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Abstract: Shading of a 20 m^2 area of San Cristobal Reef off southwestern Puerto Rico for five weeks altered community structure and function by decreasing net primary productivity and respiration and by causing bleaching and death of several hard coral species. The prolonged exclusion of light was a partial simulation of extreme turbidity. Shading significantly reduced the growth rate of the dominant coral *Acropora cervicornis* (Lamarck) although the daily application of sediments to colonies of this species did not affect growth. Ten months after shading ceased, no new corals had settled on the dead corals which were rapidly colonized by algae. Although coral reefs are adapted to transient increases in turbidity, a continuous reduction in light penetration, for example after dredging, would severely alter community function and structure by decreasing photosynthesis, particularly in deeper reef zones where light is already limiting.

INTRODUCTION

Coral reefs are complex systems which face increasing pressure from human activities. Coastal development and dredging threaten reef survival by increasing sedimentation and turbidity. Runoff from storms and heavy rains also increases the turbidity of the reef waters. Johannes (1975) states, "Exposure of reefs to brackish silt-laden water associated with flood runoff has probably been the single greatest cause of reef destruction historically". Siltation from accelerated erosion of the shore may be as critical or more critical than lowered salinities in causing the destruction observed after storms (Hedley, 1925; Rainford, 1925; Goreau, 1964; Banner, 1968).

Banner (1968) described the death of coral reef organisms following excessive rainfall during a storm in Hawaii in 1965. Low salinity, extreme turbidity (from runoff), the settling out of sediments from the water column, high concentrations of H_2S, and low concentrations of oxygen (a result of decomposition of the killed organisms) combined to cause severe damage to the reef community. Three years after the storm, hard corals were just starting to recolonize the damaged areas, and recovery in general was slow.

Dredging is particularly detrimental to coral reefs (Brock *et al.*, 1966; Grigg, 1970; Roy, 1970; Maragos, 1972; Marsh & Gordon, 1974). Aside from the localized consequences of removal and cutting of substrate, dredging affects extensive areas by introducing fine sediments into reef waters. Deterioration of the reef can continue for several years after the cessation of dredging because of continual resuspension and transport of dredged materials. Brock *et al.* (1966) document total destruction

of 440 hectares of coral reef following dredging and filling. Siltation affected six times this area. Reef flat communities in Guam succumbed to siltation after dredging of nearby areas (Marsh & Gordon, 1974).

Field studies (Edmondson, 1928; Marshall & Orr, 1931) on the response of corals to applied sediments indicate considerable resistance, although the species tested differed in susceptibility. Hubbard & Pocock (1972) discovered the sediment rejection capabilities of several species and the importance of colony and calyx morphology. Marshall & Orr's (1931) experiments on the reef flat in Low Isles, Great Barrier Reef, suggested that water movement is more important in removing sand from some coral species than from others with superior cleaning ability. Corals generally do not survive burial for more than several hours (Mayer, 1918; Marshall & Orr, 1931). Although Dodge *et al.* (1974) described the inverse correlation between natural sedimentation and coral growth rates, most previous studies have emphasized the direct effect of sediments on corals (as in smothering) rather than the indirect effects. The structural and functional response of corals and coral reefs to reduced light intensities with increases in turbidity and sedimentation has not been documented.

Turbidity, an optical property of water, is a function of the light attenuation which results from "the scattering and absorption by the water itself, by dissolved substances, and by organic and inorganic suspended matter" (McCarthy *et al.*, 1973). It is difficult to establish a direct relationship between light attenuation and suspended matter concentrations (McCarthy *et al.*, 1973) because optical properties depend on "the shape, refractive index, and size distributions of the suspended particles, as well as on their absorption spectra" (McCluney, 1975). However, suspended particles in the water column will always reduce light penetration because of the two processes of absorption and scattering (Jerlov, 1970; Wilber, 1971).

While corals may be able to tolerate turbid conditions to some extent (Stephenson *et al.*, 1958; Roy & Smith, 1971), the dependence of corals and associated zooxanthellae on light for rapid deposition of calcium carbonate and for production of oxygen indicates that the reduction of light penetration because of increased suspended matter concentrations can be critical.

In this paper, I present the results of a study of the effect of experimental shading, a simulation of one aspect of extreme turbidity, on a 20 m^2 area of San Cristobal Reef off La Parguera, Puerto Rico (Fig. 1) and the results of an experiment on sediment application to colonies of *Acropora cervicornis* (Lamarck). With artificial shading, the response to decreased light intensities can be differentiated from the response to smothering by coarse sediments. While artificial shading is not equivalent to extreme turbidity, a lowering of light intensity by either factor below the light compensation point might be expected to elicit the same response. Changes in community structure were observed and recorded during and after shading. Metabolism and coral growth rate were measured to determine the effect of the exclusion of light on reef function. In the sediment application experiment, sediments were applied

to several colonies of *A. cervicornis* in different doses and at different frequencies to determine the effect on growth rate and colony structure. This species is dominant at San Cristobal, as on many Caribbean reefs, and recently has been shown to be an important framework builder in the western Caribbean (Macintyre *et al.*, 1977).

