

***Halimeda* Investigations: Progress and Problems**

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INTRODUCTION

Although *Halimeda* has long been known as a contributor of sand- to mud-size carbonate sediment from the mid-Jurassic to the Holocene (Elliot, 1960, 1965; Johnson, 1969), its true role as a very significant organism is becoming more evident from a wide variety of investigations. Such research has shown that *Halimeda* (1) has an extensive habitat range (to depths of 150 m, Hillis-Colinvaux, 1986), (2) is capable of producing extensive biohermal accumulations (Phipps *et al.*, 1985; Davies and Marshall, 1985; Hine *et al.*, 1988; Searle and Flood, 1988) and meadows (Hillis-Colinvaux, 1988), and (3) can be evaluated in the field using a variety of techniques for growth. Other studies have demonstrated the ability of *Halimeda* to obtain nutrients directly from the sediment (Williams, 1984) which may help explain its wide distribution and rapid growth. It also appears that *Halimeda* is not only adapted to large variations in light environment, but can also take advantage of episodic nutrient pulses (Littler *et al.*, 1988). Recent findings concerning physical and chemical defense mechanisms may influence future evaluations of predation. SEM studies by Multer (1988a) indicate (1) swift initial calcification (up to 50% of new segment weight composed of CaCO₃ within 48 hours), (2) sporadic subsequent infill of intertricular spaces with two sizes of aragonite crystals, and (3) very efficient sediment-stabilizing and encrusting substrate role for filaments of the bulbous holdfast system.

Halimeda is found throughout the tropical world. In the Pacific, sites have been described by Maxwell (1968), Drew (1983), Tudhope *et al.* (1985), Phipps *et al.* (1985), Scoffin and Tudhope (1985), Hillis-Colinvaux (1986), Marshall *et al.* (1988) Roberts *et al.* (1987) and Roberts and Phipps (1988). Caribbean areas are discussed by Milliman (1973, 1974), Wefer (1980), Hillis-Colinvaux (1980), Hudson (1985), Hine *et al.* (1988), Liddell *et al.* (1988), and Multer (1988a).

Fourteen species of *Halimeda* have been described for the tropical and subtropical western Atlantic (Wynne,

1986). Included in this list is the newest (and smallest) species of *Halimeda*, as well as a new variety, both described by Ballantine (1982) from Puerto Rico. For a comprehensive description of taxonomy and ecology of *Halimeda* from the Caribbean, the reader is referred to Hillis (1959), Taylor (1960), and Hillis-Colinvaux (1980).

No single comprehensive study of *Halimeda* in the St. Croix area has been published to date. The present writers conducted various growth-rate studies (unpublished) in Tague Bay, St. Croix in 1972-73. In addition to this field work there have been a series of short-term Independent Study projects conducted by students of the West Indies Lab concerning various aspects of *Halimeda* found off of St. Croix. Hubbard *et al.* (1981) discussed the role of *Halimeda* as an important element in the carbonate sand budget of the St. Croix shelf and discussed the results of various student projects involving *Halimeda*.

In the following pages, the presently available techniques for measuring *Halimeda* growth are briefly summarized. The available data from early studies by the present authors, along with information from investigations by WIL students and faculty are also outlined. Finally, some thoughts on as-yet unresolved problems with our measurement techniques are offered. It is hoped that these will set the stage for renewed interest in this important contributor to the carbonate system on St. Croix and throughout the tropics.

MEASUREMENT TECHNIQUES

Despite the significant role that *Halimeda* plays in both ancient and modern reef environments, actual published field measurements of growth rates for individual plant species in today's tropical environments are limited. This may be due to the difficulty in measuring growth in a plant that grows by unpredictable "spurts", varies in percentage of CaCO₃ with age (Hillis-Colinvaux, 1980; Abel and Drew, 1985), and differs in growth rate by species (Goreau, 1963; Hillis-Colinvaux,

1980) and perhaps with depth (Bohn, 1973). Such variables, combined with unpredictable storm damage to sampling sites (Merten, 1971) and the patchy nature of *Halimeda* distribution (Gilmartin, 1960) have discouraged attempts to quantitatively evaluate production rates. The different physical characteristics of the two basic growth forms (1- the fast-growing, low sprawling rock-bound forms, and 2- the slower-growing, erect, Rhipsalian forms) may also sometimes necessitate different measuring procedures.

