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PHYSIOLOGICAL EFFECTS OF SEDIMENT REJECTION ON PHOTOSYNTHESIS AND RESPIRATION IN THREE CARIBBEAN REEF CORALS

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ABSTRACT

Three species of corals, Acropora palmata, Diploria strigosa, and Montastraea annularis, were exposed to the same weight of sediment. Corals were exposed to sediment during day light and darkness. Oxygen production and consumption were measured by respirometery; sediment removed by corals was collected simultaneously. All corals exposed to sediments showed an increase in respiration rate at night and a decrease in net photosynthesis during the day. Lowered net photosynthesis was due to both light shading and respiratory increase. Integrated 24 hour P/R ratios for control and sediment-exposed corals were calculated. All control corals had naturally occurring P/R ratios in excess of 1.0, but the sediment treated corals, without exception, had ratios signficantly below 1.0, mostly due to high respiration during sediment rejection. M. annularis and D. strigosa have very high clearing rates relative to A. palmata.

INTRODUCTION

Tropical coral reefs are one of the most productive of all biological communities. The bank barrier reef of St. Croix is one of the best developed reef systems in the tropical Atlantic area and is the most extensive reef on the Puerto Rican-Virgin Island shelf (Adey 1975). Due to coastal development and other human impacts, sedimentation and coastal zone turbidity appear to be increasing on many reefs around the world (Stephenson et al. 1958, Johannes 1975, Marszalek 1981).

Sedimentation and sediment resuspension are among the important factors that may influence coral abundance and coral species distribution (Marshall & Orr 1931, Loya 1976, Rogers 1983). Sediment can inhibt coral growth in three general ways: (1) sediment-covered surface may prevent planula settlement, (2) the presence of sediment in water column or on a colony's surface may slow growth, and (3) rapid sediment deposition may lead to coral burial and death (Lasker 1980). Suspended sediments decrease incident light levels and reduce photosynthesis (Squires 1962, Dodge et al. 1974, Hudson 1981, and Dallmeyer et al. 1982). Turbidity and sedimentation decreases net photosynthesis and may cause bleaching, loss of zooxanthellae, and death of several coral species (Rogers 1979). Sediment on the colony surface reduces light availability and may inhibit exchange of oxygen, carbon dioxide, and other metabolites.

Dodge et al. (1974) related the growth rate of lagoonal corals in Discovery Bay, Jamaica to higher sediment resuspension rates. In Bermuda, Dodge and Vaisnys (1977) correlated periods of reduced coral growth with extensive harbor dredging. Barnes (1973) and Jacques and Pilson (1980) reported that skeletal growth is also influenced by light intensity.

There are three active methods of sediment rejection by corals: (1) tissue swelling caused by stomodeal up-take of water, (2) tentacular and ciliary sweeping, and (3) mucus entrapment (Hubbard & Pocock 1972). Tentacular action is limited to certain genera, notably Porites; ciliary action is restricted to 62 µ particles; mucal entrapment largely affects only fine particles (62 µ or less) (Hubbard & Pocock 1972). Hydrostatic pumping, ciliary action, and mucus production can be employed simultaneously during the sediment rejection process (Hubbard & Pocock 1972). As these mechanisms all involve active responses, all should require an expenditure of energy.

The sediment rejection process is specific to both the size of the coral and the size of the sediment (Bak & Elgershuzien 1976). Hemispherical corals with a small radius have a higher probability of quickly removing particles than heads with greater radii. Larger, hence older corals, have a lower chance of survival than smaller ones (Dodge & Vaisnys 1977). The size of the particle falling on the coral also plays a role in determining how much remains on the coral surface. Fine particles act like dense fluids and flow off the colony; larger particles are more apt to remain on the colony surface. Similarly if the polyp walls of the whole colony are steep (both polyp height and polyp convexity are important), the particle is apt to roll off (Lasker 1980). Many corals are highly specific in the sizes of particles they can remove: Agaricia, Oculina, and Acropora are most competent at removing particles in the 125 to 62 µ range, whereas Diploria, Manicina, and Colpophyllia cope better with larger particles in the 2,000 µ diameter size range (Hubbard & Pocock1972).

