44	0.19
H. incrassata	6.49	0.28
H. monile	1.82	0.08
Halimeda sp.	0.60	0.03
U. cyathiformis	5.14	0.22
Udotea sp.	0.81	0.03
Rhipocephalus	1.66	0.07
Total *Penicillus*	6.99	0.30
Total *Halimeda*	8.91	0.38
Total *Udotea*	5.95	0.25
Total *Rhipocephalus*	1.66	0.07

Table 3. Algal absolute and relative density data for Rice Bay at the species and genus level.

Halimeda incrassata densities are 32 and 26 thalli/m² for Graham's Harbour during July and December, respectively, and 27 thalli/m² for Snow Bay in both July and December. These figures are comparable to Multer's (1985) figures of 26 to 36 thalli/m² in his 3 environments on Antigua. At Rice Bay, the July census showed absolute densities of *H. incrassata* at 6 thalli/m². At Snow Bay, *H. incrassata* predominated at sites with moderate to sparse grass beds and *H. opuntia* predominated at sites with dense grass beds (Figure 3). The features described by Hudson (1985) most closely resemble the nascent bioherms observed at Snow Bay, which constitute most of the

Halimeda carbonate productivity at that site. Multer (1988) also noted that the greatest overall number of rhipsalian *Halimeda* species were to be found in medium density grass beds. Davis and Fourqurean (2001) have established a relationship between the presence of sea grass and the decreased size of *H. incrassata* thalli by over 20%. They suggested that competition for nitrogen, not available light, exists between sea grass species (e.g. *Thallasia testudinum*) and *H. incrassata*. *Halimeda opuntia*, however, grew in clumps or 'nascent' bioherms within these dense grass beds (Figure 3A&B). These features are quite large and cover a fairly large area of the dense grass beds (Table 4). This growth may be due to the increase in nutrient supply from the detrital organic matter from grass blades that can be found in this very shallow area, which is subjected to vigorous wave agitation. Because *Halimeda* obtains nutrients primarily through the substrate and secondarily from the water column (Fong *et al.*, 2001) their close association with grass beds that contain higher nutrient values within the muddy substrate is not unusual. These *H. opuntia* build-ups are very similar to those described by Hudson (1985). A total of 13 build-ups were measured at Snow Bay; these data are shown in Table 4. In addition to the algae represented in Tables 1, 2 and 3, other algae and sea grasses were noted, but in most cases represented <2 thalli/m^2 and were not recorded.



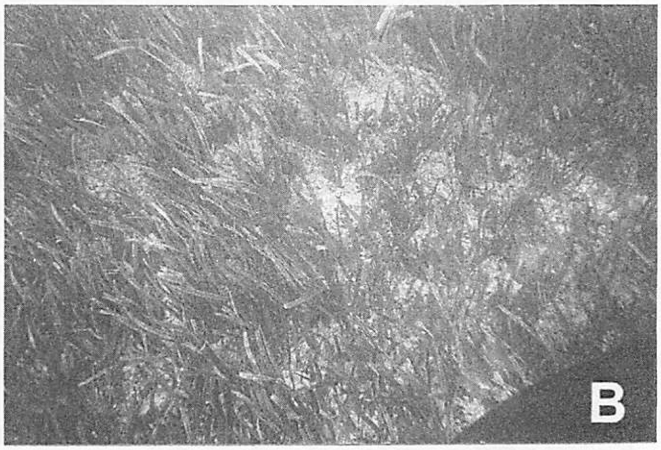


Figure 3. A) Incipient Halimeda *'bioherm' at Snow Bay. The feature is approximately 2.5 meters across and 0.75m high. B) Looking down on a* H. opuntia *'bioherm.' Note the thickness of the grass bed and the bulbous clump-like nature of the build-up.*

Length	Width	Height
2.1	1.6	0.62
2.4	2.2	0.55
5.0	3.2	1.00
1.5	1.4	0.40
2.6	1.4	0.30
5.4	3.1	0.55
1.3	1.2	0.40
2.5	2.3	0.75
2.6	1.25	0.50
1.65	1.55	n/a
1.65	1.10	n/a
1.9	1.80	n/a
1.25	1.15	n/a

Table 4. Measured H. opuntia *build-ups (nascent bioherms). All numbers are in meters.*

The time of year (July vs. December) did play a role in the total rhipsalian *Halimeda* densities measured at both Graham's Harbour and Snow Bay (Table 1,2). Relative densities of *Halimeda incrassata* for Graham's Harbour and Snow Bay are not greatly different on average; however, our results suggest that the density of *H. incrassata* may decline during the winter at GH and increase at SB. At SB there was an increase in relative density of *Halimeda* 70% (July) vs.