Specific techniques for growth measurement include (1) monitoring *Halimeda* growing upward through monofilament screens (present authors, 1973, unpublished; Bach, 1979), (2) counting segments above an Alizarin Red-S stain over time and determining turnover (Wefer 1980), (3) counting segments, measuring their surface areas and turnover rate above wire twist tags (Drew, 1983), and (4) weighing segments and determining turnover of new growth above an Alizarin Red-S stain over time (Hudson, 1985).

Each of the above techniques has some limitations and/or makes certain assumptions. Therefore calculations (e.g., grams of CaCO_3 /plant-yr) are sometimes difficult to compare with those of another investigator using a different technique.

EARLY STUDIES ON ST. CROIX (1972-1973)

Following the establishment of the West Indies Laboratory a variety of preliminary investigations were made on the distribution and growth of various flora and fauna as well as appropriate field techniques for their further study. One such study was conducted from February, 1972 to July, 1973 on various *Halimeda*, *Penicillus*, *Udotea* and coral species found in Tague Bay. Portions of these data concerning *Halimeda* are presented below. An index map to localities is given in Figure 1.

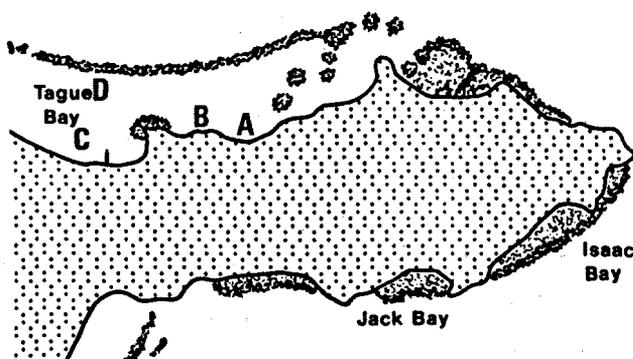


Figure 1. Index map to field localities in Tague Bay, St. Croix. Stations were (A) Smuggler's Cove, (B) Telephone Point, (C) Adey's (hurricane) Anchorage, and (D) the reef west of the W.I.L. Monument.

Erect Rhipsalian species

Stakes with assigned names were driven next to various effect species of *Halimeda* at Smugglers Cove, Telephone Pt. and Adey's Anchorage in Tague Bay (Fig. 1). Monthly observations of each plant included measurement of plant height, counting of segments and tracing of segment shape on an underwater slate.

Figure 2 illustrates segment growth of five *H. incrassata* and *H. monile* plants monitored. Observations include: (1) apparently healthy plants (e.g. Raquel, Fred, Joey) displaying no or limited senescence may totally disappear (see "?" in Figure 2) for no obvious reason within a 2-3 week period while others (e.g. Pepe, Leila) display the more expected senescent (white) stage and loss of segments before death; (2) in contrast with *Halimeda*, adjacent *Penicillus* and *Udotea* appeared to be shorter lived, less hardy and increased in total population as spring approached

Sprawling prostrate species

Field techniques differed with species. The growth pattern of *H. tuna* was observed over a two-month period from a single colony located on a reef west of the Monument in about 3 m of water in Tague Bay (Fig. 1). Large segment size and open branching growth pattern allowed this colony's segments to be counted and traced on an underwater slate. *H. opuntia*, however, due to its small segment size and multitudenous branches forming compact clumps, was studied using 2-inch long sections of 10-inch diameter concrete pipe (Fig. 3) over seven different *H. opuntia* colonies. Colonies were initially selected so that their tops would brush gently against the overlying screen. Periodic scrapings from the tops of the screens were washed, dried in an oven at 93.33° C for 30 minutes and weighed.