These behaviors act to remove the particle from the surface. Broad, flat surfaces such as those on blades of Acropra palmata increase the probability that the sediment will remain on the colony surface, and therefore these morphologies might be expected to expend more energy to remove sediment.

When sediment loading exceeds the rate of sediment removal, a sediment layer builds up which may become anoxic and kill the underlying tissue (Lasker 1980). Differential abilities at sediment removal utilizing these different morphological and behavioral means may determine which coral species can inhabit areas of high sedimentation or resus-

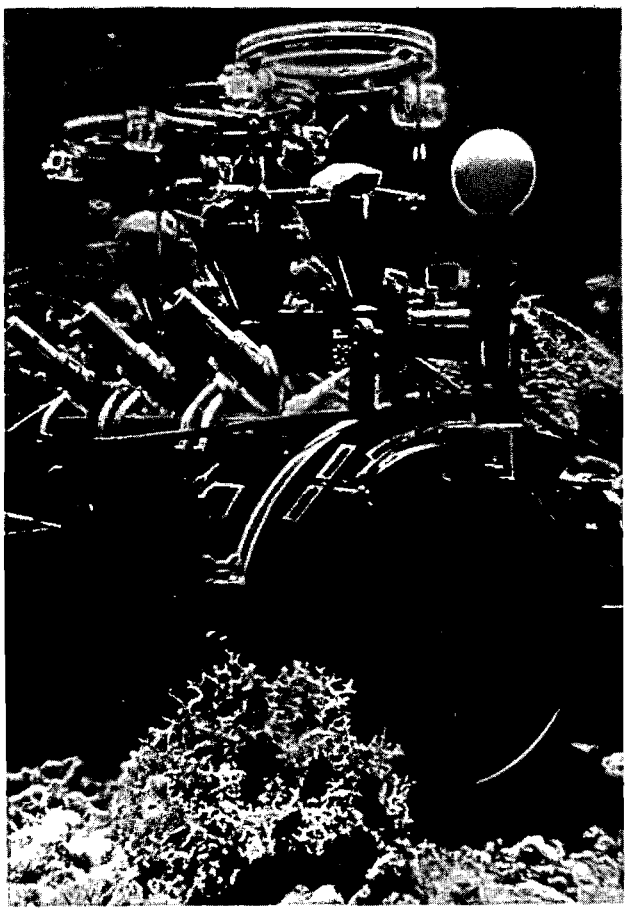

Figure 1. Bioassay respirometer showing three sediment rejection chambers with coral suspended above funnels leading to collection cups. Polarographic oxygen electrodes enter each chamber; a spherical quantum sensor measures irradiance.

pension (Roy & Smith 1971, Hubbard & Pocock 1972, Loya 1976, and Rogers 1983). In our experiments, we quantify the effects of sediments on coral respiration and photosynthesis.

MATERIALS AND METHODS

Corals were collected from a depth of 5 m off St. Croix, U.S.V.I. in August, 1984. Colonies of the three species used in these experiments were broken cleanly from substratum without damaging the coral's living tissues and without including other reef benthos. Sediments were collected from areas directly adjacent to the coral. All corals received the same weight and size class composition of sediments. We measured the oxygen flux rate of each coral colony before and after dumping 600 mg (= 5ml) of unsorted sediment on the corals.

The bioassay respirometer (Porter 1980) measured oxygen fluxes utilizing polarographic oxygen electrodes (Yellow Springs Instruments Co.) inside

