PROCEEDINGS OF THE 15TH SYMPOSIUM ON THE GEOLOGY OF THE BAHAMAS AND OTHER CARBONATE REGIONS

Edited by
Douglas W. Gamble and Pascal Kindler

Gerace Research Center
San Salvador, Bahamas
2012

Front Cover: *Porites* colony encrusted by red algae in waters of San Salvador, Bahamas; see paper by Fowler and Griffing., p. 41. Photograph by Pascal Kindler, 2011.

Back Cover:. Dr. Jörn Geister, Naturhistorisches Museum Bern, Keynote Speaker for the 15th Symposium and author of "Keynote Address – Time-Traveling in a Caribbean Coral Reef (San Andres Island, Western Caribbean, Colombia)", this volume , p. vii. Photograph by Joan Mylroie.

Press: A & A Printing

ISBN 978-0-935909-93-7

REVISITING CARBONATE PRODUCTIVITY RATES OF *HALIMEDA* IN GRAHAM'S HARBOUR, SAN SALVADOR, BAHAMAS

Deborah Freile[1], Melanie L. DeVore[2], Matthew Boyle[2] and Rob Maitner[1]

[1]Department of Geoscience
New Jersey City University, Jersey City, NJ 07305

[2]Department of Biological Sciences
Georgia College and State University, Milledgeville, GA 31061

ABSTRACT

Calcareous green algae (*Halimeda, Penicillus, Udotea* and *Rhipocephalus*) are major generators of carbonate sediments in tropical regions. A study was undertaken in July 2000 and December 2001 in Graham's Harbour on San Salvador, Bahamas, to quantify the amount of sediment produced by *Halimeda* and to establish baseline measurements for parameters of community structure including species richness and diversity of these algae (Freile, 2004; Freile et al., 2005). In May 2009 and 2010, several transects were run in the western end of Graham's Harbour and compared to the 2000-2001 data. The coverage of the previous work was extensive (180 quadrats counted for diversity vs. 37 in 2009 and 65 in 2010) and 112 specimens counted for growth in 2010 *versus* several hundred in 2000-2001. In addition, the short time spent in San Salvador in May 2009/2010 (two weeks *versus* a month in July 2000) also meant a shorter time for the *in situ* growth experiment. Preliminary work shows that a turnover rate for an algal thallus was achieved at 43.9 days *versus* 47 days for the 2000-2001 time frames. Thus, there were 8.3 algal crops/yr in 2010 vs. 7.8 algal crops/yr in 2000-2001. Also the average segments per upright or rhipsalian alga thallus (*Halimeda*) was 107 vs. 97 segments for the 2000-2001 data. Additionally, there appeared to be slightly more algae per square meter than before: 34 (2009) and 31 (2010) vs. 27 (2000-2001) than before. These data would at first glance indicate a higher photosynthetic activity on the part of the algae, but more work needs to be conducted to verify these results. To date, we have not detected any change at the community level. Community indices (e.g. species richness, the assemblage of algae *Halimeda* sp., *Penicillus* sp., *Udotea* sp. and *Rhipocephalus* sp.) have remained unchanged since 2000-2001 (Freile et al., 2005). This may be due to the fact that the community is not impacted or, alternatively, that we lack a long term set of data for both community structure and productivity. In particular, there have been few studies that provide any insight to the role sexual reproduction plays in influencing populations and communities of calcareous algae. Clifton and Clifton (1999) showed that sexual reproduction has a clear, negative impact on local algal abundance. To date, we have not noted any decrease in the abundance of *Halimeda incrassata*, and the San Salvador Island populations either are limited to asexual reproduction or populations have not been sampled after or during an episode of sexual reproduction. Future monitoring and studies will be invaluable in elucidating the relationships, if any, that exist between productivity and community structure in response to elevated levels of CO_2.

INTRODUCTION

The benthic marine macro algae (Division Chlorophyta; Order Bryopsidales) belonging to the genus *Halimeda* and the other genera (*Penicillus*, *Udotea*, and *Rhipocephalus*) (Figure

1) are all calcifying and produce copious amounts of aragonite sediment both in the >63 μm (sand-size) and <63 μm (clay and silt size) as they disintegrate.