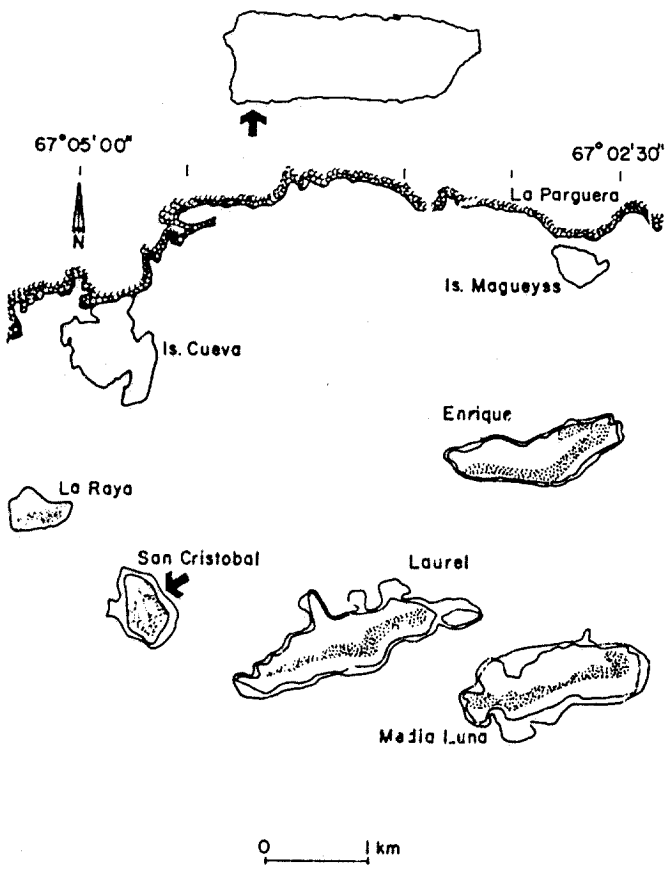

Fig. 1. Location of San Cristobal Reef, Puerto Rico.

The greatest potential threat to reefs off La Parguera lies in increases in turbidity accompanying development of Puerto Rico's southwestern coast. Because light decreases with depth, turbidity endangers deeper areas more than shallow ones. With extreme turbidity, there eventually could be a decrease in the vertical extent of a reef as deeper corals died. For these reasons, the work described here focused on a representative area 4 m deep rather than on the very shallow reef flat.

METHODS

LOCATION

San Cristobal Reef has a position centering at 17°56'30"N and 67°04'45"W, about 4.5 km southwest of La Parguera, Puerto Rico (Fig. 1). The study zone was 4 m deep and has been described elsewhere (Rogers, 1979).

METABOLISM

A modification of the upstream–downstream method used initially by Sargent & Austin (1949) and Odum & Odum (1955) was used at San Cristobal Reef and described in detail elsewhere (Rogers, 1979). The objective was to see if metabolism measurements could effectively be used to assess the response of a reef section to shading. The method involved submerged channels, open at both ends to permit water to flow over a segregated reef section (Fig. 2). One control channel (Channel

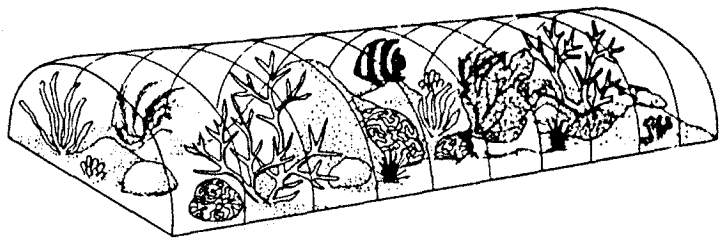

Fig. 2. Diagrammatic representation of a single metabolism channel made up of ten 1-m units.

B) and one experimental channel (Channel A) were installed at a depth of 4 m at San Cristobal. Each channel enclosed an area 10 × 2 m and had a maximum height of 1 m. When oxygen measurements were taken, transparent polyvinyl covers were used to cover the channels. During the shading experiment, Channel A was covered with black plastic. The channels, about 5 m apart, were parallel to each other and to the predominant east–west current. A map of the hard corals present in each channel appears in Rogers (1979). Upstream and downstream water samples were fixed chemically in the field with the Winkler method (Strickland & Parsons, 1972). Dye was used to monitor the movement of a water mass through the channel. Hourly rates of respiration and net photosynthesis (in g $O_2 \cdot m^{-2}$ reef area $\cdot h^{-1}$) were calculated by taking the difference between the upstream and downstream oxygen concentrations (g O_2/m^3), multiplying this figure by a value for discharge (m^3/h), and finally by dividing by 20 m^2, the area encompassed by each channel.

Light intensity was measured with a Lambda Instruments LI-170 quantum meter and an underwater sensor. The sensor was lowered to a depth of 3 m corresponding to the depth of the dominant organisms in the channels. The instrument measures quanta between 400 and 700 nm in microeinsteins $\cdot m^{-2} \cdot sec^{-1}$.

SHADING

On 31st March, 1976, Channel A was covered with a piece of black plastic. To ensure adequate water circulation, the ends of the channel were left open and the sides of the plastic were tied loosely to the steel reinforcing rod framework about 30 cm above the substrate. Because the channel was oriented parallel to the prevailing current and because water could enter the shaded area from all sides, water circulation was not significantly altered. Prior to metabolism measurements on 1st April, 27th April, and 7th June, 1976, divers secured the plastic to minimize exchange with water along the sides. Although, except during metabolism measurements, some light could enter the channel along the sides, measurements with the quantum meter indicated that photosynthetically active radiation was continuously excluded from most of the area under Channel A. The black plastic was removed on 5th May, five weeks after shading began. Channel B served as a control.

