

Disturbance and recovery of a deep-water Caribbean seagrass bed*

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ABSTRACT: The seagrass community in a deep-water (20 m) submarine canyon on St. Croix, US Virgin Islands showed strong seasonal changes in abundances (50 to 90 % of yearly maxima) of major plant species in response to predictable winter conditions of low light and storms. Major species were the seagrass *Halophila decipiens* and the green macroalga *Halimeda incrassata*. Virtual elimination of the seagrass occurred following particularly severe storms; the alga was more resistant. Seagrass and alga regained their pre-disturbance biomass or abundance within 6 to 8 mo after major storms. Addition of nutrients to the sediments had no effect on the growth or recolonization rate of the alga. The rates of recolonization of the alga and seagrass were controlled by light availability in winter. Dynamics of disturbance and recovery in this deep-water seagrass bed are very different from other Caribbean seagrass communities in shallow waters, which are more resistant to storms of similar magnitude but once disturbed take many years for recovery. The deep-water seagrass bed is an example of a tropical community that is structured by seasonal abiotic disturbances and physiological extremes, as are many temperate marine communities.

INTRODUCTION

In shallow waters, seagrasses of the genus *Halophila* are considered colonizer species and are typically found in disturbed habitats or habitats where low light/high turbidity conditions limit the distribution of other seagrass species (den Hartog 1971, Lipkin 1979, Phillips & Lewis 1983, Birch & Birch 1984, Kirkman 1985). In waters deeper than 10 m, *Halophila* spp. often form extensive beds with rhizophytic green macroalgae of the order Caulerpales. Although the biomass and thus areal productivity of *Halophila* spp. is low compared to most other tropical seagrasses (Lipkin 1979, Zieman & Wetzel 1980, Josselyn et al. 1986), the turnover of *Halophila decipiens* is rapid and can provide important sources of organic matter and habitat for other organisms (Josselyn et al. 1983, 1986). Nevertheless, there have been no long-term studies of deep water *Halophila* spp. beds. In general, long-term studies of tropical marine plant communities are few.

Here I present results of a long-term study (>2 yr) of

a deep-water plant community dominated by *Halophila decipiens* and the calcareous green macroalga *Halimeda incrassata*. The study site was the floor of Salt River submarine canyon on the north shore of St. Croix, US Virgin Islands. At least 7 species of the macroalga *Caulerpa* also occur but in lower abundance (Williams et al. 1985a). Other benthic macroalgae (excluding epiphytes) are uncommon.

Plants growing on the canyon floor are subject to environmental stress and frequent disturbance. Stress, defined *sensu* Grime (1977) as a factor that reduces the potential for growth, is caused by low light and unstable sediments (Williams et al. 1985a, Josselyn et al. 1986). Disturbance is a process that removes biomass (Grime 1977); storms, resultant surge, currents, and sediment redistribution are the most intense disturbances in Salt River canyon. Although grazers are likely responsible for the narrow band of unvegetated sediments between the canyon walls (which provide coral reef habitat) and the canyon floor, they are very rare on the canyon floor proper where no refuge is available (Williams et al. 1985a, Williams, pers. obs. of 540 h).

The study describes disturbance and subsequent recovery patterns in the deep-water seagrass bed in Salt River canyon. The results are compared to previ-

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ous studies on Caribbean seagrass beds in shallow waters where the seagrass *Thalassia testudinum* typically dominates the plant community. Patterns of disturbance and recovery in such shallow water seagrass beds are relatively well-studied in contrast to those in deep water (den Hartog 1971, Kelly et al. 1971, Patriquin 1975, Zieman 1976, Williams 1981, 1985).

METHODS

The floor of Salt River submarine canyon (17°47'N; 64°45'W) is characterized by unstable sand sediments with numerous ripple marks and a high degree of bioturbation (Williams et al. 1985a). Currents in the canyon are variable in speed and direction but generally weak ($<0.5 \text{ cm s}^{-1}$) except during storms (see 'Results'; Josselyn et al. 1983). The study site was exposed to open ocean swells, and surge was usually evident at a depth of 30 m.

In March 1984, I established a sampling grid 11 by 11 m at 20 m depth on the canyon floor. Twenty permanent 0.25 m^2 plots were assigned randomly in the grid for monthly monitoring of *Halimeda incrassata*. Individual thalli in the plots were identified with a small numbered plastic strip tied at the base of the upright portion. 'New' thalli were marked after they recruited into the permanent plots between sampling times.