Halimeda has long been recognized as a very important producer of calcium carbonate sediment on coral reefs and adjacent lagoons (Judd, 1904; Chapman and Mawson, 1906). In the last thirty years many researchers have further conducted studies attesting to its continued importance (Hillis, 1980; Wefer, 1980; Drew, 1983; Hudson, 1985; Orme, 1985;

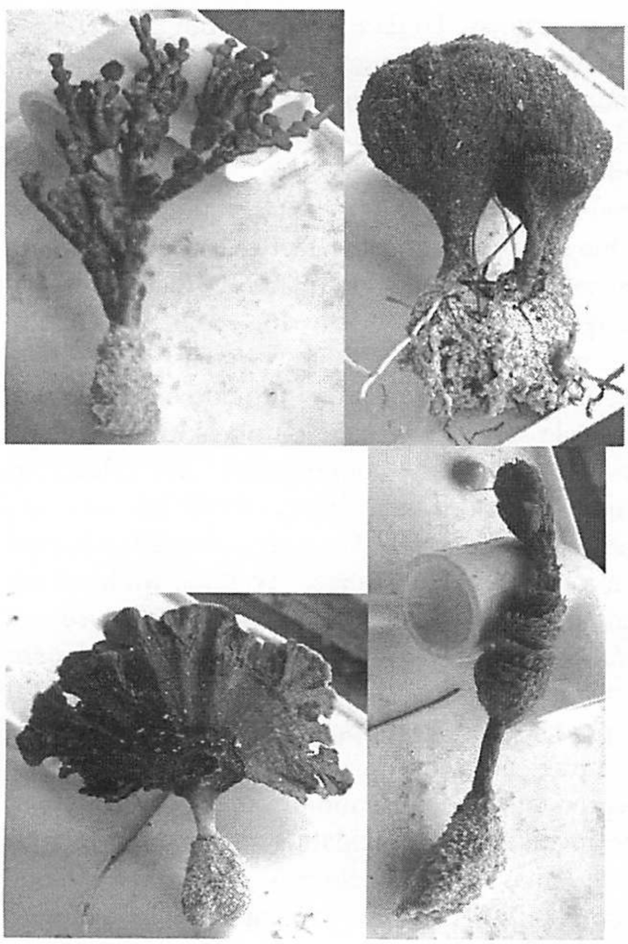

Figure 1. Benthic macro algae (Division Chlorophyta; Order Bryopsidales) counted. Different species of these genera were identified. In the figure above from topleft going clockwise Halimeda incrassata; Penicillus capitatus; Udotea flabellum; Rhipocephalus phoenix *(photographs by Sandra Voegeli).*

Hillis, 1986 a,b,c; Littler et al., 1986; Boss and Liddell, 1987; Drew and Able, 1988; Flügel, 1988; Liddell et al., 1988; Multer, 1988; Payri, 1988; Fornos et al., 1992; Freile et al., 1995; Payri, 1995; Freile and Hillis, 1997; Freile, 2004). In addition, *Halimeda* plates are the dominant skeletal component on reef-top sediments (e.g. Milliman, 1974; Bathurst, 1975).

Productivity of *Halimeda* was first measured at sites on San Salvador Island during the summer of 2000 and subsequently in the winter of 2001 (Freile, 2004; Freile et al., 2005). It is the focus of the present work to incorporate insights gained from measuring productivity of *Halimeda* during the 2009 and 2010 May field seasons.

STUDY AREA

Carbonate productivity rates of *H. incrassata*, one of the most common species of *Halimeda* in shallow (<12m), near shore environments (Littler and Littler, 2000), was re-measured at the western section of Graham's Harbour (Figure 2) near the Gerace Research Centre. Graham's Harbour is a shallow (<6m), reef-protected windward lagoon on the northeastern part of the island of San Salvador, Bahamas. San Salvador lies approximately at 23°57'N to 24°10'N and 74°23'W to 74°30'W (Figure 2). This island has a tropical marine dry climate characterized by two seasons: wet and dry (rainfall is less than 1000 mm/yr and temperatures average 23°C in the dry and 32°C in the wet season, respectively (Sealey, 1992).

