Growth and sediment disturbances of *Caulerpa* spp. (Chlorophyta) in a submarine canyon

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ABSTRACT: Growth rates of 7 species of *Caulerpa* were measured *in situ* at depths of 20 m in Salt River canyon, St. Croix, US Virgin Islands. Mean stolon elongation rate for all species of *Caulerpa* studied was approximately 1 cm d^{-1}. Dry biomass accumulated in this new growth was less than 10 mg d^{-1}, and specific growth rates were less than 10 % d^{-1}; these values are low compared to rates of many benthic macroalgae. Macrofauna (conchs, ghost shrimp, hermit crabs, urchins, rays) were observed disturbing sediment. Plants were uprooted or buried by animals that foraged, burrowed, and made excavations or sediment mounds. Plants experimentally uprooted or buried to simulate effects of animal activities had significantly lower stolon elongation, biomass accumulation, and specific growth rates than control plants. We hypothesize that the productivity of these algae is limited in part by animal-mediated sediment disturbances.

INTRODUCTION

The green coenocytic macroalgae *Caulerpa* spp. are common inhabitants of soft and hard bottoms in tropical and subtropical regions. *Caulerpa* spp. are important as colonizers in seagrass bed succession, in part because they help stabilize sediments with their rhizoids (Den Hartog, 1977; Williams, 1981). Soft bottom habitats are subjected to sediment disturbances by both physical (e.g. surge) and biological (macrofauna activities) processes. Marine animal-sediment interactions have been investigated (e.g. Ginsberg and Lowenstam, 1958; Rhoads and Young, 1970; Aller and Dodge, 1974), but their effects on plant communities have received little consideration (Suchanek, 1983). Related studies on the effects of sedimentation on macroalgae have concluded that sediment disturbances exert considerable control over the structure of these communities (Daly and Mathieson, 1977;

Devinny and Volse, 1978; Hay, 1981; Taylor and Littler 1982).

Initial observations made on the sand floor of Salt River submarine canyon, St. Croix, US Virgin Islands (17 47′ N; 64 45′ W) provided the impetus for this investigation. We recognized two major types of sediment disturbances which could affect the growth of *Caulerpa* spp. in the canyon. First, stolons and rhizoids were uprooted by surge, burrowing activities of deposit-feeding echinoids such as *Meoma ventricosa*, or excavations of rays. Second, plants could be buried by physically-created sediment movements, the activities of bottom-feeding macrofauna and callianassid shrimps, which erect volcano-like mounds and spew out large quantities of sediment. Activities of animals mentioned above have been described (Ogden, 1980; Scheibling, 1982; Suchanek, 1983).

The objective of this research was to determine the effect of uprooting and burial on the growth of *Caulerpa* spp. To accomplish this, we determined *in situ* growth rates of *Caulerpa* spp. growing on the canyon floor and compared these with experimentally uprooted and buried plants. We also identified and determined the relative importance of macrofauna which disturb the sediment.

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METHODS

This study was conducted during a 1 wk mission in April 1983 at NOAA's National Undersea Research Program at West Indies Laboratory, Fairleigh Dickinson University. This site was revisited in December 1983 for additional sampling. The program operates 'Hydrolab', an underwater laboratory and saturation diving facility. Use of 'Hydrolab' enabled us to gather data that had proven difficult to obtain in shallower areas of St. Croix waters due to boating activities, lack of adequate *Caulerpa* populations, and turbid water.

Growth measurements. All *Caulerpa* thalli within a 9 m radius from a fixed reference point at 20 m depth were identified. Apical growing points of individual stolons and branches were marked by placing numbered reference flags in the sediment next to the apex. New growth was measured as cm of stolon extending beyond the reference flag. Notes were made on necrosis or death of the thalli. At the end of 6 d, a haphazardly selected subset of plants was collected for dry weight determinations. Old growth was severed from new at the point of the reference flag; each portion was placed in a labelled plastic bag, returned to the surface, and frozen. After 2 d, these plants were thawed, cleaned of sediments, measured, dried at 90 °C for 24 h, and weighed. Specific growth rate was calculated as:

$$\mu = ((\ln W_1 - \ln W_2)/t) \times 100$$

where: W_1 = g dry weight (g dry) of whole plant including new growth; W_2 = g dry of whole plant minus g dry new growth; t = days of new growth.