Immediately following Tropical Storm 'Klaus' (6 to 13 Nov 1984), 10 of the original plots were assigned randomly to a fertilization treatment in order to test the hypothesis that the rate of recolonization was nutrient-limited. Each fertilized plot received 24 g N as NH_4^+ and 5 g P as P_2O_5 in the form of solid time-released fertilizer spikes (Jobes 'Tree Spikes', Lexington, KY, USA) placed monthly in the sediments in the center of the plot to a depth of 15 cm. Fertilization of the sediments rather than the water column was appropriate because seagrasses and rhizophytic algae absorb sediment nutrients through roots and rhizoids respectively (McRoy & McMillan 1977, Williams 1984). I determined the fertilizer mass to use in a preliminary experiment in a different but similar area of the canyon; double the amount used here killed plants. The numbers of thalli in fertilized and control treatments were compared over time using 2-way analysis of variance (ANOVA).

I sampled sediment porewaters for nutrient concentrations using miniature diffusion chambers (Williams et al. 1985b) because the coarse sediments were not amenable to coring or inserting larger diffusion chambers. Chambers were filled with $0.45 \mu\text{m}$ Millepore-filtered, de-oxygenated seawater, buried in the upper layer of sediment, and allowed to equilibrate with

porewaters for 14 d before retrieval. Chambers were placed haphazardly within a 0.25 m^2 area around a fertilizer spike and also in control areas without fertilizer. I also placed 2 chambers on opposite sides of a spike at 5 cm intervals to a radius of 20 cm to determine the effective radius of fertilization. Porewater analysis followed methods of Williams et al. (1985b). Because the sediments were reducing and I assumed that nitrogen was limiting to plant growth, I measured ammonium, although recent evidence shows that under some circumstances, phosphorus limits the growth of some macroalgae and perhaps a seagrass (Short et al. 1985, LaPointe 1986, 1987). However, the fertilizer spikes raise sediment phosphorus as well as nitrogen concentrations (Williams 1987).

The growth of fertilized versus unfertilized *Halimeda incrassata* was determined during Hydrolab Mission #84-14 from 26 Nov to 6 Dec 1984. Hydrolab is an underwater laboratory and saturation diving facility. A total of 30 plants were selected haphazardly from within fertilized plots. Likewise, 30 control plants were selected at least 2 m away from the fertilized plots and outside of the permanent unfertilized plots. Growth was measured by marking the terminal segment of all branches on a plant with a $1 \times 5 \text{ mm}$ aluminum tag and counting all new segments 5 d later. The control plants were removed, separated into new versus old growth, decalcified in 20% glacial acetic acid, briefly rinsed in freshwater, dried at 80°C , and weighed. A regression between the number of segments and dry weight ($n = 60$; $r = 0.96$) was calculated and used to estimate the biomass of new growth of the unsacrificed fertilized plants. Growth rates of fertilized versus control plants were compared using a Student's t-test.

At each sampling time, 20 1.0 m^2 areas of the grid were randomly selected for collection of biomass of *Halophila decipiens*. Plots established for monitoring *Halimeda incrassata* were left undisturbed. No areas were resampled for at least 5 mo. Above plus below ground biomass was taken by tossing a plexiglass ring corer (0.0165 m^2) into each 1 m^2 area and collecting all *H. decipiens* within the ring. Sediments were washed from the seagrass, and visible epiphytes (primarily a summer phenomenon) were removed. The material was rinsed briefly in freshwater, dried at 80°C , and weighed.

Water temperature 1 m above the sediments was recorded with a Ryan thermograph. Terrestrial and submarine photosynthetically active radiation (PAR) were measured using a LI-COR terrestrial cosine-corrected quantum sensor, a 4π underwater quantum sensor, a Solar Monitor, and integrating quantum meter. From January 1985 through May 1986, incoming irradiance was integrated at hourly intervals throughout the daily light period. The extinction coeffi-

cient k was derived from vertical profiles of submarine light using the equation

$$I_z = I_0 e^{-kz},$$

where I_z = quantum irradiance at depth z ; I_0 = quantum irradiance at the surface of the water.