METHODS

Diversity and Density Counts

In 2000 and 2001, eight transects both shore parallel (4) and shore perpendicular (4) were established along several areas in Graham's Harbour (Figure 2). Each transect consisted of up to 12 stations, located 15 m apart. Several randomly selected quadrats were also sampled as well. Density counts were made using a 0.5 m x 0.5 m frame (0.25 m^2 quadrat). The stations on

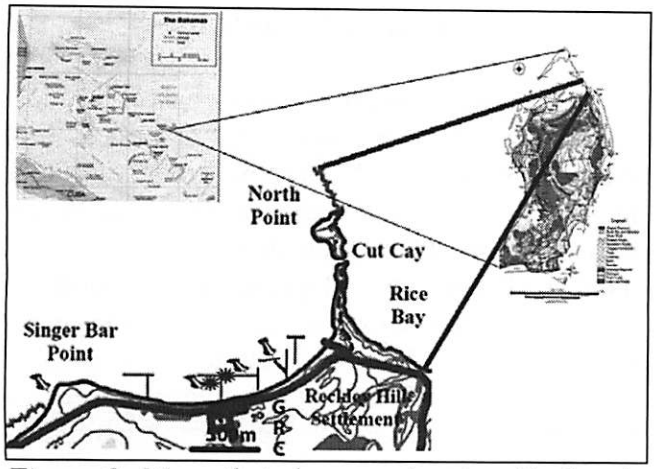

Figure 2. Map of study area showing Graham's Harbour and the island of San Salvador, Bahamas. The transect areas surveyed in May are directly north-west of the Gerace Research Centre (GRC) and those surveyed in 2000/2001 are both north, west and east of GRC. The plots that were employed in the dye experiments in 2009/2010 are marked by stars whereas those in 2000/2001 are marked by push-pins. (Map modified from Robinson and Davis, 1999)

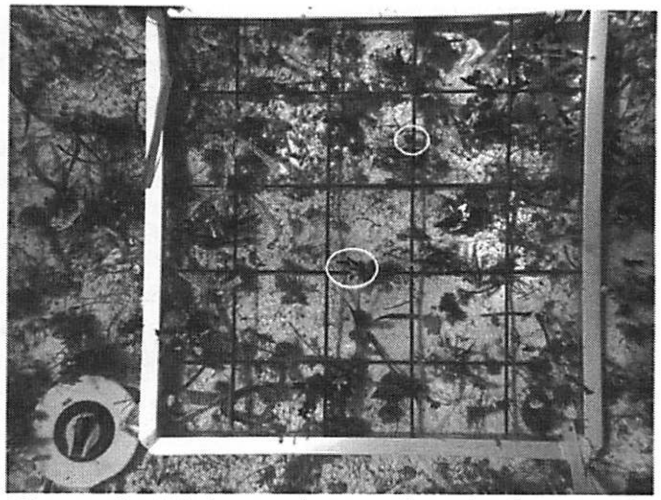

Figure 3. High resolution digital photograph used to count algal quadrats in 2010. The methodology was ground-truthed for accuracy. The counts in 2000/2001 and 2009 were counted by 2 divers; all species when possible were identified. For example, the circles on the photographs are illustrating <u>Penicillus</u> *(top) and* <u>Halimeda</u> *(bottom). The quadrat is 0.50 m on each side giving an area of 0.25 m^2.*

the transect were surveyed in the following manner: the frame was shifted one unit length to the right and left of the station marker and densities were counted a total of three times by two divers and a fourth quadrat was sampled for laboratory work. In total, 180 quadrats were counted at Graham's Harbour. In May 2009 and 2010, only the western end of Graham's Harbour was re-examined; three short transects were run in 2009 accounting for 37 quadrat counts and six short transects were run in 2010 accounting for 65 quadrat counts. In 2010, high resolution digital photography was used to count the algae within the quadrats (Figure 3). The methodology was ground-truthed for accuracy. *Halimeda*, *Penicillus*, *Udotea* and *Rhipocephalus* were counted. Select species were identified whenever individuals were intact and possessed identifiable features.

Dye Experiment

The algae were dyed *in situ* using a solution of 2.5% Alizarin Red S stain (Sigma® Alizarin Sodium Sulfonate) dissolved in seawater (Wefer, 1980; Hudson, 1985; Payri, 1988; Freile and Hillis, 1997). Plastic or Plexiglas® aquaria were inverted over at least 15 algal thalli. The aquaria were banked with surrounding sediment and weighed down with lead weights and injected through a hose and syringe combination until the water within the aquaria was red (Figure 4). The dye was left in the inverted aquaria for 24 hours before removal. The concentration of dye is greater than that used by Wefer (1980) or Payri (1988) and was determined to be effective, after various attempts (Freile and Hillis, 1997) at lesser concentrations failed to give observable results.