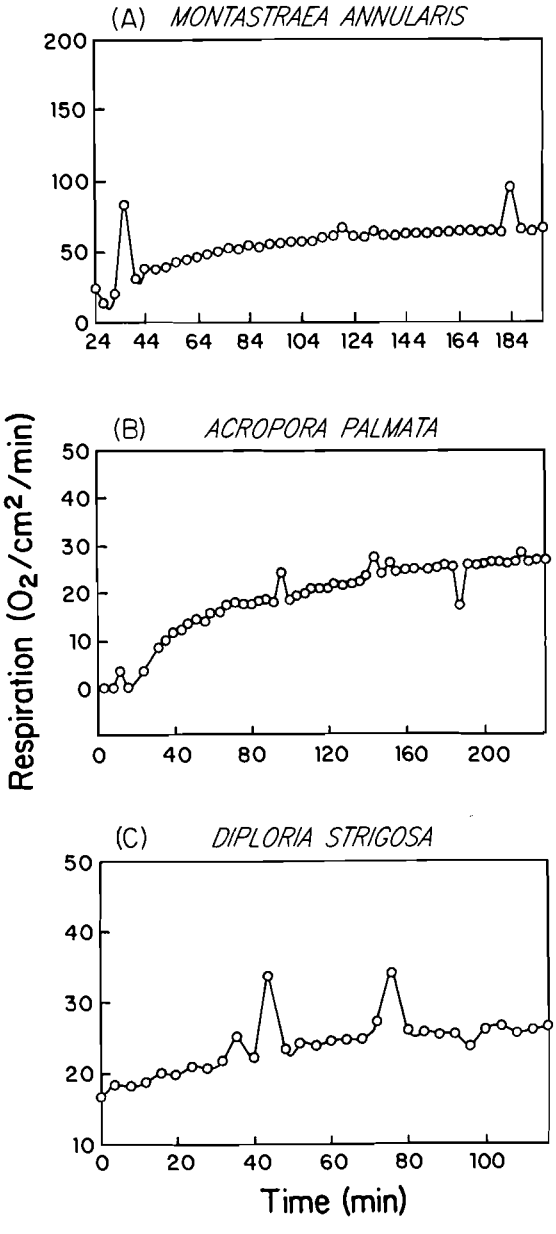

Figure 2. Coral respiration rate in the dark under sediment stress is plotted against time in minutes after the application of sediment.

three replicate experimental chambers into which single coral colonies were placed. The coral colony in each chamber was suspended over a funnel leading down to four cups on a "lazy susan" turn style (Fig. 1). Each cup was the size of a small 35mm film canister. The four cups were swung sequentially into place directly under funnel at hourly intervals; each experiment ran for four hours. The chambers were continuously stirred at a rate of 80-100 RPM by stir magnets. Ambient photosynthetically active radiation (PAR) was measured by an external 4-π spherical quantum

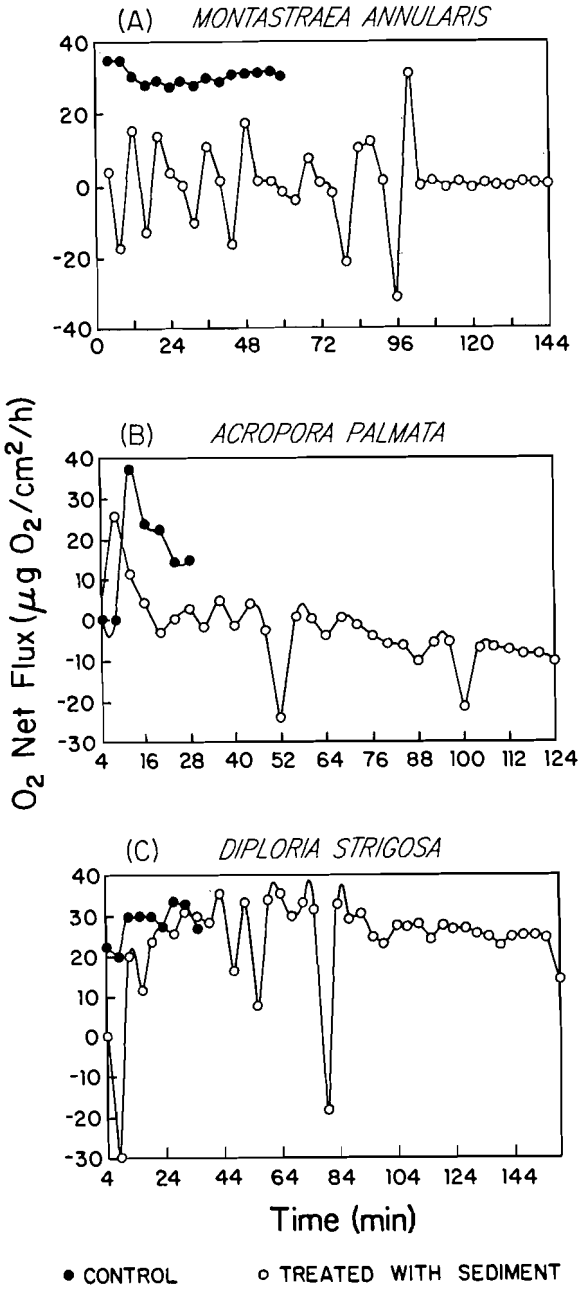

Figure 3. Net photosynthesis in the light with sediment stress (open circles) and without sediment stress (solid dots) is plotted against time after sediment application for three species of reef coral.

sensor attached to a quantum radiometer (Licor Instruments, Inc.). Sensor and meter were calibrated to each other prior to field use and checked again following the expedition.