CORAL GROWTH

Measurements of the growth rates of *A. cervicornis* colonies were made with a modification of the method originally described by Shinn (1966). Numbered plastic electrical ties were pulled around coral branches of various lengths. This method permitted in situ growth measurements without damage to the colonies. A diver can carefully measure the growth of the main branch and offshoot branches with a flexible plastic ruler, using the tie as a fixed baseline. Growth rates of corals in the two channels were determined as well as the growth rates of nearby corals to which sediments were applied.

APPLICATION OF SEDIMENTS

Calcareous sediments from the reef were applied to *A. cervicornis* colonies to determine their response to different sediment doses and to various frequencies of application. All the corals grew at a depth of 2–3 m in an area near the metabolism channels described above. In the frequency experiment which ran for 45 days, nine colonies received doses of 200 mg/cm^2, three colonies receiving sediment once a day, three once a week, and three once a month. Three other colonies were controls. For the dosage experiment, single doses of 200, 400, and 800 mg/cm^2 were applied to nine colonies, three colonies receiving each dose.

By collecting, drying, and weighing known volumes of sediment, it was found that 1.5-l containers held approximately 2000 g of sediments. A 1-m^2 quadrat was placed around each colony to be stressed. The sediments were applied from the container as evenly as possible. In this manner, doses of 200 mg/cm^2 were placed on the corals. For higher doses of 400 and 800 mg/cm^2, two and four containers were used respectively. Sediments were applied wet. All sediments were calcareous, consisting mostly of *Halimeda* plates, and all came from a barren area 2–3 m deep in the

reef's lagoon where living corals are scarce. The particle size distribution of these sediments appears in Fig. 3.

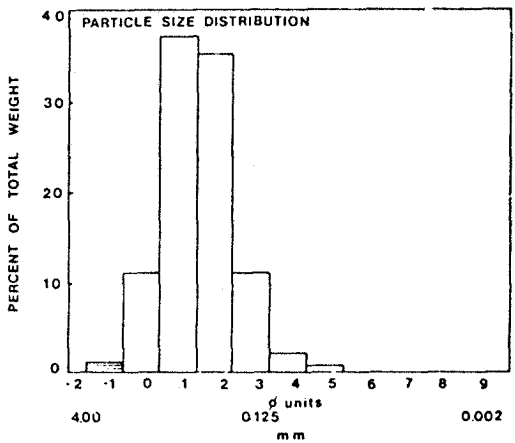

Fig. 3. Particle size distribution of the calcareous sediments applied to corals at San Cristobal Reef: bars with horizontal lines represent gravel; bars with no lines represent sand; Ø is equal to $-\log_2$ (diameter of the particle in mm).

RESULTS

EFFECT OF SHADING ON COMMUNITY STRUCTURE

Table I summarizes the effect of shading on the hard corals in Channel A and reveals the pattern of coral bleaching followed by limited recovery or by algal colonization of stressed or dead areas. The dominant coral, *Acropora cervicornis*, was the first to respond to shading. Three weeks after shading began, virtually all of the *A. cervicornis* colonies were white, indicating loss of zooxanthellae. This species contributed 45% of the total living coral cover in Channel A (Rogers, 1979). There was less macroscopic algae and algal turf growing on the bases of *A. cervicornis* branches than when the experiment began. *Diploria labyrinthiformis* (Linnaeus) and *Montastrea annularis* (Ellis & Solander) colonies were pale, although not white.

The only corals that appeared normal after removal of the black plastic at the end of the five-week experiment were near the edges of the channel and received some light during the experiment. The single exception was a colony of *Mussa angulosa* (Pallas) in the middle of the channel which appeared normal until three weeks later when it began to get progressively paler.

In general, the gorgonians appeared normal, although many grew near the channel edges and received some light. A few colonies were pale. A large sea fan, *Gorgonia flabellum* Linnaeus, which received very little light, seemed normal.

TABLE I

Structural responses of hard corals in Channel A to shading: shading ended after 5 weeks.

Coral species	Time after shading began						
	3 weeks	5 weeks	6 weeks	7 weeks	8 weeks	9 weeks	15 weeks
A. cervicornis	All colonies white; less algae on branch bases than before shading	All colonies white; only coralline algae on branch bases	Growth tips deteriorating or grazed off; algal colonization of some bleached branches; partial recovery of a few branches	Almost all colonies covered with algae	More algae on branches; further disintegration of branch tips	No change	No change
A. agaricites		Some pale areas	Some recovery	No change	No change	No change	Algae on dead areas; some areas still white
M. alcicornis		Some pale areas	Algal growth on bleached sections	No change	No change	No change	No change
M. annularis	A few pale colonies	Colonies near channel edges normal; all others pale	Some recovery	Little change	Further recovery of some bleached areas; some white areas secreting mucus	Little change; one colony about 40% recovered	Algae with fine sediments on some bleached areas; some areas still white and without algae
D. labyrinthiformis	A few pale colonies	Colonies near channel edges normal; all others pale	No sign of recovery	Little change	No further recovery	Further recovery	Algae with fine sediments on some bleached areas on all colonies; some areas still white and without algae
S. siderea		Some pale areas	Limited recovery	Little change	Further recovery	Little change	One colony completely recovered
C. natans		Some pale areas	Limited recovery	Little change	Little change	Little change	Algae with fine sediments on some colonies
E. fastigiata ***M. cavernosa*** ***M. angulosa***		No response; unaffected visibly			A single colony of *M. angulosa* paler		

A week after removal of the black plastic, the growth tips of several *Acropora cervicornis* colonies had been destroyed or had deteriorated, and fish were grazing on them. Parrotfish grazed on both partially bleached and completely dead *A. cervicornis* branches. Although damselfish were the most abundant fish in the study area prior to shading, only a few were observed near Channel A after the experiment; however, they were still abundant at Channel B. During shading, there was a decrease in algal biomass which presumably affected damselfish territories.