In 2000-2001, 56 thalli were dyed at Graham's Harbour and harvested from 4 to 17 days. In 2009, 51 thalli were dyed, but only harvested at 5 and 12 days due to weather. However, in 2010, 112 thalli were dyed and harvested at 3, 6 and 10 days. The algae were removed completely (thalli plus holdfast), air-dried and stored for further analysis. Once in the laboratory, the algae were soaked in a mixture of

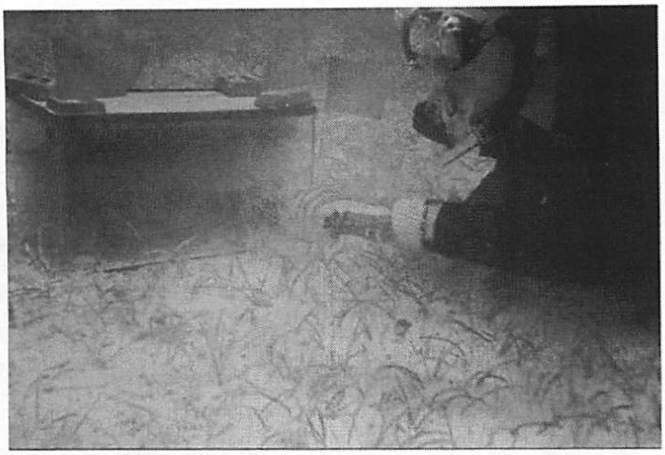

Figure 4. In situ *dyeing experiment. Plexiglas or plastic aquaria were inverted over a patch of 15 or more algae and sea grass and Alazarin Red S stain was introduced through a syringe and hose. The dye remained over a period of 24 hours in the tanks and the tanks were weighed down with lead diving weights. The aquaria were flagged and marked by buoys.*

seawater and bleach for 10 minutes at a neutral pH to remove all the organic matter. The algae were allowed to air-dry. Old segments (dyed) and new growth was clearly observed (Figure 5). All segments were counted. Growth rate was measured as the ratio of new segments to total segments (Wefer, 1980; Multer, 1988; Freile and Hillis, 1997; Freile, 2004).

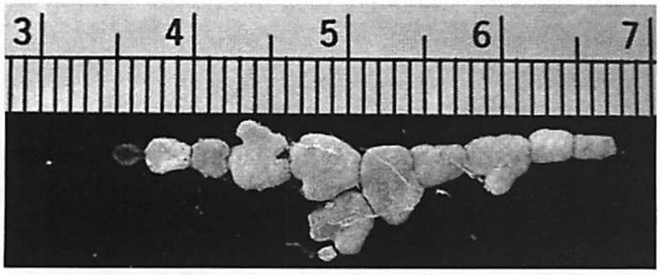

Figure 5. Part of an algal thallus showing old (dyed, grayish color) segments and new growth (white at the 4 cm mark). The apical segment starting at the 3.7 cm mark is not calcified and therefore is green (or appears dark in the photograph). The new calcified segment is white and is clearly visible between the 4 and the 3.7 cm mark.

Carbonate Productivity

Multiple quadrats were harvested near station markers. In 2000-2001, 216 thalli were picked from Graham's Harbour compared to 51 in 2009 and 145 in 2010. Different measurements were taken (height, branches and number of segments). Representative samples of segments of the rhipsalian species of *Halimeda incrassata* (n = 150 from 2000-2001 and n = 500 from 2009) were bleached, cleaned, and weighed to obtained a typical figure in grams of $CaCO_3$/segment.

RESULTS

Density Counts

Two species of *Halimeda*, the erect sand-growing taxa *H. incrassata* and *H. monile* (Section Rhipsalis) were present. *H. scabra* and *H. simulans* were also present in 2000-2001, but constituted a very small amount of the taxa present. They were absent in 2009/2010. *H. monile* was also sparse in 2010. *Halimeda incrassata* predominated at sites with moderate to sparse grass beds as compared to other calcareous green algae (i.e. *Penicillus*). *Halimeda incrassata* was the species used to determine carbonate productivity rates. The 2000-2001 and 2009-2010, density data are illustrated in Table 1. It shows a slight increase in the rhipsalian *Halimeda* density in Graham's Harbour (34 vs 27 thalli/m^2) for 2009 and 31 thalli/m^2 for 2010. The other algal taxa remain the same with the exception of *Penicillus capitatus* in 2010 (24 thalli/m^2 vs 14 thalli/m^2 for both 2000-2001 and 2009). It is important to note that the competition between *Halimeda* and the seagrass *Thalassia* is known to be influenced by nitrogen and the growth rate of the former can decrease by 33.3% (Davis and Fourqurean, 2001) with the presence of the later. How the presence of *Penicillus,* which is abundant in quadrats with seagrass, interferes with the growth of *Halimeda,* needs to be understood in Graham's Harbour.