The portion of the daily light period in which light exceeds the saturation irradiance, i.e. the minimum irradiance at which the maximum photosynthetic rate is achieved, is defined as H_{sat} (Dennison & Alberte 1985). H_{sat} predicts the effect of light on seagrass growth better than does light intensity alone (Dennison & Alberte 1985, Dennison 1987). Here, H_{sat} is defined as the portion of the daily light period in which irradiance at 20 m water depth exceeded $100 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. This intensity was chosen because the saturation irradiance of photosynthesis of *Halophila* spp. is 70 to $175 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ (Josselyn et al. 1986, Dennison 1987). Previous experiments in Salt River canyon (Williams & Dennison unpubl.) determined that the growth of *Halophila decipiens* is no longer dependent on light (i.e. growth was 'light-satu-

rated') when H_{sat} was ≥ 9 h; below 9 h, growth is light-limited. Using the maximum k measured, H_{sat} was determined during the period when hourly integrations of surface irradiance were made.

RESULTS

The 40 knot winds of Tropical Storm 'Klaus' were a major disturbance to the plants in Salt River canyon. During the storm, waves 3 m high broke on Salt River barrier reef (at the head of the canyon) and currents up to 2 knots were measured in the canyon (Wood, pers. comm.). Transmittance of light through the water was reduced to zero for several days. The upper 0.6 m of sediment was removed down-canyon in a sheet flow, dislodging cement blocks that anchored equipment. Surge whipped upright macroalgal thalli back and forth from prone positions on the sediment surface. Plants were uprooted, buried, and broken. At the end of the storm, marine sediments were covered with a thin layer of brown, terrestrially-derived sediment and

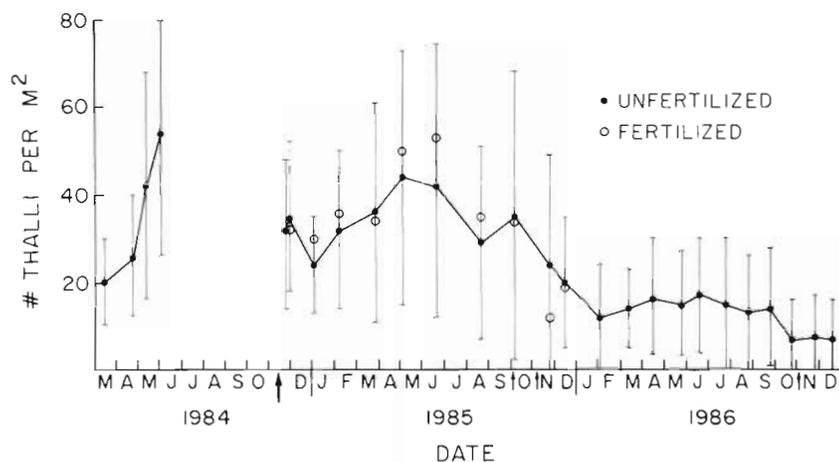


Fig. 1 *Halimeda incrassata*. Abundance of old plus new thalli at 20 m water depth in the permanent quadrats. Mean values ± 1 standard deviation for unfertilized plots; mean values for fertilized plots. Heavy arrow: Tropical Storm 'Klaus'; small arrows: other storms

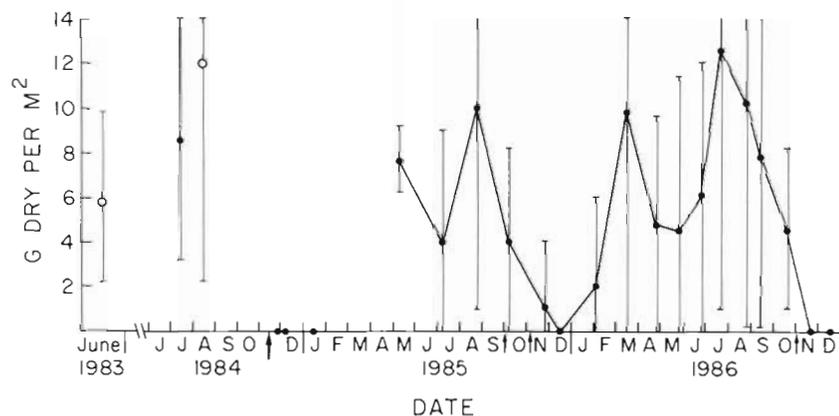


Fig. 2 *Halophila decipiens*. Biomass at 20 m water depth. Mean values ± 1 standard deviation. Heavy arrow: Tropical Storm 'Klaus'; small arrows: other storms. (o) data taken from Josselyn et al. 1986

other debris and were littered with sponges and gorgonians dislodged from the reef and canyon walls.