82% (December). This is opposite of what Lirman and Biber (2000) showed for the northern Florida reef tract. It is also contrary to experiments done by Payri (1988) and Ballesteros (1991) that showed a strong seasonality in the number of thalli produced by Halimeda. They show maximal productivity in the summers. They measured maximum percent cover of macro algae (*Halimeda* and *Dictyota*) in July vs. December (56.7% vs. 25.8%). The trends in GH were opposite to those at SB. Relative densities for *Halimeda* in GH were 59% (July) vs. 43% (December). *Penicillus*, however, showed an increase in GH in December (47%) vs. July (28%).

Halimeda is consistently a dominant element of both the Snow Bay and Graham's Harbour communities. Though at Snow Bay, *H. opuntia* is a major element and a dominant sediment contributor. However, determination of individual thalli of *H. opuntia* is difficult and thus the relative densities calculated do not accurately reflect the major role the species plays in the community. Relative density values show that *H. incrassata* is by far the most abundant of the algae present (Tables 1, 2, 3). At RB it accounts for 28% of the community in July while at GH they account for 57% and 42% in July and December, respectively. At SB *H. incrassata* accounts for 51% of the community year-around. If all *Halimeda* species were lumped together, the genera as a whole represents 70% (July) and 82% (December) of the community at SB and 59% (July) and 43% (December) at GH (Table 1, 2). Even at RB they account for 38% of the community (Table 3). Obviously more pairs of data sets for December and July would be needed to determine if this is a trend or not.

The community similarity indices used showed very little difference between the GH and SB sites. Very little difference also existed within each site at different times of year. The Jaccard coefficient of community ($CC_j = c/S$; where c is the number of species common to both communities and S is the total number of species found in the two communities) for GH July vs. December is 0.78 for SB it is 0.80. Thus there is very little difference between the communities at different times of the year. The Morisita index of community similarity ($I_M = (2\Sigma x_i y_i)/((l_1 + l_2) N_1 N_2)$ where; x_i is the number of individuals in species (i) in community 1 and N_1 is the total number of individuals in community 1, l_1 and l_2 are the Simpson's dominance indices for community 1 and 2, respectively, y_i is the abundance of species (i) and N_2 the total number of individuals in community 2) refers to the probability that individuals randomly drawn from each of the two communities will belong to the same species. The Morisita index for SB (July vs. December) is 96%. For GH it is 90% and between SB and GH it is 94% for July and 85% for December (Table 5). Once again a great similarity exists between and within the sites.

A comparison of algal morphological data was also conducted between the different sites within Graham's Harbour and Snow Bay. Also a comparison was done between Snow Bay (SB) and Graham's Harbour (GH) for the December data set. Mean, mode and median segment number (*Halimeda*) and capitula circumference (*Penicillus*) of the algae were measured. Because the standard deviation in most cases was so great, a T-test was employed to see if any differences existed. The T-test employed showed no significant differences of morphological features within and between the sites (Table 6). At both SB and GH there is no significant difference in variation.