Sediment disturbance experiments. Growth was similarly determined for *Caulerpa* thalli that were uprooted and buried experimentally. Treated plants were chosen haphazardly from the populations. The apex and adjacent 10 cm of stolon were uprooted in 30 plants. Other plants were partially covered with sediments, simulating the effects of the ghost shrimp *Callianassa rathbunae*. Sediment (mean grain size = 0.325 mm) was collected from the study site, dried and packaged into doses of 369 g dry (250 cm³), the average amount ejected daily by *C. rathbunae* in Salt River canyon (Suchanek, 1983). The sediment doses were applied once to the apical region and adjacent stolon of 18 plants and likewise daily to another 14. At the end of 6 d, plants were uncovered and measured. The daily sediment dosage experiment was repeated at the same site for 7 d in December 1983 when 20 treated and 20 untreated plants were measured and collected on Day 8.

Macrofauna observations. An attempt was made to determine abundances and activities of animals which could affect the growth of *Caulerpa* spp. by disturbing sediment. Four permanent belt transects (30 × 3 m)

were surveyed to the northeast, northwest, southeast, and southwest of the fixed reference point during 4 consecutive days and nights. All animals observed on the transects were counted and their activities noted.

Statistical analyses. One-way ANOVA's were used to test for significant differences in growth data, first using Bartlett's test for homogeneity of variance (Sokal and Rohlf, 1969). Growth data with nonhomogeneous variances were log transformed. Means are reported as untransformed values. Confidence limits are reported as back-transformed values and thus, are asymmetrical. *A posteriori* comparisons among stolon elongation rates were made using a sum of squares simultaneous test procedure (Sokal and Rohlf, 1969). A log-likelihood test (G statistic) was used to assess differences other than growth rates in the April sediment disturbance experiment (Sokal and Rohlf, 1969). A Friedman test extended to several observations per treatment was applied to animal distribution data (Conover, 1971).

RESULTS

Growth rates

Most of the seven *Caulerpa* species identified in the study area grew approximately 1 cm d^{-1} during April (Table 1). There were no significant differences in stolon elongation rates among the different species (p > 0.90). New growth contributed an average of less than 10 mg dry biomass d^{-1} and specific growth rates were less than 10 % d^{-1} (Table 1). There were no significant differences in specific growth rates among species (p > 0.90). Biomass accumulation, however, differed significantly among the species (p < 0.05). This difference probably reflects the greater weight of individuals of *C. cupressoides* v. *lycopodium* f. *elegans* (2 g dry individual^{-1}) in contrast to the other species (1 g dry indiv.$^{-1}$).

Sediment disturbance effects

Growth rates in experimentally disturbed (i.e. uprooted or covered with sediments once or daily) *Caulerpa sertularioides* and *C. cupressoides* v. *lycopodium* f. *elegans* differed significantly from untreated plants (p < 0.01) in the April experiment (Table 2). Only a few individuals of other species were disturbed and thus not included in the results. Daily burial reduced stolon elongation significantly more than burial once or uprooting (p < 0.05). Growth of uprooted *C. cupressoides* v. *lycopodium* f. *elegans* did not differ significantly from uprooted *C. sertularioides* (p > 0.90) however the former species grew signifi-

Table 1 Relative abundances and growth rates of undisturbed *Caulerpa* spp., April 1983. Mean values (95% confidence interval), n = sample size. Mean exclude nongrowing plants. Dashes indicate no data

Species	% Total no. plants	Stolon elongation cm d^{-1}	n	Biomass accumulation mg dry d^{-1}	n	Specific growth % d^{-1}	n
C. sertulariodes	51	1.6 (0.93–1.92)	84	1.43 (0.00–7.78)	21	7.17 (1.75–20.16)	21
C. cupressoides v. lycopodium f. elegans	31	1.8 (0.22–7.51)	45	0.35 (0.02–0.76)	15	7.38 (0.66–13.68)	15
C. mexicana	9	1.0 (0.26–2.48)	8	0.23 (0.00–2.60)	4	2.04 (0.14–35.58)	4
C. cupressoides v. flabellata	4	1.0 (0.09–8.81)	13	–		–	
C. cupressoides	3	0.8 (0.12–4.93)	6	0.28 (0.00–0.76)	4	7.62 (0.33–84.37)	4
C. prolifera	2	0.4 (0.09–5.11)	5	–		–	
C. taxifolia	< 1	0.0 (0.00)	2	–		–	