Although some corals recovered partially, algae gradually colonized most of the bleached coral sections beginning with the *A. cervicornis* branches. Three weeks after Channel A was exposed to light again, there was a heavy incrustation of algal turf species on the basal branches of *A. cervicornis* colonies, especially on the areas which had supported a large algal biomass prior to shading. A lighter covering of algae grew on *A. cervicornis* branches which were killed by lack of light. *Polysiphonia* sp., *Centroceras clavulatum* (C. Agardh) Montagne, *Ceramium byssoideum* Harvey, *Hormothamnion enteromorphoides* Grunow; Bornet & Blahault, and an ectocarpoid were all found on coral areas which were dead prior to shading. Two of the red algal species, *Polysiphonia* sp. and *Ceramium byssoideum*, were also found growing on the freshly killed coral branches along with several species of pennate diatoms.

When observed in June and July 1976, six and ten weeks after shading ceased, Channel A corals showed no marked increase in recovery. In March 1977, eight months later, algae grew on all corals which had been killed by the prolonged exclusion of light. There had been no further recovery. No new corals were seen in Channel A.

EFFECT OF SHADING ON COMMUNITY METABOLISM

Prior to the shading experiment, the metabolism of Channel A and Channel B measured on several days and under many different light intensities appeared similar, with net primary productivity of Channel A ranging from 0.03 to 1.43 g $O_2 \cdot m^{-2}$ reef area $\cdot h^{-1}$ ($n = 27$), and net primary productivity of Channel B ranging from 0.02–1.85 g O_2/m^2 reef area $\cdot$ h ($n = 21$) (Rogers, 1979). Metabolism measurements for one day appear in Fig. 4. On 1st April, a metabolism study was done after covering Channel A with black plastic. Channel B was the control. Channel A exhibited no significant net primary productivity although Channel B did (Fig. 5). Four weeks after shading began, another set of metabolism measurements indicated less respiration in Channel A (Fig. 6) than on April 1 (Fig. 5). By this time, zooxanthellae had been expelled, algae had died, and some of the hard corals were badly stressed or dead. Five weeks after removal of the black plastic, measurements indicated higher production in Channel A than in B, possibly reflecting the abundance of new algae growing on freshly killed corals (Fig. 7). For the time period examined, there was a production of 1.7 g O_2 in Channel A and 1.0 g O_2 in Channel B. Channel A organisms appeared to be more sensitive to the changes in light intensity.

EFFECT OF SHADING ON CORAL GROWTH

Prior to shading, the mean growth rates of *Acropora cervicornis* colonies in the two channels did not differ significantly ($P < 0.01$, $t = 0.05$, d.f. = 22) (Table II). After removal of the black plastic, measurements of 15 branches (including main branches and offshoots) revealed that all but three decreased in length during the shading experiment (presumably from fish grazing or disintegration). None of

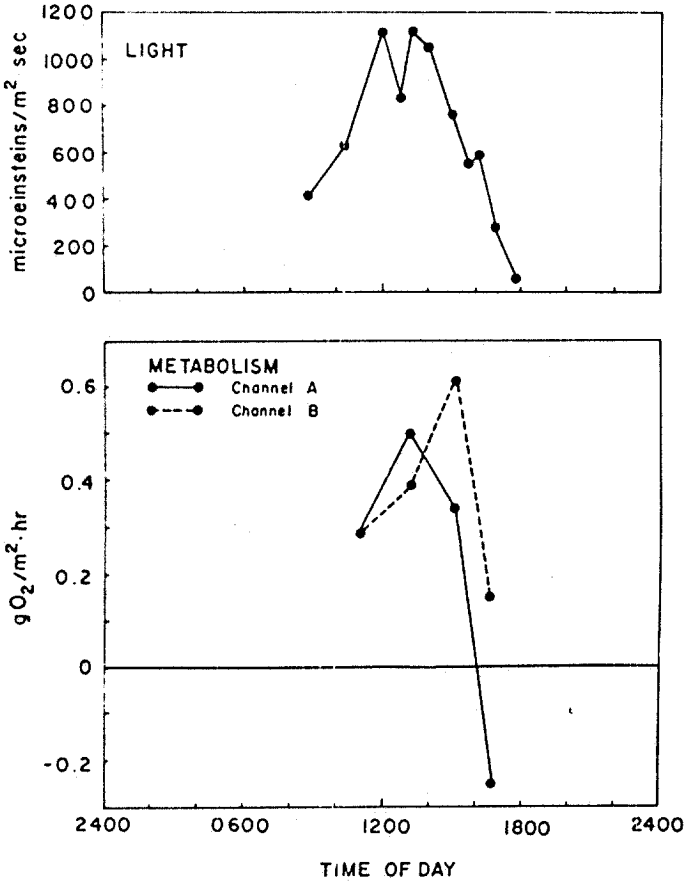

Fig. 4. Metabolism of Channel A and Channel B, 20th January, 1976.

the 13 branches measured in Channel B had decreased in length (Table III). The mean extrapolated growth rate for Channel B corals (including one branch with no growth) was 8.0 cm/yr while that for Channel A corals (calculating negative results as zero growth) was 0.5 (Table III). There was a highly significant difference in the two means ($P < 0.01$, $t = 5.34$, d.f. = 26).