Figure 4 displays the growth and segment evolution of one *H. tuna* colony over a two month period; Figure 5 and Table 1 tabulate growth data of seven different monitored *H. opuntia* colonies. Data indicate: (1) three (A, B, C; Fig. 5) of the seven colonies evaluated showed periods of consistent decrease in growth which were marked by appearance of senescent (white) segments; each of these observed decreases occurred at different times of the year; (2) five (B, C, D, E, F) of the seven colonies evaluated showed periods of consistent increases in growth, each again sporadically, at different times of the year; (3) one colony (C) displayed consistent growth followed by consistent decline over a period of a year (359 days) to an apparently dead (all white with loose holdfasts) stage providing a minimum lifespan estimate for that colony; (4) although colonies B and C peaked in segment production in September and November, as do *H. Opuntia* in the Florida Keys (Hudson, 1985) where greater seasonal temperature fluctuations appear to be a major control, other St. Croix colonies (D, F, G) increased production throughout the winter (November through February) months suggesting less seasonal control than found in Florida; (5) this field technique is believed to yield a

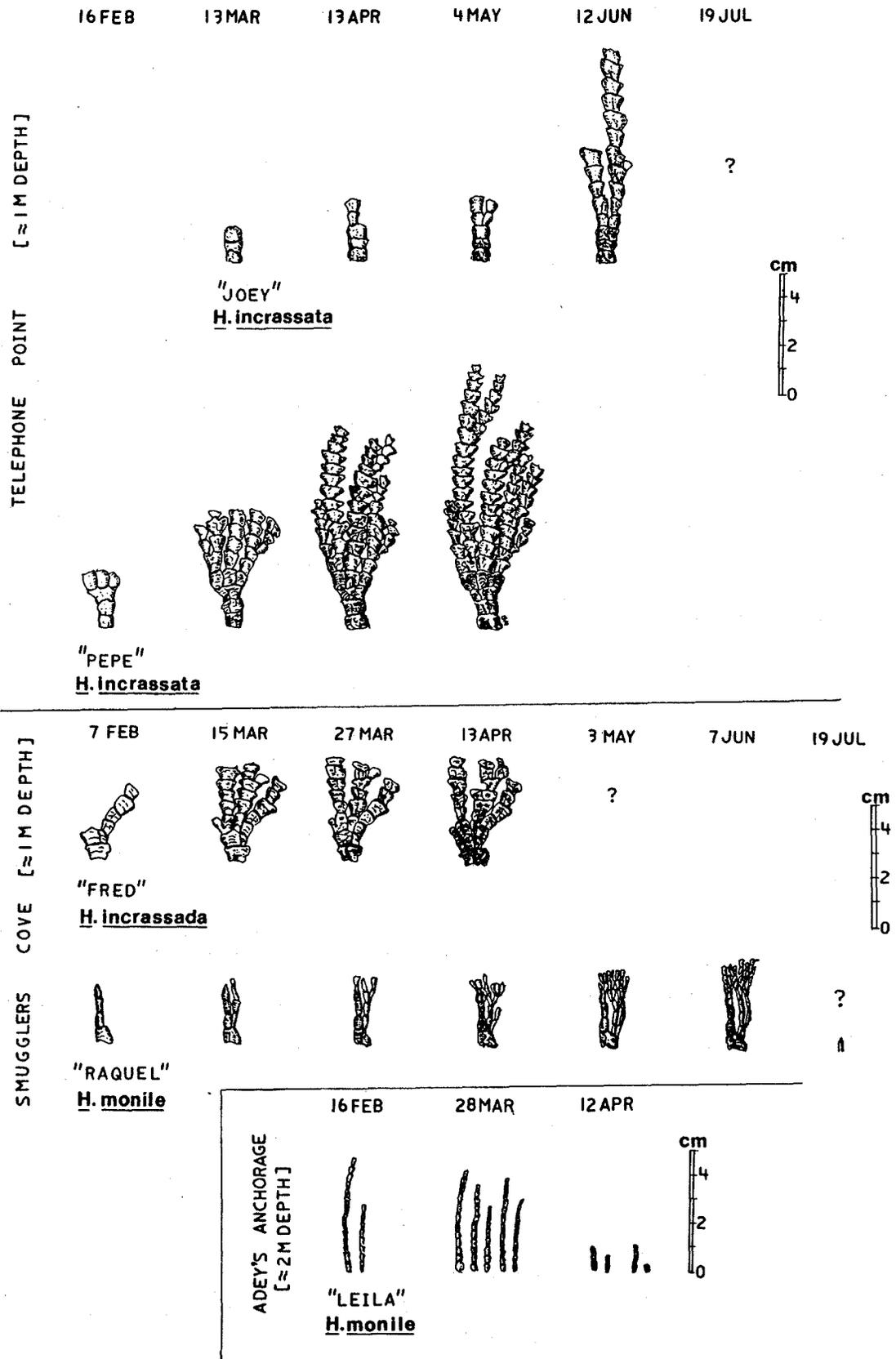


Figure 2. Sequential tracings of various Rhipsalian species.

minimum figure for growth rates as it (a) does not account for natural spalling or predation during the test period, (b) screens decrease available light for the initial growth after each scraping and (c) growth calculations do not include unobserved (i.e. lateral) growth of the plant beneath the screen.