Table 2. Effects of experimental sediment disturbances on stolon elongation rates of *Caulerpa sertulariodes* and *C. cupressoides* v. *lycopodium* f. *elegans*, April 1983. $\overline{X}$ = cm d^{-1}; n = sample size; CI = 95% confidence interval

Treatment	All plants			Excluding non-growing plants		
	n	$\overline{X}$	CI	n	$\overline{X}$	CI
Control	153	1.4	1.0–1.5	129	1.7	1.2–1.8
Uprooted	29	1.5	1.0–1.6	28	1.5	1.1–1.7
Sediments applied: once	15	1.0	0.0–4.9	9	1.3	0.9–1.6
daily (5 d)	14	0.8	0.2–1.1	9	1.3	0.4–1.9

Table 3. Effects of experimental sediment disturbances on *Caulerpa sertulariodes* and *C. cupressoides* v. *lycopodium* f. *elegans*, April 1983. Sample size = n

Treatment	n	% of n		
		Zero growth	Partially decomposed*	Dead**
Control	153	16	7	3
Uprooted	29	3	17	0
Sediments applied: once	15	40	35	6
daily	14	36	14	7

* Includes growing and nongrowing plants
** Subset of zero growth

cantly less than *C. sertularoides* (p < 0.005) when both were buried. The proportion of plants which were partially decomposed, did not grow, or died was higher in the experimentally disturbed than in the undisturbed plants (p < 0.005; Table 3). Some plants having partially decomposed thalli grew and some apparently healthy thalli did not grow. The significant differences in growth rates mentioned above included the increased proportion of non-growing plants. In order to ascertain whether disturbed individuals grew more slowly than undisturbed ones, the non-growers were eliminated from the data set. In this case, the mean growth rate of disturbed plants was numerically lower but not statistically different than undisturbed ones.

This result confirmed our observations that certain individuals did not appear to be affected during the disturbances.

Many individuals of *Caulerpa* spp. responded rapidly to the sediment disturbances. Uprooted plants appeared healthiest. Uprooted stolons reattached to sand by growth of new rhizoids usually within 3 d. Rhizoids of the uprooted portion did not reattach to sediments. Some of the buried upright blades differentiated into a new stolon or produced a new upright (Fig. 1). Most plants which were completely buried were green when uncovered and had grown. Within 2 d growing apices of buried plants had turned up, often extending through the sediment mound. Plant

Fig. 1. *Caulerpa cupressoides* v. *lycopodium* f. *elegans.*
Arrow: buried upright blade which initiated 2 new uprights.
Scale = 1 mm

Table 4. Growth of sediment-treated *Caulerpa sertulariodes*,
December 1983, including non-growing plants. Mean values
(95 % confidence interval). Sample size = n*

Parameter	Controls (no sediments) (n = 11)	Sediments applied daily for 7 d (n = 9)
Stolon elongation (cm d⁻¹)	1.23 (1.13–1.58)	0.53 (0.27–0.98)
Biomass accumulation (mg d⁻¹)	3.44 (1.58–4.63)	1.59 (0.20–2.11)
Specific growth rate (% d⁻¹)	1.38 (1.10–3.47)	0.46 (0.01–1.77)
Zero growth (% n)	0	22

* Number of original 20 marked that were measureable

growth essentially kept pace with the rate of experimental sedimentation, which delivered 369 g dry to an area of about 79 cm² and typically 30 cm of stolon.

Daily observation of all plants enabled a rough estimation of the frequency of natural sediment disturbances. Of the control plants, 11 % (n = 201) were broken, uprooted, or at least partially buried by *Callianassa* mounds. Of these disturbed plants, 52 % (controls: 6 %) exhibited partial decomposition associated with the site of disturbance, zero growth, or death. These percentage values are conservative; there was an approximately equal number of questionable disturbances.