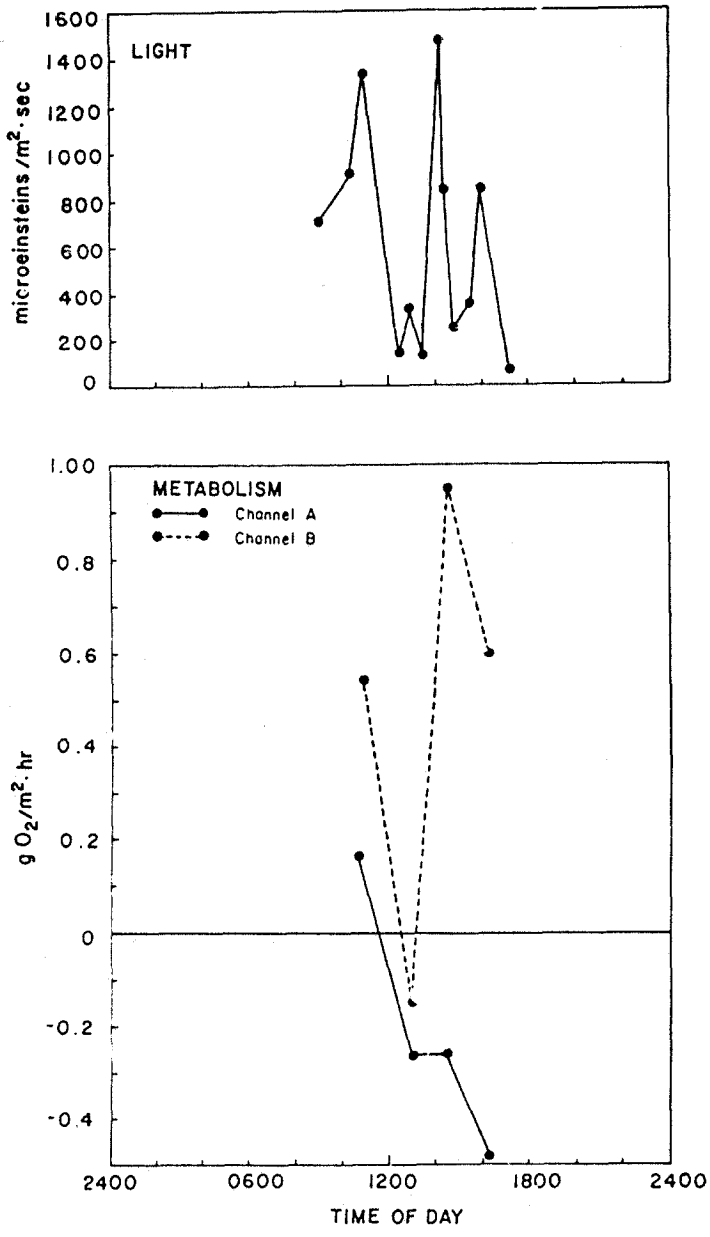

Fig. 5. Metabolism of control Channel B and shaded Channel A, 1st April, 1976, one day after shading of Channel A began.

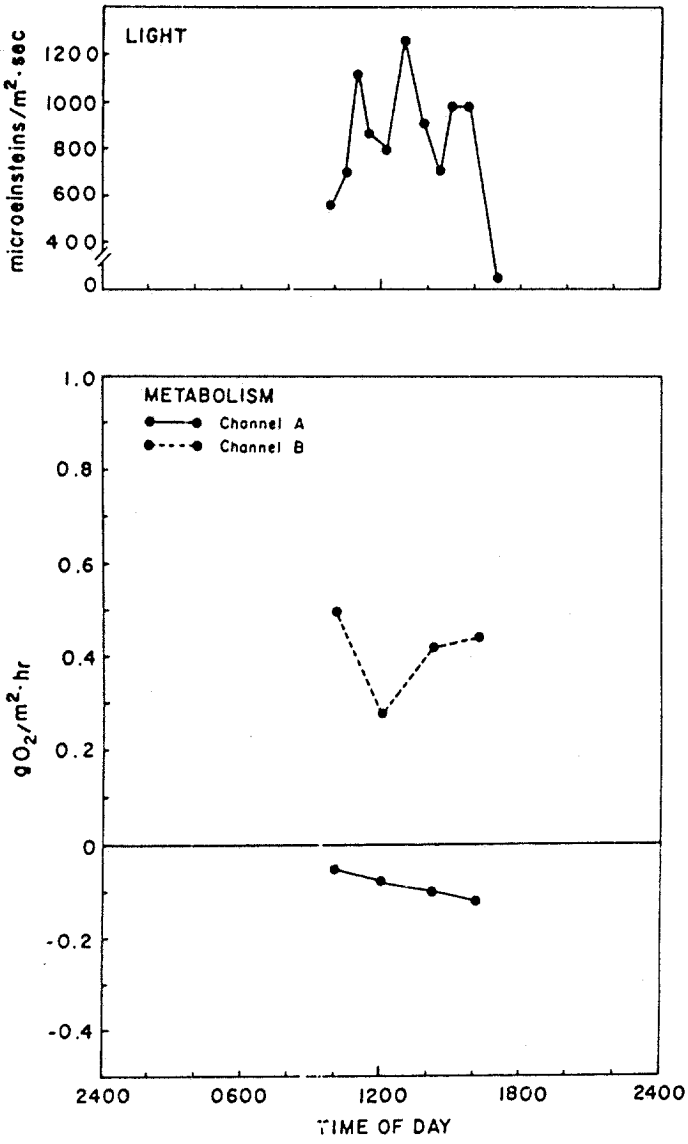

Fig. 6. Metabolism of control Channel B and shaded Channel A, 27th April, 1976, 28 days after shading of Channel A began.