Snow Bay vs. Graham's Harbour			
Time of Year	Jaccard	Morisita	% similarity
July species	0.89	0.94	77.06
December species	0.89	0.85	61.26
July genus	1	98	88.64
December genus	1	0.75	61
Snow Bay			
July vs. December species	0.8	0.96	80
July vs. December genus	1	0.98	87
Graham's Harbour			
July vs. December species	0.78	0.9	71.87
July vs. December genus	1	0.92	78.88

Table 5. Community similarity indices between sites and within a site at different times of the year (July vs. December)

Location	Season	Species	Mean (seg or head width in cm)	Std. Dev.	Mode	Median
Snow Bay	July	*P. dumetosus*	0.87	0.34	0.5	0.9
Graham's Harbour	July	*P. dumetosus*	1.62	0.98	1	1.4
Snow Bay	July	*H. incrassata*	42.83	35.94	15	29
Graham's Harbour	July	*H. incrassata*	57.23	43.48	37	42.5
Snow Bay	July	*P. capitatus*	1.17	0.55	1	1
Graham's Harbour	July	*P. capitatus*	1.56	0.66	1	1.5
Snow Bay	Dec	*P. dumetosus*	2.62	2.31	N/A	1.7
Graham's Harbour	Dec	*P. dumetosus*	2	Only 1 ind		
Graham's Harbour	Dec	*H. incrassata*	37	31.39	25	26
Snow Bay	Dec	*H. incrassata*	87.52	99.25	23	54
Graham's Harbour	Dec	*P. capitatus*	1.48	0.77	1.6	1.5
Snow Bay	Dec	*P. capitatus*	1.73	1.05	1.7	1.6

Table 6. Statistical parameters on algal morphological data from December 2001.

These results are preliminary and we would like to continue to monitor these communities in the future in the hope of establishing a longer-term record of algal diversity.

Dyeing Experiment

New growth as indicated by absence of pink (alizarin stained) segments was documented in approximately 70% of *H. incrassata* thalli. It was difficult to observe on *H. monile* and *H. opuntia* thalli, whereas *H. simulans* and *H. scabra* did not constitute a large enough population in the aquaria experiment to analyze statistically. Growth rate for *Halimeda incrassata* is measured as a function of new segments/total segments per unit time (Wefer, 1980; Drew, 1983; Hudson, 1985 ; Multer, 1988; Freile and Hillis, 1997). Regression analysis (R=0.918 and R=0.797) of the data are shown in Figure 7 for Graham's Harbour and Snow Bay, respectively. The best-fit regression lines show a doubling time (100% replacement) of 46.7 days (GH) and 19.8 days (SB). If this figure represents one crop of segments, then a figure of 7.8 and 18.4 crops per year are obtained for these areas respectively. The term 'crop' is a helpful concept when considering production; yet in terms of growth pattern it may be misleading. A new thallus may be produced, or the equivalent in new segments may be added to an older, perennial type of base. The data indicate that conditions for *Halimeda* growth at these sites remain similar throughout the year, 7.8 and 18.4 'crops' (*sensu lato*) would be produced. There appeared to be no statistically valid changes in the growth rate between July and December. These figures are within the range of the general 3 to 19 crops per year provided by Hillis (1991) for *Halimeda* (most species and environments).

The growth rates for *H. incrassata* at Snow Bay is 50 to 100% greater than what other researchers have found in other regions of the Caribbean (Wefer, 1980; Multer, 1988; Freile and Hillis, 1997) (Figure 8), while those of Graham's Harbour correlate well with the figure of Multer (1988). Doubling rates in Bermuda (Wefer, 1980) and Panama (Freile and Hillis, 1997) were 32 days and in Antigua, W.I., 39 days (Multer, 1988). In making these comparisons, it should be remembered that physico-chemical parameters for these different study areas may be very different and are based on extrapolations from a few months of data. Turnover figures must be applied with care until more data on different species, and the impact of temperature, salinity, currents, and photosynthetic photon flux are known.

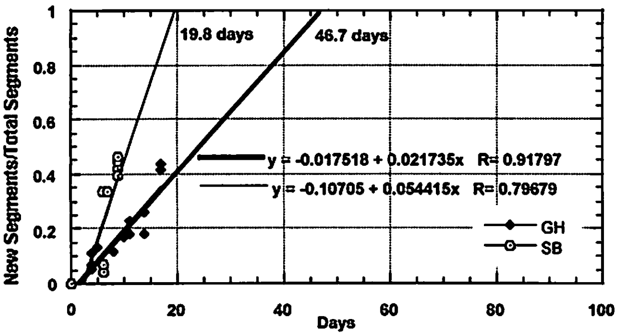


Figure 7. In situ *growth rate for* Halimeda incrassata *at Graham's Harbour and Snow Bay. Growth rate is expressed as a ratio between new segments/dyed segments over a maximum period of 17 days.*