Halimeda incrassata declined to 58% of its density of the previous summer but was more resistant to the disturbances than were the other plants (Fig. 1). Greater than 99% of *Halophila decipiens* and also *Caulerpa* spp. was eliminated from the shallow apex of the canyon at 15 m to at least 23 m. The biomass of *H. decipiens* declined from >5 g to <1 mg m⁻² (Fig. 2). Increased resistance of *H. incrassata* resulted from its deeper (10 cm), more massive rhizoidal holdfast compared with the fine, superficial rhizomes and roots (5 cm long) of the seagrass.

In each successive year, a less intense storm disturbed the plant populations in Salt River canyon. In 1985, a cyclonic storm occurred in October and in November. The loss of *Halophila decipiens* after these storms was less severe than after 'Klaus'; more and larger patches of the seagrass were left (Fig. 2). *Halimeda incrassata* lost only 27% of its pre-storm abundance (Fig. 1). However, most of the upper portions of the thalli were lost. Many thalli were almost completely buried by ripple marks 30 cm high. In December 1986, large swells from a non-cyclonic storm virtually eliminated *H. decipiens*, similarly to 'Klaus', but the abundance of *H. incrassata* changed little. The abundance of *H. incrassata* declined to 50% of the summer maximum just prior to the storm. Although bioturbation by macrofauna is stressful to the plants (Williams et al. 1985a), it is not responsible for the observed seasonal declines in plant abundances because bioturbation also declines during the winter when animals are less active and conch (*Strombus gigas*) remain buried (M. Coulston pers. comm., Williams pers. obs.).

Within 6 mo after 'Klaus', *Halimeda incrassata* regained its pre-storm abundance but declined thereafter (Fig. 1). Both loss of mature thalli and reduced recruitment of new thalli occurred (Fig. 3). Apparently regrowth was by vegetative propagation; I observed only a single individual with gametangia, and *Halimeda* spp. lack zoospores. *Halimeda* spp. are clonal plants that propagate well from rhizoidal filaments, buried branches, and holdfasts (Hillis-Colinvaux 1980, Williams pers. obs.). For several reasons, it is unlikely that the initially high recruitment of the alga came from vegetative propagules washed into the canyon from shallow water during the storm. The peak of recruitment occurred 6 mo later and correlated with increased light availability. By this time, individuals washed into the canyon would have completed their lifespan; marked individuals typically died within 4 to 8 mo. Also, I have observed no dormancy in *Halimeda* spp. Viable plants that are buried regenerate new upright thalli within 1 mo.

Ammonium concentrations in sediment porewaters were 4 times higher in fertilized versus control areas (1-sided t-test, $p < 0.001$). Maximum ammonium concentrations in fertilized sediments reached 177 μ M in fertilized versus 9.8 ± 3.2 μ M. Mean ammonium concentrations (± 1 standard deviation) were 38 ± 46 μ M in unfertilized sediments. These concentrations were reasonable estimates of the average concentrations because they were taken midway between successive applications of fertilizer. Concentrations of 36 μ M occurred at least 20 cm from the point source. I did not measure soluble phosphate concentrations. However, in a similar study in a shallow seagrass bed on St. Croix, I demonstrated that an equal mass of the same fertilizer spikes raised soluble phosphate concentrations over 200 times ambient concentrations (Williams 1987). There is no reason that phosphorus would not diffuse from the fertilizer spikes in Salt River canyon. Although phosphate is strongly adsorbed to pure calcite and aragonite crystals in the laboratory (DeKanel & Morse 1987), this process is dependent on the concentration of soluble phosphate. Furthermore, carbonate sediments of coral reefs and seagrass beds are not purely carbonate but contain organic matter (Williams et al. 1985b) and also significant soluble phosphorus pools (Entsch et al. 1983).