The respirometer was stationed at 2 m depth on the reef in full sunlight for the photosynthetic experiments with Montastraea annularis. Nocturnal experiments with this species, and both diurnal and nocturnal experiments for Diploria strigosa and Acropora palmata, were done in a large tank filled with running seawater. Diurnal irradiance levels for the tank experiments were similar to those encountered on the reef during the experiments there with M. annularis.

After incubation, surface area of the coral was measured by wrapping aluminum foil around the branches of the colony (Marsh 1970), and computing the foil area on a digitizer (Hewlett-Packard 9815A-9864A).

Analysis of Oxygen Flux Data

Data were recorded on a Datel-Intersil magnetic-tape data logger in serial hexadecimal. Readings of oxygen concentrations (ppm ± 0.1 ppm) inside the three chambers, and light intensity by the in situ light sensor ($\mu E\ m^{-2}s^{-1} \pm 1.0\ \mu E\ m^{-2}s^{-1}$) were made every four minutes. The magentic tape from the bioassay respirometer was read into a Tektronix 4054 micro-computer for analysis. Oxygen concentrations were converted to weight of oxygen by multiplying the recorded oxygen concentration by the volume of the chamber minus the displacement volume of the experimental coral. These values were converted to oxygen flux rates per coral biomass by dividing the flux rates per four minutes by the surface area of living coral tissue.

Photosynthetic rates of the whole coral head (p_c net and p_c gross) and hourly respiration rates for the whole coral head (r_c) were established by using interpretative models for coral-zooxanthellae symbiosis (Muscatine & Porter 1977, McCloskey et al. 1978, Porter 1980, Muscatine et al. 1981, Chalker 1981):

p_c net = p_c gross max [tan ($\alpha I/p_c$ gross max)] - r_c where p_c net equals the net coral photosynthetic oxygen flux as $\mu g\ O_2 h^{-1} cm^{-2}$, and p_c gross max equals the light saturated photosynthetic oxygen flux. α is the initial slope of the P:I curve where I is light intensity.

Total respiration (Rc 24 hrs) was obtained by multiplying the average hourly night-time respiration rate by 24 hours. The total production values (P_c gross, idealized light) were obtained by using idealized irradiances generated from a sine function:

$$I = Imax\ [\sin \alpha(T/D)]$$

where Imax = maximum intensity at solar noon ($\mu Em^{-2} s^{-1}$), D = day length in hours, and T = hours since sunrise; for 1 m, Imax = 1990. Idealized values were used as a basis for comparison between experiments conducted under variable irradiance conditions.

RESULTS

Because the sediment dumped onto the coral contained air, the first 40 minutes of the oxygen

Table 1. Oxygen flux rates (µg O_2 $cm^{-2}h^{-1}$) for p_c gross, p_c net, r_c max and 24 hr P/R ratio (N = 3; x ± S.E.)

	p_c net	p_c net	r_c max	24 hr P/R
(1) *Montastraea annularis*				
Control	26.92 ± 2.80	35.04 ± 2.47	-8.12 ± 0.42	2.10 ± 0.06
Sediment	3.00 ± 2.55	32.55 ± 1.95	-29.55 ± 0.54	0.54 ± 0.04
(2) *Acropora palmata*				
Control	20.47 ± 13.20	30.83 ± 9.86	-10.36 ± 2.52	1.88 ± 1.04
Sediment	-8.51 ± 2.69	32.61 ± 3.70	-41.12 ± 4.27	0.37 ± 0.03
(3) *Diploria strigosa*				
Control	28.02 ± 3.20	57.44 ± 7.90	-29.42 ± 1.15	0.91 ± 0.05
Sediment	23.39 ± 2.20	108.09 ± 8.30	-84.70 ± 3.60	0.56 ± 0.03

Table 2. Clearing rate (mg $cm^{-2}h^{-1}$) for three Caribbean coral species (N = 3; x ± S.E.) as a function of time after application (hr).