SHORT-TERM STUDENT PROJECTS

Gill (1978), working at three sites in Tague Bay, found the average production rate for *H. incrassata* to be 2.46 lobes/day (at 15.2 m depth) and 0.63 (at 4.6 m depths). He found that predation by parrotfishes decreases gradually away from patch reefs at 15.2-m depth and thus predation at 4.6-m depths is negligible. *Callianassa* bioturbation and current-induced transport caused burial of *Halimeda*.

Allen (1980) worked at a patch reef in Tague Bay at 5.5 m depths and found average production of *H. incrassata* to be 0.0309 g CaCO_3 /plant-day and 2.5338 g CaCO_3/m^2 -day using a density of 82 plants/ m^2 . She

also noted that 10-30% of segments were lost due to spalling.

Meares (1980) compiled data along a cross-section from Smugglers Cove to the bank-barrier reef. He noted densities of *Halimeda* ranging from 0 - 55 plants/ m^2 , and indicated that *Halimeda* decreased in population seaward. He also estimated the potential role of *Halimeda* in total carbonate product (see below under Hubbard *et al.*, 1981).

Pret (1983) worked in Tague Bay at 4.6-m depths with *H. incrassata* densities of 20 - 30 plants/ m^2 . She found that epiphytization did not affect rates of calcification and that calcification rates did not vary during the daytime. First-day segments averaged 30-54% CaCO_3 .

Comprehensive carbonate sand study

A detailed study of the production, transport and deposition of carbonate sediments on the St. Croix shelf by Hubbard *et al.* (1981) includes many references to the essential role of *Halimeda* in the carbonate budget of the area and a detailed bibliography including listing of pertinent student theses and special projects. Two summary paragraphs from this report describing the role of *Halimeda* are quoted below.

"The carbonate production of *Halimeda* is generally far lower than that of coral reef systems in St. Croix. The estimates of Allen (1980) and Meares (1980) lie between 1.2 and 0.43 Kg CaCO_3/m^2 -yr. This is to be compared to reefal carbonate production of 18.3 Kg CaCO_3/m^2 -yr for Cane Bay reef (this study). When considered by total area, however, production rates of reefs and grass bed systems may be far closer. *Halimeda* flourishes in a wide variety of environments, and is widespread in shallow lagoonal and shelf zones. Using our estimated *Halimeda* density of 1- 6 plants per m^2 for the south shore sand bodyand Allen's growth rate, a productivity rate of only 0.015 - 0.090 Kg/ m^2 -yr results. If this low *Halimeda*-productivity rate is applied evenly to the entire 10-7 m^2 area of the south shore sand body, however, then a total annual productivity figure of 1.56 - 9.0 X 10⁻⁵ Kg emerges.

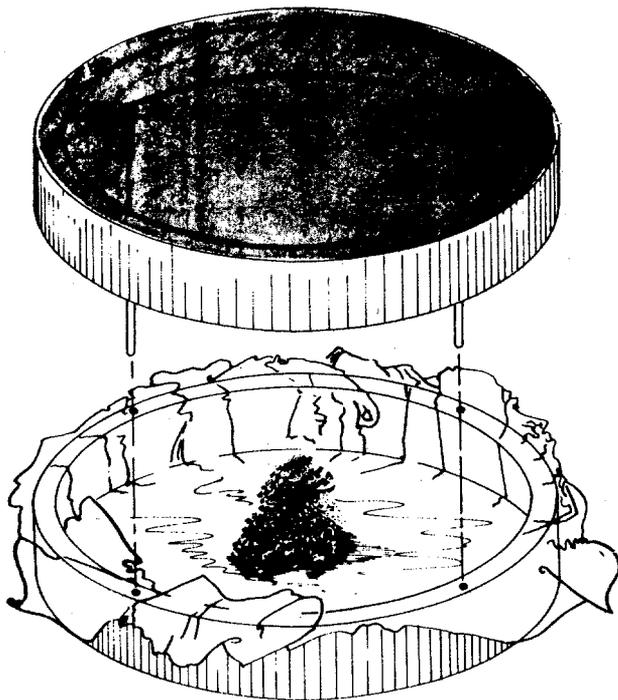


Figure 3. One technique used by the present authors for evaluating spalling employs sawed cross-sections of cement pipe. A monofilament screen over the top half prevents predation (but also reduces sunlight) while a plastic liner in the bottom half collects spalled segments. After prostrate types of *Halimeda* grow vertically through the top screen, periodic scraping of the screen can yield growth rate information.