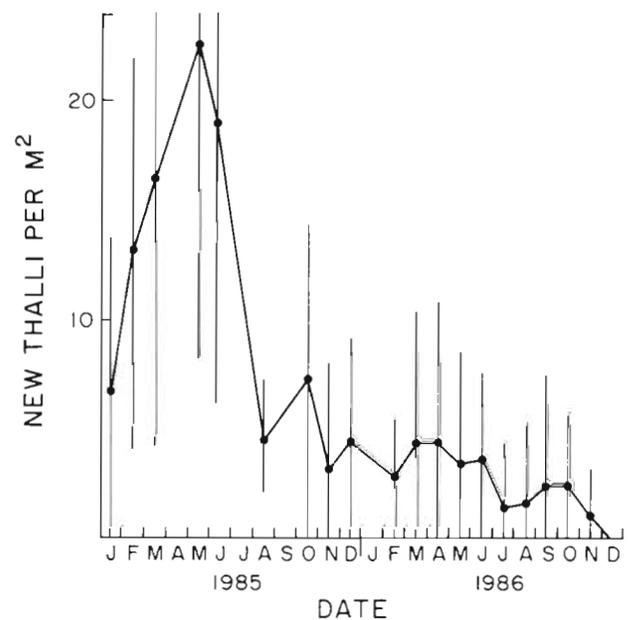


Fig. 3. *Halimeda incrassata*. Recruitment of new upright thalli in permanent quadrats. Mean values ± 1 standard deviation

Increased sediment nutrients had no effect on the abundance (2-way ANOVA, $p > 0.10$) or growth (2-tailed t-test, $p > 0.10$, Table 1) of *Halimeda incrassata*, providing indirect evidence for light limita-

Table 1. *Halimeda incrassata*. Growth in Salt River canyon, St. Croix, from 30 Nov to 5 Dec 1984. Values = means \pm 1 standard deviation

Sample size	Fertilized 23	Control 22
New segments plant ⁻¹ d ⁻¹	1.0 \pm 1.0	0.8 \pm 1.4
μg (dry plant) ⁻¹ d ⁻¹	385 \pm 427	311 \pm 520
% Plants not growing	39	59

tion. *Halophila decipiens* in the unfertilized areas was not qualitatively different in or around the fertilized plots.

Halophila decipiens recovered its pre-'Klaus' biomass within 6 to 8 mo or conceivably earlier as no measurements were taken between Jan and Apr 1985 (Fig. 2). More rapid recovery after subsequent storms occurred because more seagrass remained to recolonize (Fig. 2). Recovery occurred through vegetative extension and coalescence of patches of seagrass but sexual reproduction also may have played a role. Flowers and mature fruits were abundant in each biomass collection, and seedlings have been found in the canyon (Josselyn pers. comm.).

Changes in plant abundances rather than species diversity and composition occurred following disturbance in Salt River canyon where species diversity is low. The canyon is below the depth limits of *Halodule wrightii*, *Syringodium filiforme*, and *Thalassia testudinum* (Phillips & Lewis 1983), species that typically form a successional series in shallow waters (Patriquin 1975, Zieman 1976, den Hartog 1977). Seeds and seedlings of *S. filiforme* and *T. testudinum* and vegetative pieces of these species and *H. wrightii* did not survive more than 1 mo in the canyon (pers. obs.). *S. filiforme* and *T. testudinum* transplanted into the canyon in

summer did not survive past September (Dennison & Williams, unpubl.), presumably due to insufficient light.

The long-term decline in *Halimeda incrassata* in Salt River canyon was correlated with increased coverage of the sediments by *Halophila decipiens*. Although biomass of the seagrass recovered each year, the plant community appeared patchy until the fall of 1986 when *H. decipiens* covered the sediments almost completely, as it had before Tropical Storm 'Klaus' and when *Caulerpa* spp. finally regained their former abundance and diversity.

Within the long-term trends described above, plant abundances declined seasonally during October through February when light decreased (Figs. 1, 2 and 4) and swells increased, intensifying disturbance of the sediments (Williams et al. 1985a). The extinction coefficient k at 20 m ranged from 0.005 to 0.023. From April through August, H_{sat} was ≥ 9 h, sufficient for growth of *Halophila decipiens* (Table 2). From October through February, the growth of *H. decipiens* was light-limited when H_{sat} was < 9 h for 14 to 35% of the time. The seasonal difference in temperature of 2°C was probably insufficient to cause the seasonal changes in abundance. Seasonal changes were more pronounced in *H. decipiens* than *Halimeda incrassata*. In addition to being more resistant to storms, the alga may tolerate low light better than the seagrass. *H. incrassata* grew deeper than the 40 m limit of the seagrass. Because storms occurred each year, their effect cannot be fully separated from low light in winter.