Table 1. Density count data for Graham's Harbour variations in species through the period from 2000-2010.

SPECIES	RANGE 2000/2001 Thalli / m²	MEAN 2000/2001 Thalli / m²	RANGE 2009 Thalli / m²	MEAN 2009 Thalli / m²	RANGE 2010 Thalli / m²	MEAN 2010 Thalli / m²
H. incrassata	0 – 164	26	0 – 168	32	0 – 104	31
Halimeda sp.	0 – 8	1				
H. monile	0 – 132	1	0 – 48	2	None	
Rhipsalian Hal	N/A	27	N/A	34	N/A	31
P. capitatus	0 – 52	14	0 – 44	14	0 – 76	24
P. dumetosus	0 – 44	9	0 – 20	8	0 -32	10
P. pyriformis		6	0 – 12	1		
Penicillus sp.	0 – 32	3	0 – 20	5		
U. cyanthiformis	0 – 40		0 – 28	3	0 -8	2
U. flabellum			0 – 4	< 0.5	0 -8	1
Udotea sp.	0 – 20	1	0 – 4	< 0.2		
R. phoenix			0 – 16	4	0 -16	2
Rhipocephalus sp.	0 – 24	3				

Dye Experiment

New growth, indicated by the presence of white (Alizarin unstained) segments, was clearly observed on the *H. incrassata* thalli (Figure 5). 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; Freile, 2004). The best-fit regression line shows a doubling time (100% replacement) of 43.9 days (Figure 6).

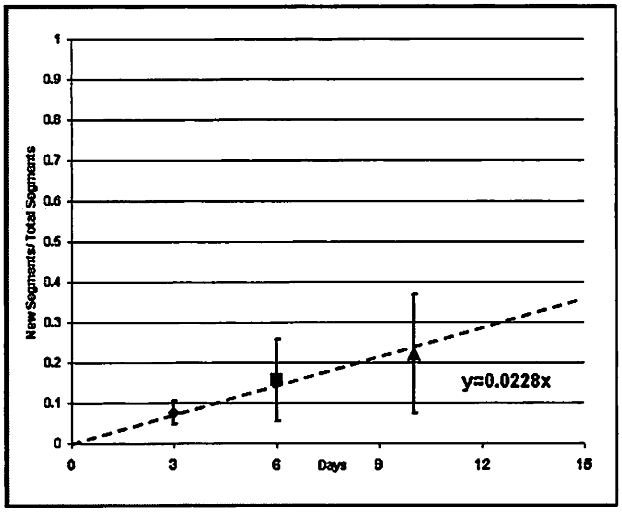

Figure 6. Best fit regression line doubling rate (100% replacement) is at 43.9 days for Halimeda incrassata (2010) data. The highly variable growth rate is probably due to variation among individuals.

Carbonate Productivity

From the measurements of 216 thalli from 2000-2001, it was determined that *H. incrassata* contained an average of 97 segments/thalli and from the measurement of 51 thalli from 2009 and 145 thalli in 2010 it was determined that *H. incrassata* contained an average of 107 segments/thalli. Total carbonate content of the segments is calculated using the weight of representative segments (n = 500) and is calculated at 0.0057 +/- 0.0035 g/segment of

$CaCO_3$; in contrast, a value of (n = 150) 0.0111 +/- 0.0052 g/segment $CaCO_3$ was obtained for the 2000-2001 data. Multer (1988) obtained a value of 0.009 grams; no range of mass was given. It is important to understand that the variation in mass of individual segments is due to inherent variations in the size of the individual organism. Additionally, $CaCO_3$ accounts for 81% of the total algal biomass of *H. incrassata*. This value is obtained by measuring total dry weight of the algae before and after oxidation with bleach (Freile and Hillis, 1997; Freile, 2004)

Carbonate productivity can be determined from density counts, turnover rates, and calculations based on the number of segments/thallus and the weight in grams of $CaCO_3$/segment. For Graham's Harbour this translates to 232 g $CaCO_3/m^2/y$ in 2000-2001 (Freile, 2004) and 162 g $CaCO_3/m^2/y$ in 2009/2010, a decrease of 30% in 10 years for *Halimeda incrassata*, but an increase in growth rate and segment production.