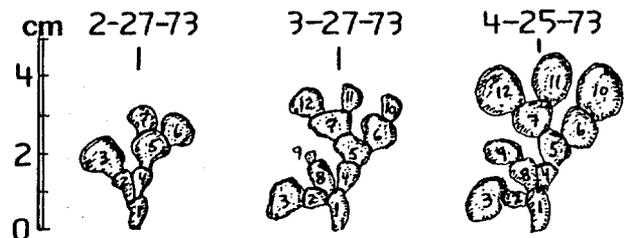


Figure 4. Segment evolution (indicated by numbers) of *H. tuna* on reef, West Monument area, Tague Bay.

Table I. Segment production data from seven *H. opuntia* colonies, Smuggler's Cove, Tague Bay.

Plant colony	No. days growth	Dry weight (g) produced	CaCO ₃ (g)* produced	CaCO ₃ (g) produced/day
A	183	76.3	66.4	0.362
B	232	273.6	238.0	1.025
C	359	86.4	75.2	0.209
D	157	33.1	28.7	0.182
E	157	14.7	12.8	0.081
F	157	122.8	106.8	0.680
G	157	145.6	126.7	0.807

Average production per colony = 0.478 g CaCO₃/day
or 174.470 g CaCO₃/year

*Assuming that *H. opuntia* yields 87% (dry wt.) CaCO₃ as found by Bohmn (1973) for this species in 2-m depths in Jamaica.

"The aerial extent of these environments may therefore well make up for a large part of the difference between grassbed and reef-related productivity. In censusing a transect from the shoreline seaward beyond the reef crest, Mearns (1980) found that in Tague Bay carbonate production by *Halimeda* was close to 15% of total production along the transect. *Halimeda* was responsible for nearly 50% of total carbonate production within the grassbed zones."

REMAINING PROBLEMS FOR FUTURE RESEARCH

Role and cause of spalling

Breaking off of individual segments or parts of whole branches occurs at unpredictable intervals with growth and can cause errors during growth-rate studies. The rates of spalling for different species are unknown. Allen (1980) in a limited field study using macrophotography found a 10 to 30% loss of segments from spalling. Environmental factors such as high-energy (storm) events and/or excessive drag during these events due to attached epiphytes may influence spalling rates. Careful monitoring of weather and epiphyte conditions at staked plots using macrophotography over long time periods may help evaluate this process.

Role of predation on *Halimeda*

Both growth-rate and segment-production data could be negatively influenced by predation upon *Halimeda* during field measurement periods. Only limited data exist on this subject. Hillis-Colinvaux (1974) reported predation by the echinoid *Diadema antillarum* in Jamaica. Gill (1978) reported crescent-shaped bites located toward the distal ends of *H. incrassata* branches and observed feeding by parrotfishes (Fig 6a) on highly epiphytized *Halimeda* from St. Croix. Multer (1988a) reported low

fish predation from one 6-week experiment in Antigua (Fig 6b).

Recent investigations have shown that various *Halimeda* possess multicomponent (physical and chemical) defenses against predation, which may account not only for low fish predation but also for the success of *Halimeda* as a major tropical green alga. Its high level of calcification provides a coarse and not-too-palatable texture which has been described as a major defense against predation (Ogden and Lobel, 1978; Lobel and Ogden, 1981; Hay, 1981). Chemical adaptations against herbivory (Fig. 7) can include production of larval toxicity, ichthyotoxicity and feeding deterrent effects (Paul and Fenical, 1983; Paul, 1985; Paul and van Alstyne, 1988).