	DAY			
Species	1 hr	2 hr	3 hr	4 hr
1)	28.60	46.50 ± 20.97	66.327 ± 20.00	28.40 ± 6.16
2)	1.32 ± 0.20	0.97 ± 0.15	1.70 ± 0.15	7.49 ± 3.41
3)	74.27 ± 2.68	24.18 ± 1.54	14.69 ± 3.92	23.92 ± 7.24
	NIGHT			
1)	29.30 ± 3.42	54.29 ± 9.55	12.33 ± 2.84	18.47 ± 16.79
2)	4.59 ± 2.70	1.26 ± 0.34	0.82 ± 0.19	0.95 ± 0.12
3)	27.04 ± 8.27	13.48 ± 3.79	14.21 ± 4.43	11.09 ± 1.52

1) *Montastraea annularis* 2) *Acropora palmata* 3) *Diploria strigosa*.

flux experiment had to be eliminated as the air trapped inside the sand grains bubbled off or dissolved. Large bubbles emerging from the sand grains could be seen for up to 20 minutes after sediment dumping. All three chambers responded identically in this respect. All coral colonies also responded similarly in another fashion. A burst of oxygen comsumption occurred as soon as the living coral tissue emerged from the sediment during sloughing. Oxygen rates of up to 218 µg O_2 $h^{-1}cm^{-2}$ were measured at this time. We speculate that this reflects the liberation of oxygen-depleted water from around the coral tissue rather than an order of magnitude increase in respiration during that particular four-minute interval.

Table 3. Mean of combined day and night clearing rate (mg $cm^{-2}h^{-1}$) for three Caribbean coral species (N = 6; x ± S.E.)

Species	1 hr	2 hr	3 hr	4 hr
1)	28.92 ± 9.31	50.42 ± 25.57	39.33 ± 36.94	23.44 ± 20.33
2)	2.96 ± 3.50	1.29 ± 0.43	1.26 ± 0.55	4.22 ± 5.18
3)	50.66 ± 27.53	18.83 ± 7.94	14.45 ± 6.49	12.51 ± 8.25

1) Montastraea annularis 2) Acropora palmata 3)Diploria strigosa

Respiration rates showed significant increases for all three species tested. Since the respiration rate rose slowly as sediment was sloughed off, we calculated a maximum respiration rate ($\mu gO_2 cm^{-2}h^{-1}$) as the asymptote of this curve (Fig. 2). For Montastraea annularis (Table 1; Fig. 2a) the mean of r_c max for sediment treated corals was much higher than for control specimens: -29.55 ± 0.54 for coral with sediment versus -8.12 ± 0.42 for control specimens. For Acropora palmata (Table 1; Fig. 2b), r_c max was -41.12 ± 4.27 for sediment-exposed specimens, and -10.41 ± 2.55 for control specimens. For Diploria strigosa (Table 1; Fig. 2c), r_c max was -84.7 ± 3.6 for sediment exposed specimens, and -29.42 ± 1.15 for control specimen.

Net photosynthesis shows significant differences between control corals and sediment stressed corals for Montastraea annularis and Acropora palmata (t-test, $p \leq 0.05$), (Table 1; Figs. 3a and b), but curiously not for Diploria strigosa. In the photosynthetic experiments with Montastraea annularis, there was a pronounced oscillation in oxygen flux between positive and negative values (Fig. 3a). The mean p_c net production was 26.92 ± 2.80 $\mu g\ O_2 cm^{-2}h^{-1}$ for the control specimens, and 3.00 ± 2.55 for treated specimens.

In Acropora palmata most of the oxygen flux values of the treated specimens were negative. The mean net pnotosynthesis of the control specimens was 20.47 ± 13.20, and for the treated corals was -8.51 ± 2.69.

In Diploria strigosa, however, the mean was +28.02 ± 3.20 for control specimens, and +23.39 ± 2.20 for sediment-treated corals (Table 1; Fig 3c), a lower value, but not significantly.