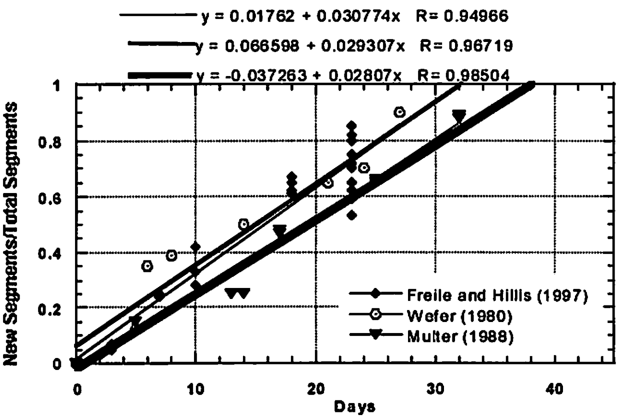


Figure 8. In situ *growth rate for* Halimeda incrassata *data from Freile and Hillis (1997), Multer (1988) and Wefer (1980). Growth rate is expressed as a ratio between new segments/dyed segments over a maximum period of 32 days.*

DISCUSSION AND CONCLUSIONS

Previous studies of calcareous green algae's contribution to sediment formation in tropical near shore environments have focused on a single study site in a particular region. Rarely have researchers looked at the way productivity is impacted due to the following factors: 1) differences in productivity in relation to the diversity of a community and 2) microhabitats present in near shore environments. At most these studies have concentrated on seasonality and productivity (Drew and Abel, 1988; Payri, 1988; Ballesteros, 1991).

Time of year: Differences in productivity are apparent for some species based on the time of year. These do not appear to be at the generic level, but rather at the specific level. *Penicillus dumetosus* head size was rather large December 2001 as compared to July 2000 measurements. It is important to note that there was a wide range of head sizes as indicated by the large standard deviation. *Halimeda incrassata* likewise increased the number of segments produced in the winter at Snow Bay. This is opposite of what other researchers have found (Drew and Abel, 1988; Payri, 1988; Ballesteros, 1991). However, *Halimeda sp.* and *Penicillus sp.* as a whole did not increase in size.

Differences in productivity in relation to the diversity of the community: There are no significant differences among the communities sampled on San Salvador. However, clearly some species are more productive and thus dominant. If the communities are not significantly different, we can consider this a controlled variable.

Microhabitats: Previous studies may assume that nearshore environments are relatively homogenous and that one study site may be representative of a particular region. Our studies suggest that very different rates of calcium carbonate production are found in different microhabitats of a region. An example of these different rates was suggested between the wave-dominated shallow lagoon of Snow Bay compared to the low-energy lagoon at Graham's Harbour. If no abiotic factors such as nutrient upwelling can account for this change in productivity, then different species of calcareous green algae have different enzymes that perform better at different times of the year cold vs. warm. In a six-year laboratory and field study by Drew and Abel (1988) they investigated the gametangia formation of 17 species of *Halimeda*. Most of the species showed a distinct fertility in the summer; however, *H. opuntia* showed a preference for winter spawning. Similarly, Carpenter *et al.* (1991) measured primary productivity and nitrogenase activity of algae in tanks. Their data indicate that rates of photosynthesis are not only dependent on flow speed but also on flow mode. Oscillatory flow, they summarize, is especially important for primary producers because it creates more turbulent flow in the vicinity of the thallus. Wave action is especially strong in Snow Bay during the winter and that oscillatory flow can affect the growth rate of the algae. Furthermore, Littler *et al.* (1988) stated that shallow water species of *Halimeda* are very well adapted to take advantage of episodic nutrient pulses.

Most rates of carbonate sedimentation contributions are based on estimates of a steady rate of production. Our findings in San Salvador suggest that significant peaks in production associated with short term phenomena may contribute significantly to carbonate production. Therefore, rates based on a steady rate of calcium carbonate production may be underestimated if the contributions of these short periods of high production are not taken into account.

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