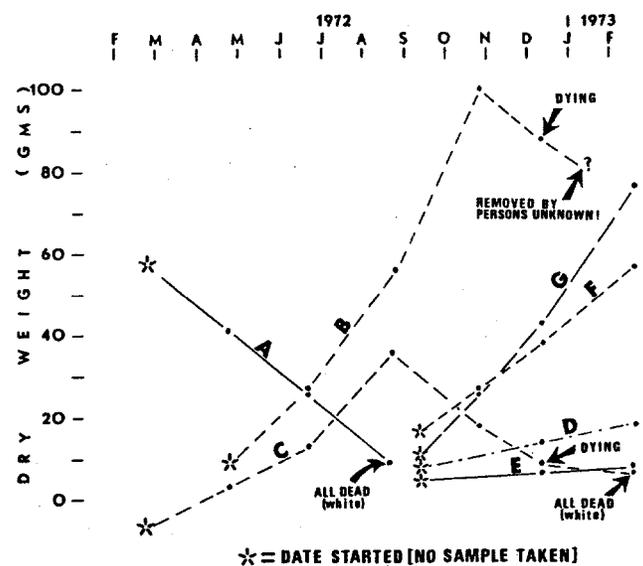


Figure 5. Dry weight of monthly scrapings from seven *H. opuntia* colonies, Smuggler's Cove, Tague Bay.

Paul and Hay (1986) indicate low susceptibility to grazing by herbivorous fishes in the Florida Keys due to a combination of secondary metabolites and calcification. This co-occurrence of defense mechanisms resulted in low percentages of individual thalli being consumed during periods of up to 22.5 hours of observation.

Although the above-described chemical/physical natural defenses found in some species may reduce attack by various organisms, the true role of predation on *Halimeda* at specific sites and with different species is still difficult to determine.

Choice of growth measuring techniques

Growth of sprawling, rock-bound species such as *H. opuntia* is difficult to measure due to the nature of the small multitudinous branching segments. Monofilament screen overlays (Bach, 1979) provide only the vertically growing portion of new growth for collecting and weighing. Although tedious, the Alizarin Red-S technique (Fig. 8) described by Hudson (1985), may be the best method developed to date for these sprawlers. Rates of spalling or some accounting of this process should be incorporated into the final analysis.



Figure 7. Chemical defense.

Growth of the erect Rhipsalian species is more easily monitored. If using colored plastic ties or wire twists, the individual plant and site must be well marked for subsequent periodic sampling. Care must also be taken that ties do not provide undue stress to the plant under heavy wave action nor too attractive a target for predators.

Alizarin Red-S staining of 1-m square plots provides a definitive time line above which new growth can be identified and collected at periodic intervals. Proper concentration of the stain and duration of staining period should be determined on an experimental basis before long-term projects are started. Periodic collecting should always include different-sized plants to compensate for non-linear growth.

Lab procedures should include a freshwater rinse of collected specimens and removal of epiphytes. When calculating percent carbonate, caution is necessary as not all organic material may be removed by immersion of plants in a commercial bleach solution (Multer 1988a). It is recommended that selected plants that have been bleached and weighed also be dissolved in 20% HCl and reweighed to confirm organic removal.

Role of epiphytes

Various epiphytes are found on *Halimeda* in concentrations which appear to fluctuate throughout the year (Fig. 9). *Dictyota*, *Wrangelia*, and *Amphiroa*, together with unidentified thread-like masses (which occasionally produce positive floatation that can tear off segments and whole branches) have been observed clinging to erect *Halimeda* plants in St. Croix, Antigua and the Florida Keys. The origin and positive and/or negative roles that these epiphytes play in the life cycle of *Halimeda* need additional study.