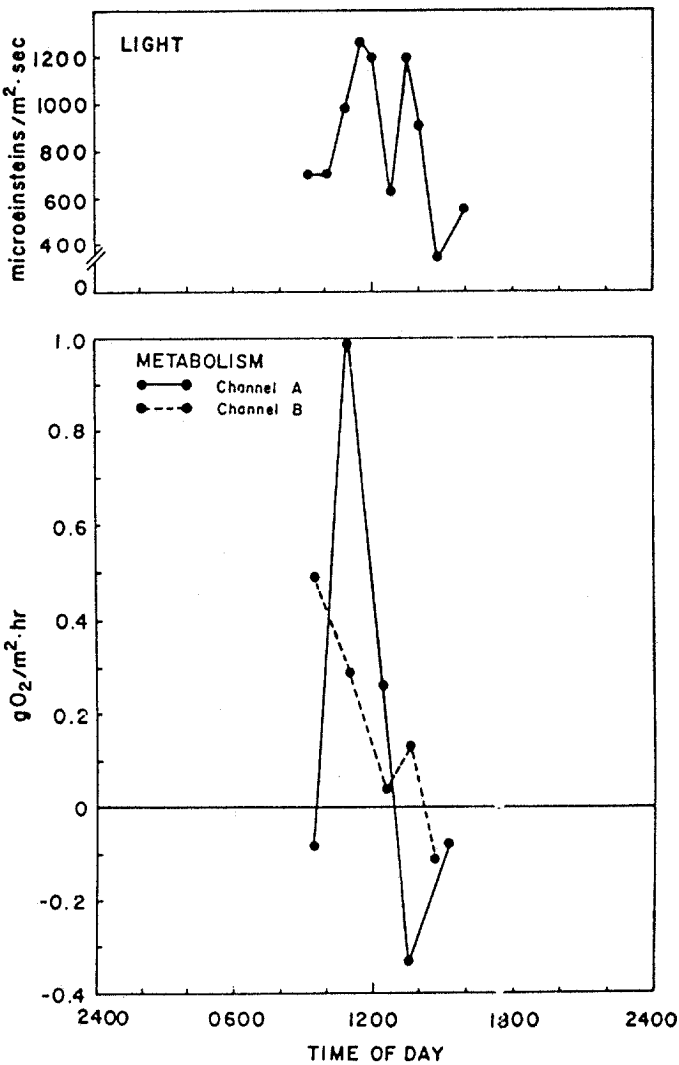

Fig. 7. Metabolism of Channel A and Channel B, 7th June 1976, 33 days after termination of the shading experiment.

SEDIMENTATION EXPERIMENTS

In contrast to shading, the application of sediments to the *A. cervicornis* colonies did not adversely affect them structurally or functionally. The numerous sediment particles which remained on colonies receiving 800 mg/cm^2 were scattered and did not smother large portions of the corals. There was no visible damage to the corals other than small bleached areas which appeared even on controls.

Extrapolated rates of growth for the 47 individual branches on the twelve *A. cervicornis* colonies ranged from 0 to 22.8 cm/yr (Table IV). The average growth for all marked branches was 8.3 cm/yr (zeros excluded) and 7.6 cm/yr (zeros included).

A one-way analysis of variance revealed no significant differences between the growth rates of individual corals (without zeros, $F = 0.96$, 11, 34 and with zeros, $F = 0.44$, 3, 46) or between the four experimental groups (without zeros, $F = 0.57$, 3, 8, and with zeros $F = 0.39$, 3, 8). The application of sediments did not alter growth rates.

TABLE IV

The rate of growth of *Acropora cervicornis* colonies prior to shading.

Channel	Time period	Change in branch length (cm)	Extrapolated growth rate (cm/yr)	Mean growth rate ±S.D. (cm/yr)
A	11-IX to 15-XII-75	1.0	10.7	3.3 ± 4.8
		1.4	15.0	
		0.7	7.5	
		0.4	4.3	
		0.8	8.6	
		1.0	10.7	
		0.0	0.0	
		0.8	8.6	
		1.0	10.7	
		1.0	10.7	
		1.4	15.0	
		0.2	2.1	
		0.5	5.4	
		1.4	15.0	
		0.6	6.4	
		1.0	10.7	
		0.0	0.0	
B	22-X to 15-XII-75	1.2	8.2	8.4 ± 4.0
		0.4	2.7	
		0.6	4.1	
		1.9	12.9	
		1.6	10.0	
		1.2	8.2	
		1.9	12.9	

DISCUSSION

The shading experiment at San Cristobal elucidated the response of an ecosystem to the shutting off of the main energy source, solar radiation. Structural changes included damage to the hard corals, particularly the dominant species, and subsequent colonization of all bare surfaces by algae. Functional changes included a

decrease in community metabolism and in the growth rate of *A. cervicornis*. The limited metabolism data presented here indicate that the exclusion of light decreased net primary productivity and respiration. Oxygen consumption decreased after several weeks of shading as the organisms died or left the area.

TABLE III

The rate of growth of *Acropora cervicornis* colonies during the shading experiment, 31st March to 5th May, 1976.