DISCUSSION

The highly variable growth rate among and between individuals is probably due to competition for nutrients between algae and seagrass (Davis and Fourqurean, 2001). One set of data needed to address this question would be observations of *Halimeda incrassata* during periods of sexual reproduction. Only one study (Clifton and Clifton, 1999), conducted at the Smithsonian Tropical Research Institute's San Blas station between October 1994 and May 1997, has ever documented periods of sexual reproduction (March-May) of *Halimeda*, *Penicillus*, *Rhipocephalus*, and *Udotea*. All four taxa are holocarpic and disintegrate after completing sexual reproduction. We often tend to view algae in terms of having homogenous growth rates and not in terms of having genetically based differences among individuals in terms of productivity. The numbers of genetically different individuals and their clones would be expected to have variable growth rates. The overall genetic structure of populations of *Halimeda* is a question that has not been explored and no studies using molecular markers comparing variation within and among populations of these algae have been completed.

If the figure of 43.9 days represents a doubling rate or one crop; then a figure of 8.3 crops per year is obtained for Graham's Harbour. Similarly, the data for Graham's Harbour in 2000-2001 showed a turnover rate of 47 days or 7.8 crops per year. 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, as new leaves are added to trees. These preliminary data indicate that if conditions for *Halimeda* growth at this site remain similar throughout the year, 8.3 'crops' (*sensu lato*) would be produced. This figure is within the range of 3 to 12 crops per year provided by Hillis (1991) for *Halimeda* (most species and environments).

This growth rate for *H. incrassata* correlates well with previous work (Wefer, 1980; Multer, 1988; Freile and Hillis, 1997). The doubling rate in Bermuda, a subtropical area (Wefer, 1980) was 32 days; in Antigua, W.I., 39 days (Multer, 1988) and in the land proximal lagoon in Panama, 32 days (Freile and Hillis, 1997). 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 limited data. Also, the nature of sexual stages of *Halimeda* sorely needs to be addressed. In May, some individuals were observed with gametangia and clearly were in sexual stages. It is not known if entire populations sexually reproduce and die; if only certain genetically distinct subpopulations sexually reproduce and die; or if individuals within populations stagger their sexual reproduction across the March-May time frame when environmental cues are present to signal the onset of sexual reproduction.

Based on five consecutive years of measurements of *Halimeda opuntia* and *H. tuna* populations on Conch Reef, Florida Keys, Beach et al. (2003) found evidence that a potential dynamic relationship indeed exists between nutrients, irradiance and algal productivity. Their study further illustrated that long-term monitoring over spatial and temporal gradients is needed to fully disentangle the factors that impact productivity. One factor that clearly influenced productivity of these algae was cold-water upwelling events. It is not clear what the patterns of cold-water circulation events are on San Salvador Island or their potential impact on shallow-water *Halimeda* populations. The isolated nature of San Salvador Island makes it a prime site to initiate long term studies that incorporate measurements of both growth and water temperatures.

Examining Acidification and Impact on Carbonate Production in *Halimeda*

Robbins and colleagues (2009) conducted both laboratory and field studies examining the response of *Halimeda* to ocean acidification on the west Florida shelf. One of the responses they documented was a link between increased pCO_2 and decreased pH with the form of aragonite crystals produced. In essence, these researchers noted a decrease in crystal size (width), but an increase in the abundance of crystals produced. Because the morphology and crystal abundance in *Halimeda* segments can vary with species, segment age, and even within site, only apical segments were examined during the study (Robbins et al., 2009). Examination of apical segments from specimens of *Halimeda* collected over the last 40+ yrs also indicated this change of shape and increase in crystal concentration. A second significant insight was gained by measuring percentage of organic and inorganic carbon per sample weight. In pooled species no significant changes in the ratio were noted. However, in the most recent samples (2007-2008) of *H. incrassata*, increased levels of organic carbon and decreased levels of inorganic carbon were observed.