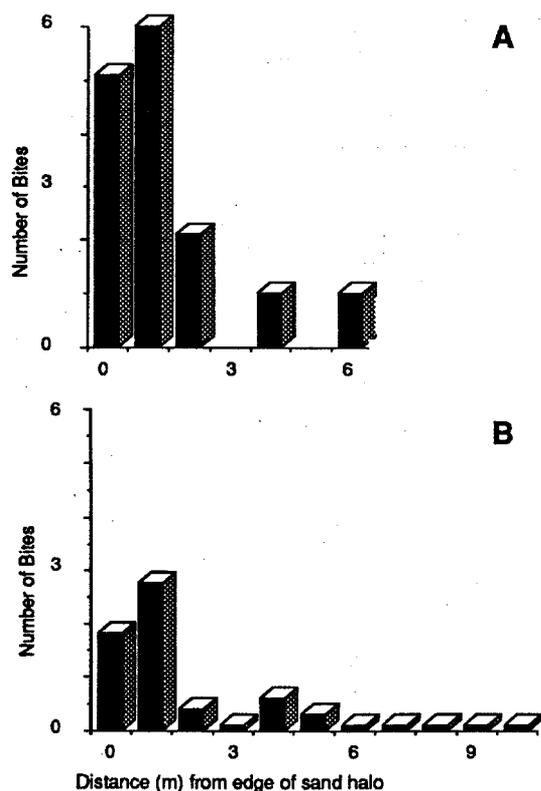


Figure 6. Summary of predation found along transects radiating out from patch reefs with known fish populations. A. Predation on *H. incrassata* and *H. monile* found in Nonsuch Bay, Antigua (after Mutter, 1988a). B. Number of crescent-shaped bites of *H. incrassata*, Tague Bay, St. Croix (after Gill, 1978).



Figure 8. (above) *Halimeda incassata* and *Halimeda monile* undergoing Alizaren Red-S staining beneath plastic frame secured with heavy anchor chain and four PVC corner stakes.

Figure 9. (below) Various epiphytes encrusting and surrounding *Halimeda*-rich substrate, Smuggler's Cove, Tague Bay, St. Croix.

Life span of *Halimeda*

Literature dealing with the study of *Halimeda* contains very little information on life span (the number of days or months an individual plant actually lives). There is also a paucity of information on the average life span of one species compared to another (Fig. 10).

Although life span was not the objective of the research in Antigua (Multer 1988a), it was noted that the average number of days that recognizable stained plants remained at the 25 sites studied was 33 days. If one makes the assumption that an average plant was one month old at the time of staining, lives 33 additional days as a stained plant and another month through late senescence until its stump falls over, then 3 months may be the average life span of *H. incrassata* and *H. Monile* in Antigua. Six individual unstained plants that were monitored averaged a life span of 96 days (range of 72 to 121 days).

On St. Croix the present writers found the minimum life span of 7 individual clusters or colonies of *H. opuntia* to be much longer (range of 6 to 12 months) than that of *H. incrassata* and *H. monile*. The life span of *H. incrassata* and *H. monile* in St. Croix varied according to locations (Susan Williams, pers. commun., 1988). She estimated a 1-4 month life span for these *Halimeda* in shallow areas of Tague Bay, but a longer (4-8 month) life span for the same species in deeper Salt River Canyon. She further notes this is probably due to decreased light and absence of a nutrient-rich *Thalassia* substrate in the canyon.

The stress-recovery potential of *Halimeda*

One reason for *Halimeda's* widespread distribution today may be its ability to survive natural stresses such as animal-mediated disturbances and high-energy (storm) events. Uprooting and burial of *Halimeda* by various macrofauna (e.g. conchs, callianassid shrimp, hermit crabs, urchins, and rays) can result in lower carbonate production by algae in the disturbed areas. Suchanek (1983) noted the negative influence of *Callianassa* on

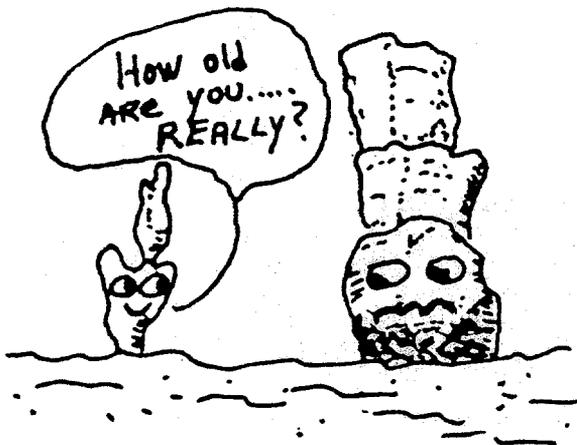


Figure 10. Age problems.