Channel	Change in branch length (cm)	Extrapolated growth rate (cm/yr)	Mean growth rate ± S.D. (cm/yr)
A (shaded)	−0.1	0.0	0.5 ± 1.4
	−1.2	0.0	
	−0.2	0.0	
	0.1	1.0	
	−0.1	0.0	
	0.1	1.0	
	−0.4	0.0	
	−0.1	0.0	
	−0.3	0.0	
	−0.1	0.0	
	0.5	5.2	
	−0.8	0.0	
	−0.9	0.0	
	−0.9	0.0	
	−0.8	0.0	
B (control)	1.4	14.6	8.0 ± 5.3
	0.7	7.3	
	1.4	14.6	
	0.5	5.2	
	0.0	0.0	
	0.1	1.0	
	1.0	10.4	
	0.7	7.3	
	1.6	16.6	
	0.4	4.2	
	1.0	10.4	
	0.3	3.1	
	0.9	9.4	

As light was excluded but zooplankton and other food sources were not, one would expect different responses from the various species of coral. Large-polyped corals with greater efficiency in zooplankton capture would be expected to be more resistant to shading than corals with small polyps which presumably depend more on light (see Porter, 1976). In fact, there was a fairly close correlation of increasing susceptibility to shading (demonstrated by bleaching) with decreasing polyp size.

TABLE IV

Growth rates of *Acropora cervicornis* colonies in sediment stress experiments: values under column a are means with zeros excluded; values under column b are means with zeros included; N.D. = no data.

Coral	Branch	Increment	Branch growth rate (cm yr)	Average colony growth rate (cm yr)		Average growth rate for group (cm/yr)		Frequency of sediment application
				a	b	a	b	
C1	1	0.8	9.1	8.6 ± 0.6	5.7 ± 4.4	9.0 ± 1.2	8.0 ± 2.3	Once/day
		0.0	0.0					
	2	0.8	9.1					
		0.0	0.0					
	3	0.7	8.0					
		0.7	8.0					
C2	1	0.7	8.0	8.0 ± 3.4	8.0 ± 3.4			
	2	0.3	3.4					
	3	1.0	11.4					
		0.8	9.1					
C8	1	0.5	5.7	10.3 ± 6.4	10.3 ± 6.4			
	2	1.3	14.8					
	3		N.D.					
C5	1	1.2	13.7	8.5 ± 3.4	8.5 ± 3.4	7.8 ± 1.1	7.8 ± 1.1	Once/week
		0.8	9.1					
	2	0.6	6.8					
		0.8	9.1					
		0.4	4.6					
	3	1.0	11.4					
		0.4	4.6					
C6	1	0.4	4.6	8.4 ± 3.3	8.4 ± 3.3			
	2	0.9	10.3					
	3	0.9	10.3					
C11	1	0.5	5.7	6.5 ± 1.3	6.5 ± 1.3			
	2	0.7	8.0					
	3	0.5	5.7					
C3	1	1.7	19.4	10.3 ± 5.8	10.3 ± 5.8	9.3 ± 2.1	8.5 ± 1.7	Once/month
		0.7	8.0					
	2	1.1	12.5					
		0.5	5.7					
	3	0.5	5.7					
C4	1	0.5	5.7	6.9 ± 3.6	6.9 ± 3.6			
	2	0.9	10.3					
		0.8	9.1					
	3	0.2	2.3					
C7	1	0.6	6.8	10.6 ± 8.3	8.4 ± 8.6			
	2	2.0	22.8					
		0.0	0.0					
		0.4	4.6					
	3	0.7	8.0					

TABLE IV (continued)

Coral	Branch	Increment	Branch growth rate (cm/yr)	Average colony growth rate (cm/yr) a	Average colony growth rate (cm/yr) b	Average growth rate for group (cm/yr) a	Average growth rate for group (cm/yr) b	Frequency of sediment application
C9	1	0.7	8.0	11.4 ± 7.1	11.4 ± 7.1	6.9 ± 4.2	6.2 ± 4.5	Zero (control)
		0.3	3.4					
	2	1.3	14.8					
	3	1.7	19.4					
C10	1	0.2	2.3	6.3 ± 5.7	4.2 ± 5.4			
	2	0.0	0.0					
	3	0.9	10.3					
C12	1	0.2	2.3	3.1 ± 2.9	3.1 ± 2.0			
		0.5	5.7					
	2	0.3	3.4					
	3	0.1	1.1					
		Mean	8.3*					
			7.6**					

* Zeros excluded. ** Zeros included.

A. cervicornis with small polyps was the first species to bleach, indicating a loss of its zooxanthellae. *Montastrea annularis*, with medium-sized polyps, later lost its normal coloration, as did *Diploria labyrinthiformis* and *D. strigosa*. The large polyped species, *Eusmilia fastigiata* (Pallas), *Mussa angulosa*, and *Montastrea cavernosa*, appeared unaffected by the shading, although there were only a few colonies of these species and some grew near the edge of the channel where they may have received some light. Franzisket (1970) documented the bleaching of coral as the result of the extrusion of zooxanthellae under stressed conditions and suggested that hermatypic corals with large polyps survive in the absence of light better than those with small polyps because they can more readily receive nutrition from sources other than their zooxanthellae. Goreau (1964) observed differential bleaching in several scleractinians exposed to low salinity water following torrential rains, but noted no correlation with polyp size.