Because of disparate sample sizes and lack of information on other growth parameters such as biomass accumulation, the daily sediment application experiment was repeated in December on the most common species, *Caulerpa sertulariodes*. Treated plants had significantly lower mean stolon elongation (p < 0.01), biomass accumulation (p < 0.05), and specific growth rates (p < 0.001) than controls (Table 4). When non-growers were excluded from the data, stolon elongation and specific growth rates were different between treated and control plants (p < 0.05) although biomass accumulation was not. Nine control and 11 treated plants of the original 20 marked of each type could not be recovered. The plants or flags had disappeared or the flags were obviously moved by heavy surge and movement of sediment ridges. In April, when seas

where much calmer, only 3 plants had disappeared and 1 flag had moved of the original 263.

Macrofauna and effects on *Caulerpa*

Thirteen species of animals were classified according to the nature of their disturbance of the sediment (Table 5). Major disturbers uprooted plants, excavated holes which broke or undermined plants, trampled plants, or caused large-scale sediment redistributions affecting at least a 0.25 m² area or 5 cm of sediment depth. These included all taxa with densities greater than one per 360 m² (area covered by 4 transects). Minor disturbers were estimated to have minimal effects on *Caulerpa* spp. They caused only the top 1 to 3 cm of sediment to be redistributed during feeding activities (peacock flounder *Bothus lunatus*, flying gurnard *Dactylopterus volitans*) or grazed on *Caulerpa* spp. or associated biota (Bermuda chub *Kyphosus sectratrix*, French angelfish *Pomacanthus paru*).

There were no significant differences in frequencies of occurrence of each major disturber (*Callianassa rathbunae* not tested) among the 4 transects or between day and night (p > 0.90). Accordingly, counts were combined from all 4 transects per sampling period to yield densities (Table 5). *Strombus gigas* (conch) and *Meoma ventricosa* (heart urchins) were the most frequently encountered disturbers.

Ghost shrimp *Callianassa rathbunare* and rays *Dasyatis americana* caused the greatest sediment disturbance. The activities and densities of ghost shrimp in Salt River canyon have been described by Suchanek (1983). Rays continually disturbed the bottom, creating sediment plumes up to 1 m from the site of their activity. Frequently they left 1 to 2 cylindrical excavation

Table 5. Animals observed on Salt river canyon floor, grouped according to their effect on *Caulerpa* spp. Mean densities ± 1 standard deviation, n = 8 surveys

Major disturbers	# $(360 \text{ m})^{-2}$
Mollusca	
Strombas gigas (conch)	5 ± 3
Crustacea	
Callianassa rathbunae (ghost shrimp)[*]	1 ± 1
Petrochirus diogenes (conch hermit crab)	1 ± 2
Echinodermata	
Meoma ventricosa (heart urchin)	4 ± 3
Chordata	
Dasyatis americana (southern stingray)	1 ± 1
Minor disturbers	
Mollusca	
Natica canrena (colorful moon snail)[**]	–
Chordata	
Dactylopterus volitans (flying gurnard)[**]	–
Pomacanthus paru (French angelfish)[**]	–
Bothus lunatus (peacock flounder)	1
Others (effect unknown)	
Crustacea	
Decapoda (shrimp)	1
Echinodermata	
Tripnuestes esculentus (urchin)	1
Chordata	
Caranx ruber (bar jack)	1
Kyphosus sectarix (Bermuda chub)	1

[*] Only sediment mounds seen on transects. Densities from Suchanek (1983)
[**] Not found on transects

holes (8 cm wide × 10 cm deep). Large depressions (1 m wide × 20 cm deep) on the bottom with *Caulerpa* undermined at the edges frequently were noted and were assumed to be the result of buried rays. Heart urchins *Meoma ventricosa* uprooted *Caulerpa* and produced sediment ridges (3 cm high × 2 cm wide) on both sides of their paths. Conch *Strombus gigas* and hermit crabs *Petrochirus diogenes* inhabited large heavy shells which they dragged over and rested on the vegetation. Conch were found in shell-sized depressions up to 7 cm deep. Hermit crabs actively excavated shell-sized depressions up to 10 cm deep.