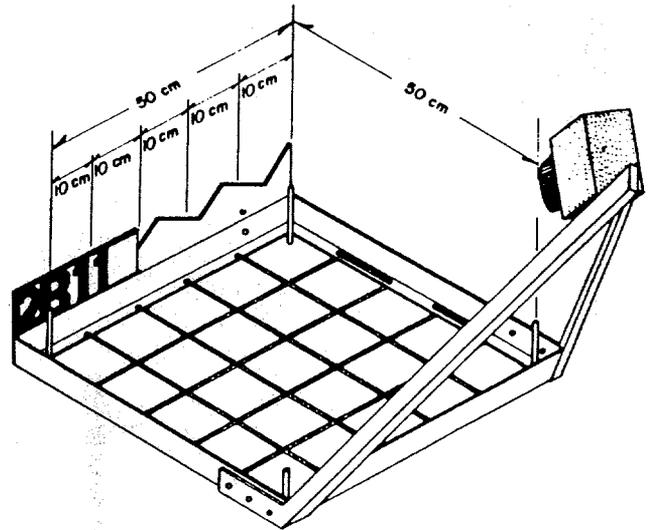


Figure 11. When set over established stakes, an aluminum frame with yellow plastic line grid and camera mount, provides one method for periodic monitoring of natural and animal-mediated stress.

plant communities by burial and reduction of available light from suspended sediment production. At 20-m depths in St. Croix, Williams (1988) found stressful disturbances on *Caulerpa* by macrofauna to be seasonal, declining in winter months when animals are less active and conch remain buried. Details of quick recovery from these disturbances are described by Williams (1985) from a study of *Caulerpa* occurring in Salt River Canyon, St. Croix. Williams (pers. commun., 1988) noted that similar quick responses were found with *Halimeda*.

The effect of tropical storm Klaus on *H. incrassata* at 20 m depth in Salt River Canyon is described by Williams (1988) in which the plants were uprooted, buried and broken. Survival surpassed other bottom algae due to the deeper (10 cm) and more massive rhizoidal holdfast network of *H. incrassata*. Within 6 months after "Klaus", *H. incrassata* had regained its pre-storm abundance.

In some preliminary field studies of stress on *Halimeda* in Antigua, Multer (1988b) found that the time for regeneration of new, upright thalli after natural animal-mediated disturbances and experimental uprooting of *Halimeda* was longer (1-2 months) than that following natural (storm) and experimental sand burial (2-6 weeks).

A fruitful avenue for future studies would be monitoring environmental stresses that might affect *Halimeda* growth. Two possible pieces of instrumentation are shown in figures 11 and 12.

Abnormal Growth

H. incrassata growing to 30 cm heights can be found in a shallow (1 m) isolated portion of Nonsuch Bay, Antigua (Muller, 1988b). These "giants" are three times the average height of all other members of this genus in the same Bay. A possible cause of this abnormal growth

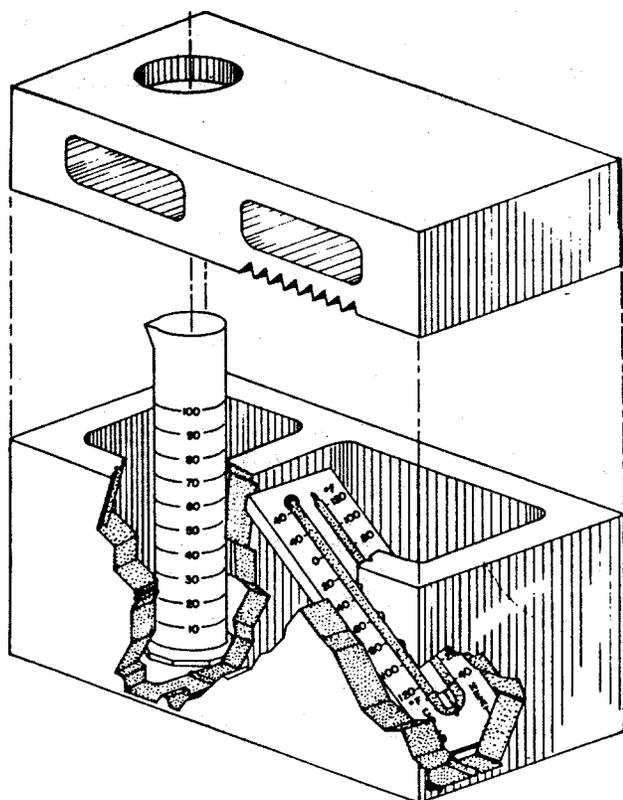


Figure 12. An inexpensive monitoring station for temperature and suspended-sediment measurement. The enclosure is constructed of two concrete blocks.

(local substrate and/or water column enrichment due to runoff from a bird rookery) has not been identified.

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