Experimental manipulation of the environment in which a coral grows, e.g., the exclusion of light (this study) or transplant experiments (Shinn, 1966), can help to clarify the role of the environment in controlling coral growth. Shading drastically reduced the growth rate of *A. cervicornis* colonies, finally killing them. In contrast, even daily sediment doses of 200 mg/cm^2 for 45 days did not lower growth rates. Growth rates for control and treatment colonies did not differ significantly. The cylindrical branches of this species make it less susceptible to damage by excessive sedimentation (when light intensities remain high) than other coral species with flattened areas or depressions where sediment particles can settle.

The average growth rate of *A. cervicornis* at San Cristobal fell between the minimum and maximum rates previously reported for this species being most similar

to those found by Gladfelter *et al.* (1978) for St. Croix colonies at a depth of 10 m (Table V). Growth rates at San Cristobal varied from 0 to 22.8 cm/yr. Even branches from the same colony grew at very different rates (Table IV). When using growth as an index of stress or environmental conditions, measurements are only

TABLE V

The mean rate of growth of *Acropora cervicornis* in different western Atlantic localities.

Locality	Rate (cm/yr)	Study
Florida	4.0	Vaughan, 1915
Florida	10.0	Shinn, 1966
Bahamas	4.5	Vaughan, 1915
Barbados	14.5	Lewis *et al.*, 1968
Jamaica	26.6	Lewis *et al.*, 1968
Puerto Rico	8.3	This study
St Croix	7.1	Gladfelter *et al.*, 1978

reliable when made on several colonies and several branches from these colonies. Gladfelter *et al.* (1978) note that rates reported for *Montastrea annularis* are quite consistent, but that *Acropora cervicornis* rates vary greatly, possibly reflecting a greater response to local conditions.

In laboratory experiments, Hubbard & Pocock (1972) found that *A. cervicornis* could effectively remove sediments 0.25 mm or finer and that larger particles either fell between the corallites or wedged in the intercorallite area. In a field study, Marshall & Orr (1931) found that *Acropora* sp. cleaned itself in 24 h even when virtually buried in sand, although the experiment lasted only a few days. In a study of *Montastrea annularis* in Discovery Bay, Jamaica, Dodge *et al.* (1974) found an inverse correlation between both maximum and average coral growth rates and the resuspension of sediments. Rogers (1977) found that single sediment doses of 800 mg/cm^2 killed portions of *M. annularis* while a single application of 200 mg/cm^2 was sufficient to kill underlying portions of *Acropora palmata* branches.

The exclusion of light was an extreme situation. However, any increase in turbidity or decrease in light penetration could inhibit or prevent photosynthesis, especially in deeper reef areas where light is already limiting. Rogers (1979) found that the light compensation point for the Puerto Rican reef zone described here was 400–600 microeinsteins $\cdot$ m^{-2} $\cdot$ sec^{-1}. With decreasing light intensities below this point, there was no detectable net productivity. With no measurable light, maximum respiration was recorded.

High suspended matter concentrations can reduce light intensities below the compensation point even in shallow water. For example, Rogers (unpubl. data) found that suspended matter concentrations of 9–16 mg/l in a dredged lagoon off the north coast of St Croix decreased light intensities such that only 65 micro-

insteins · m^{-2} · sec^{-1} reached a depth of 2 m in full sunlight at noon. The Secchi disk depth was 0.9 m. At the mouth of this lagoon, dilution with ocean water lowered the mean concentration of suspended sediments to 1.4 mg/l and increased light penetration to 700 microeinsteins · m^{-2} · sec^{-1} at a depth of 2 m.

Increases in turbidity may affect competition between reef organisms. In eastern Martinique, carbonate pavements covered with fleshy algae, predominantly *Sargassum*, have replaced *Acropora palmata* on the reef crest, presumably because the corals could not compete with algae in turbid water with high nutrient concentrations (Adey *et al.*, 1976).

The point in an ecosystem at which a stress operates will determine at least partially the magnitude of the response it elicits. A stress can act by shutting off the main energy source (as in the shading experiment at San Cristobal); by removing structure (e.g., harvesting of coral for the making of cement); by accelerating the energy drains (e.g., thermal effluent increases respiration rates); and by changing the existing balance of inputs and outputs (e.g., sewage increases the phosphate concentrations on reefs leading to a takeover by algae). The type, intensity, and duration of a stress influence the impact it will have on a given system. For example, mangroves are adapted to live in high salinity areas, and cacti are adapted to live in deserts. Yet, there is an energy cost associated with these adaptations to the continuous natural stresses of high salinity or of water shortage. In these cases, the stresses have existed as part of the environment for so long that the organisms which are present are necessarily those that can withstand these stresses. Similarly, sediments are a natural part of the reef environment, and reef organisms have adapted to the continuous input of sediments. However, an increase in the intensity of a stress above a certain level, for example the acceleration of sedimentation rates through dredging, will lead to greater energy drains, and the system may become less stable, reverting to an earlier successional stage.

Stresses may be classified as chronic or acute. In general, given two stresses of equal intensity per unit time, the chronic stress will have a greater impact than the acute stress. San Cristobal Reef was found to be resistant to the transient stress from Tropical Storm Eloise in September, 1975 (Rogers, 1977). During this storm, virtually no photosynthetically active light reached the reef organisms for two days. There was no obvious damage after this temporary interruption of the main energy source. Energy stores in the system were sufficient to maintain homeostasis for the time that the system was subject to stress. In contrast, shading, a chronic stress, was lethal because it was continuous. There was a decrease in energy available for repair and only partial recovery after the stress. Extreme chronic turbidity is particularly detrimental to coral reefs because it limits the solar radiation energy flowing into and organizing the reef ecosystem and can severely alter both coral reef function and structure.

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