The results of our 2009/2010 survey of *Halimeda incrassata* populations in Graham's Harbour suggests that the loss of carbonate per segment could be due to acidification, and the overall increase in carbonate sedimentation represents an increase in the rate of organic carbon generation as evidenced by the increase in crops of algae per year. This supports the results from the west Florida study (Robbins et al., 2009).

Still, the monitoring and measurements needed to document impacts of acidification on *Halimeda* are in their infancy and more long term data sets from regions outside the Caribbean are essential. In regards to San Salvador Island monitoring, we will continue the present field studies, but will also be initiating the necessary SEM studies to document the abundance and size of crystals within segments. Because of the significant role calcareous algae play in the carbon budget of tropical marine ecosystems, an understanding of their responses to declining, global pH values is significant for predicting how carbonate production will be altered.

ACKNOWLEDGMENTS

The author's would like to thank Dr. Dwight Call and the staff of the GCSU International Education Center and the students participants from the 2009 and 2010 Bahamas Study Abroad Program for their help and in particular GCSU students Christopher Edenfield, Zachary Gilbert, Seth Strzyzewskil, and Evan Boitet and NJCU Students Melissa Palacios and Mandy Edgecombe, who was funded through a CCRAA grant for the summer.

REFERENCES

Bathurst, R.G.C., 1975, Carbonate Sediments and their Diagenesis: Amsterdam, Elsevier, Developments in Sedimentary Petrology, v.12, 659 p.

Beach, K., Walters, L., Vroom, P., Smith, C., Coyer, J., and Hunter, C., 2003, Variability in the ecophysiology of *Halimeda* spp. (Chlorophyta, Bryopsidales) on Conch Reef, Florida

Keys: Journal of Phycology, v. 39, p. 633-643.

Boss, S.K., and Liddell, W.D., 1987, Patterns of sediment composition of Jamaica fringing reef facies: Sedimentology, v. 34, p.77-87.

Chapman, F., and Mawson, D., 1906, On the importance of *Halimeda* as a reef forming organism: with a description of *Halimeda*-limestones of the New Hebrides: Quarterly Journal of the Geological Society of London, v. 62, p. 702-711.

Clifton, K.E., and Clifton, L.M., 1999, The phenology of sexual reproduction by green algae (Bryopsidales) on Caribbean coral reefs: Journal of Phycology, v. 35, p. 24-34.

Davis, B.C., and Fourqurean, J.W., 2001, Competition between the tropical alga, *Halimeda incrassata*, and the seagrass, *Thalassia testudinum*: Aquatic Botany, v. 71, p. 217-232.

Drew, E.A. 1983. *Halimeda* biomass, growth rates and sediment generation on reefs in the central Great Barrier Reef Province. Coral Reefs, 2:101-110.

Drew, E.A., and Able, K.M., 1988, Studies on *Halimeda*: The distribution and species composition of *Halimeda* meadows throughout the Great Barrier Reef Province: Coral Reefs, v. 6, p. 195-205.

Flügel, E., 1988. *Halimeda*: Paleontological record and palaeoenvironmental significance: Coral Reefs, v. 6, p.123-130.

Fornos J.J., Forteza, V., Jaume, C., and Martinez-Taberner, A., 1992, Present-day *Halimeda* carbonate sediments in temperate Mediterranean embayments: Fornells, Balearic Islands: Sedimentary Geology, v. 75, p. 283-293.

Freile, D., DeVore, M.L., and Lowe, B., 2005, Comparison of calcareous green algae community structure and carbonate production of Graham's Harbour, Rice Bay and Snow Bay: San Salvador Island, Bahamas, *in* Buckner, S.D., and McGrath, T.A., eds, Proceedings of the 10th Symposium on the Natural History of the Bahamas, p. 37-47.

Freile, D., 2004, Carbonate productivity rates of *Halimeda* in two different locations, San Salvador, Bahamas, *in* Lewis, R.D., and Panuska, B.C., eds, Proceedings of the 11th Symposium on the Geology of the Bahamas and Other Carbonate Regions, p. 95-106.

Freile, D., Milliman, J.D., and Hillis, L., 1995, Leeward bank margin *Halimeda* meadows and draperies and their sedimentary importance on the western Great Bahama Bank slope: Coral Reefs, v. 14, p. 27-33.