DISCUSSION

Temporal variation in the abundance of seagrasses is not well-documented in areas undisturbed by man, particularly in the tropics, but natural temporal varia-

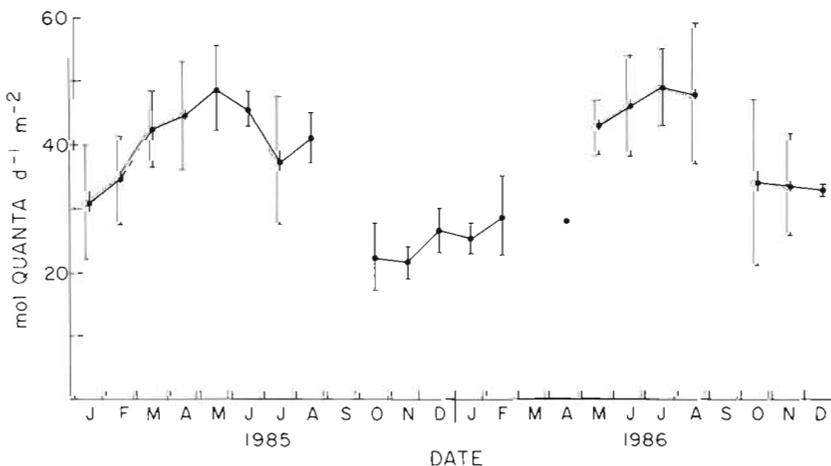


Fig. 4. Incoming solar irradiance (PAR), Salt River canyon, St. Croix. Mean values \pm 1 standard deviation. Missing data due to malfunction or factory calibration of sensors or meters

Table 2. H_{sat} : length of the daily light period during which irradiance at 20 m water depth in Salt River submarine canyon was above $100 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$, the saturation level of *Halophila decipiens* photosynthesis. $H_{\text{sat}} = 9 \text{ h}$ is the saturation level for growth of *H. decipiens*. Values are percentages of days per month when light was measured on an hourly basis

Month	Light limitation				H_{sat} (h)					
	4	5	6	7	8	9	10	11	12	
Jan	0	0	0	0	14	72	14	0	0	
Feb	0	0	0	0	5	23	69	3	0	
Mar	0	0	0	0	0	4	13	83	0	
Apr	0	0	0	0	0	6	6	88	0	
May	0	0	0	0	0	0	0	100	0	
Jun	0	0	0	0	0	0	0	100	0	
Jul	0	0	0	0	0	0	13	87	0	
Aug	0	0	0	0	0	0	6	88	6	
Oct	5	5	0	10	15	20	45	0	0	
Nov	0	0	6	0	19	75	0	0	0	
Dec	0	0	0	0	33	57	10	0	0	

tions of >30% of macroalgal abundance commonly occur over a wide geographical gradient (e.g. Sears & Wilce 1975, Prince & O'Neal 1979, Peckol 1982, Virnstein & Carbonara 1985, Brouns 1987, Payri 1987). The abundance of marine plants (i.e. density of individuals, coverage, or biomass), is the net effect of biomass accumulation (growth) and removal (disturbance). Temporal variation in abundance occurs when a change in one of these parameters is not compensated for by a change in the other. Given constant disturbance, fluctuations in an environmental condition (e.g. light, temperature, salinity, nutrients) produce temporal changes in growth only when fluctuations occur within: (1) the effective response time of the plant, (2) a critical region that limits plant growth, and (3) outside the range of plant acclimation or ecotypic differentiation. Temporal changes in plant abundance will be irregular when no seasonality is exhibited in factors that limit growth, when seasonal changes fall outside the critical region for growth, or when disturbance does not compensate exactly for changing growth (Doty 1971, Santelices 1977, Dethier 1982). Where changes in factors that limit growth are minimal or outside the critical region, disturbance will have a proportionally greater effect on plant abundances. The myriad factors that affect growth, the types of disturbance, and the interaction between growth and disturbance are represented by a wide variety of habitat-specific temporal patterns in plant abundance.

In Salt River canyon, plant abundances change predictably in winter when storms coincide with light availability that falls into the critical region for growth and thus maintenance of biomass of *Halophila decipiens* and probably *Halimeda incrassata* (Figs. 1, 2 and 4; Table 2). Biological disturbances of bioturbation and grazing are not responsible for the seasonal patterns in

plant abundance. The coincidence of low light and winter storms similarly controls macroalgal abundance on a sand plain at 10 to 14 m at Galeta Point, Panama, although the effect of light was not critically assessed (Hay 1981). There grazers are likewise rare. Macroalgal abundance in the intertidal regions of Galeta Point also respond to winter storms that occur during periods of the greatest tidal emersion and thus physiological stress (Kilar & McLachlan 1986). The habitats discussed above share the feature that times of maximum stress in the form of physiological extremes coincide with abiotic disturbances to control plant abundance, as occurs in temperate rocky intertidal habitats (Dayton 1971, Sousa 1979, Paine & Levin 1981, Dethier 1984).