DISCUSSION

The sediment disturbance experiments were superimposed on natural disturbances since all plants were unprotected from surge or macrofaunal activities. Surge was greater in December than April and created sediment ridges 18 cm high by 28 cm wide. This increase perhaps accounted for the difference in the results from the two disturbance experiments. Another contributing factor may be that the daily sedimentation treatment continued an additional two days in December. In April, the growing plants in disturbed and control populations were not significantly different. In December, mean growth rates for the disturbed population were significantly lower than controls as a result of both an increased proportion of non-growers and lower growth rates. At this time, almost one-third of the plants had their stolon apices uprooted during the experiment and several had damaged apices. The difference in the 2 experiments cannot be attributed to deletion of 1 species in the December experiment (see 'Results').

Sedimentation decreased the growth of *Caulerpa* spp. more than uprooting. This suggests that the activities of heart urchins have minor effects on *Caulerpa* spp. compared to those of rays and callianassid shrimps. Similarly, the effects of a one-time heavy sedimentation were less severe than chronic sedimentation (e.g. *Callianassa* mounds). A seasonal pattern to sediment disturbance effects in Salt River canyon may occur if surge in winter augments the effects of macrofauna.

The ability of *Caulerpa* spp. to survive sediment disturbances is probably related to many generic factors. Our findings confirmed the observation that thallus differentiation is very plastic (Jacobs, 1964, 1970). Buried thalli develop new growing apices that can differentiate into stolons or upright blades (Fig. 1). The apices grow turned up, thus away from a sediment mound. *Caulerpa* spp. also have a remarkable healing response to wounding (Dawes and Goddard, 1978), which would serve to minimize frequently observed mechanical damage. Finally, chloroplasts move into the uncovered portions of partially buried coenocytic thalli (Williams, pers. obs.), possibly maximizing productivity.

The energetic cost of partial burial may be reflected in the lower biomass accumulation and specific growth rates. Burial involves respiration of the buried portions, movement of chloroplasts away from, and photosynthate to, those portions, and a possible reduction of photosynthetic area. The pattern of *Caulerpa* spp. growth, i.e. rapid stolon elongation with very little biomass invested, perhaps serves to ensure 'escape' from a sediment disturbance at minimal cost.

Soft unconsolidated sediment habitats such as Salt River canyon are subjected to frequent disturbances in the form of sediment redistribution from storm, surge, and bioturbation. Sediment disturbances were found to limit the productivity of the seagrass *Thalassia testudinum* on a similar substratum (Suchanek, 1983). We have shown that biomass accumulation, specific growth rates and the number of growing *Caulerpa* plants were decreased by sediment disturbances, serv-

ing to reduce productivity of these algae. The magnitude and frequency of natural sediment disturbances are needed to evaluate fully the impact on *Caulerpa* productivity. Without measuring these directly, we feel natural sediment disturbances exert a major effect on the populations, given our estimate that at least 6 % of the control population was impacted within 6 d and our ongoing observations. The productivity of *Caulerpa* spp. in Salt River canyon was estimated to be 1–7 mg dry m^{-2} d^{-1}, using the average plant density of 0.8 m^{-2}. This rate can be converted to 0.3 to 1.0 mg C m^{-2} d^{-1}, assuming a carbon content of 27 % dry weight (Williams, 1984). This productivity is very low compared to that of many hard bottom macroalgae (e.g. Mann, 1973; DeBoer et al., 1978; Rogers and Salesky, 1981; Gerard, 1982). *Caulerpa* spp. productivity in Salt River canyon is apparently not low due to factors intrinsic to the canyon. Mean stolon elongation rates found for most *Caulerpa* spp. growing there were higher than maximum rates previously reported (Chen and Jacobs 1966, 1968; Mishra and Kefford, 1969; O'Neal and Prince, 1982) and similar to rates from shallower (1 to 5 m) population on St. Croix (Williams, unpubl.). Compared to Salt River canyon, higher biomass on certain hard bottoms contributes to their higher productivity, but higher specific growth rates also contribute. For example, coral-reef algae typically have low biomass but high areal productivity (Carpenter, 1984). This comparison reinforces the suggestion that sediment disturbances cause a major difference not only in the structure but function of primary producers in each type of bottom.

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