Freile, D., and Hillis, L., 1997, Carbonate productivity by *Halimeda incrassata* in a land proximal lagoon, Pico Feo, San Blas, Panama, *in* Lessios, H.A., and Macintyre, I.G., eds., Proceedings of the 8th International Coral Reef Symposium: Balboa, Panama, Smithsonian Tropical Research Institute, v. 1, p. 767-772.

Hillis (as Hillis-Colinvaux), L., 1980, Ecology and taxonomy of *Halimeda*: primary producer of coral reefs: Advances in Marine Biology, v. 17, p. 1-327.

Hillis (as Hillis-Colinvaux), L., 1986a, Historical perspective on algae and reefs: have reefs been misnamed?: Oceanus, v. 28, p.43-48.

Hillis (as Hillis-Colinvaux), L., 1986b, *Halimeda* growth and diversity on the deep fore-reef of Enewetak Atoll: Coral Reef, v. 5, p. 19-21.

Hillis (as Hillis-Colinvaux), L., 1986c, Deep water populations of *Halimeda* in the economy of an atoll: Bulletin of Marine Science, v. 38, p. 155-169.

Hillis, L., 1991, Recent calcified Halimedaceae, *in* Riding, R., ed., Calcareous Algae and Stromatolites: Springer-Verlag, Berlin, p. 167-188.

Hudson, J.H., 1985, Growth rates and carbonate production in *Halimeda opuntia*: Marquesas Keys, Florida, *in* Toomey, D.F., and Nitecki, M.H., eds., Paleoalgology: Contemporary Research and Applications: Springer-Verlag, Berlin, p. 257-263.

Judd, J.W., 1904, Report on the materials from the borings at the Funafuti Atoll: Report on Coral Reef Communities, Royal Society of London, p. 167-185.

Liddell, W.D., Ohlhorst, S.L., and Boss, S.K., 1988, The significance of *Halimeda* as a space-occupier and sediment producer, 1-75M, north Jamaica, in Choat, J.H. et al., eds, Proceedings of the 6th International Coral Reef Symposium, v. 3, p. 127-132.

Littler, M.M., Littler, D.S., Blair, S.M., and Norris, J.N., 1986, Deep water plant communities from an unchartered seamount off San Salvador Island, Bahamas: Distribution, abundance and primary productivity: Deep Sea Research, v. 33, p. 881-892.

Littler, D.S., and Littler, M.M., 2000, Caribbean Reef Plants: An Identification Guide to the Reef Plants of the Caribbean, Bahamas, Florida and Gulf of Mexico: OffShore Graphics, Inc., Washington, DC, 542 p.

Milliman, J.D., 1974, Recent Sedimentary Carbonates: Part 1 Marine Carbonates: Springer-Verlag, Berlin, 375 p.

Multer, H.G., 1988, Growth rate ultrastructure, and sediment contribution of *Halimeda incrassata* and *Halimeda monile*, Nonsuch and Falmouth Bays, Antigua, W.I.: Coral Reefs, v. 6, p. 179-186.

Orme, G.R., 1985, The sedimentological importance of *Halimeda* in the development of back reef lithofacies, northern Great Barrier Reef (Australia), in Harmelin-Vivien, M., and Salvat, B., eds, Proceedings of the 5th International Coral Reef Symposium, v. 5, p. 31-37.

Payri, C.E., 1988, *Halimeda* contribution to organic and inorganic production in a Tahitian reef system: Coral Reef, v. 6, p. 251-262.

Payri, C.E., 1995, Production carbonatée de quelques algues calcifiées sur un récif corallien de Polynésie française: Bulletin de la Société Géologique de France, t. 166, p. 77-84.

Robbins, L.L., Knorr, P.O., and Hallock, P., 2009, Response of *Halimeda* to ocean acidification: field and laboratory evidence: Biogeosciences Discussions, v. 6, p. 4895-4918.

Robinson, M.C., and Davis, R.L., 1999, GIS topographic map, University of New Haven and Gerace Research Centre (available for download) http://www.newhaven.edu/sansalvador/gis/topo.htm.

Sealey, N.E., 1992, Caribbean World: A Complete Geography: Cambridge University Press, 256 p.

Wefer, G., 1980, Carbonate production by algae *Halimeda*, *Penicillus*, and *Padina*: Nature, v. 285, p. 323-324.