In shallow subtidal regions of the same shore of St. Croix as Salt River canyon, factors that affect plant growth, e.g. light and temperature, do not fall into critical limiting regions. I found no significant seasonal patterns in leaf shoot density or growth of seagrasses, or density of *Halimeda incrassata* and other rhizophytic algae, although plant abundances vary up to 40% of their yearly maxima (Williams 1987 and unpubl.). Light is sufficient and the physical environment is more benign than that in Salt River canyon. The effects of sea swells and storms are buffered by a barrier reef, and current velocities are reduced by the extensive canopy of seagrass leaves.

In this and other shallow subtidal environments in the Caribbean where the physical environment is comparatively benign and conditions favor high growth rates of plants, disturbance from grazing is a major factor affecting temporal changes in plant abundances (Sammarco et al. 1974, Ogden 1980, Hay 1981, Thayer et al. 1985, Carpenter 1986, Lewis 1986). For example, in a shallow backreef/reef flat on St. Croix, grazers

consume up to 97% of the annual algal primary production and algal biomass fluctuates aseasonally throughout the year in response to herbivore abundance rather than algal productivity patterns (Carpenter 1986). In fact, algal biomass increases in November–December when storms and strong swells occur. At this time, light reaches a yearly minimum but is still sufficient for maximum photosynthetic rates (Carpenter 1986).

Grazers remove probably less than 50% of the primary productivity of seagrass leaves in the Caribbean (Greenway 1976, Ogden 1980). Although estimates of loss of seagrass productivity to grazers are few, grazing in shallow subtidal seagrass beds is unlikely to be as disastrous a disturbance as storms are to the seagrass bed in Salt River canyon. Seagrass leaves regrow from a basal meristem, and the belowground biomass and associated critical nutrient remineralization processes (Klug 1980) are unaffected by grazing.

Only intense, infrequent storms disturb *Thalassia* spp. and similar shallow water seagrasses because they have massive rhizome systems that are notably resistant to disturbance from waves (Thomas et al. 1961, Birch & Birch 1984). For example, blowouts (erosional gaps created in a seagrass bed) are restricted to <4 m of water, are rare where vegetation is well-developed, and are formed every 5 to 15 yr (Patriquin 1975). Neither the storms of this study nor the record-breaking storms of the century, Hurricanes 'David' and 'Frederick' (1979, pers. obs.) substantially disturbed the shallow seagrass beds on the same shore of St. Croix as Salt River canyon. Hurricanes occur about every 5 to 6 yr (Neumann et al. 1981); significant disturbance to the shallow seagrass beds will occur even less frequently.

Although the deep water seagrass bed in Salt River canyon is disturbed more frequently and intensely (i. e. more biomass, including belowground, is removed) than many shallower seagrass beds, it recovers more rapidly (Patriquin 1975, Zieman 1976, Birch & Birch 1984, Kirkman 1985). Rapid recovery is possible because: (1) rhizomes of *Halophila decipiens* branch profusely and grow almost 1 cm d⁻¹ in Salt River canyon (Josselyn et al. 1986), (2) sexual reproduction is prolific (see 'Results'), and (3) light, the factor controlling recolonization, increases during each summer to levels allowing effective regrowth. In contrast, shallow water seagrass beds of *Syringodium filiforme* and *Thalassia testudinum* are resistant to disturbances from storms but once disturbed, take many years to recolonize areas of only 1 m² (Patriquin 1975, Zieman 1976, Williams 1985). Rhizomes of *T. testudinum* and *S. filiforme* branch infrequently and grow only a few mm d⁻¹ (Patriquin 1973, 1975). Sexual reproduction of these species is limited to a few months of the year and seedling success is poor (Lewis & Phillips 1980, McMillan 1981,

Johnson & Williams 1982, Williams & Adey 1983). Finally, the slow accumulation of nutrients in the sediments limits the rate of recolonization of shallow *T. testudinum* beds (McRoy & Lloyd 1981, Williams 1985).

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