In order to evaluate the integrated effects of sediment on corals, we calculated P/R ratios for all three species. This value was 0.54 ± 0.04 versus 2.10 + 0.06 for sediment and control specimens of Montastraea annularis; 0.37 ± 0.03 versus 1.88 ± 1.04 for sediment and control specimens of Acropora palmata; and 0.56 ± 0.03 versus 0.91 ± 0.04 for sediment and control specimens of Diploria strigosa.

While oxygen flux was being monitored in the chambers, we measured the sediment removal rate for each species (Table 2). Table 3 demonstrates that there were no significant differences between day and night clearing rates for any of the three species. Finally, if we take the mean of the removal rate during both the daytime and nighttime values (Table 3; Fig. 4), we see that Montastraea annularis and Diploria strigosa have very high clearing rates relative to Acropora palmata (ANOVA, P § 0.1).

DISCUSSION

All experimental corals in this study showed an increase in respiration rate compared to the control specimens (Table 1). There was also a significant decrease in net production in experimental versus control specimens for Montastraea annularis and Acropora palmata. This loss of photosynthetic capacity may be due in part to a reduction in light reaching the symbiotic zooxanthellae within the coral. Our results agree with the results of Dallmeyer et al. (1982), Szmant-Froelich et al. (1981), and the observations of Bak (1978) who found that particulate peat and oil-drilling muds respectively also reduce photosynthesis in Montastraea annularis. These experiments clearly demonstrate the negative effect of light reduction on coral photosynthesis no matter what the source of the shade, whether it is peat, mud, or sand.

The rate of calcification in corals is light-dependent process (Chalker 1981); impairment of the photosynthetic activity of the algal symbionts could reduce the calcification rate of corals due to the expulsion of zooxanthellae (Yonge & Nicholls 1931a and b). This impairment can be caused by naturally suspended bottom sediments (Roy & Smith 1971, Dodge et al. 1974, Aller & Dodge 1974, Loya 1976) or by dredging, filling, and mining actitivies (Johannes 1975, Endean 1976). Dodge et al. (1974) found that calcification rates of corals living in naturally turbid areas are reduced by as much as 40%. Bak (1978) reported a 33% reduction in clacification rates for two species of reef building corals in Curacao after the reefs were exposed to silt from a dredging operation for four days. Chronic exposure to sedimentation may induce drastic changes in the character of coral community (Loya 1976). Dodge & Vaisnys (1977) reported that 35 years after dredging occurred in Castle Harbour, Bermuda, the coral community was still in a phase of high recruitment with many large dead colonies

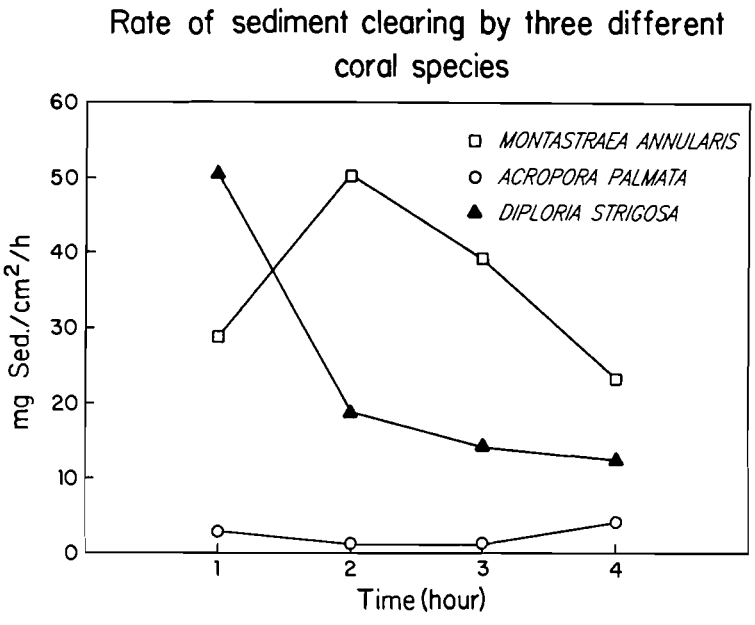

Figure 4. Clearing rate for three species of reef coral is plotted against time. Rates for Montastraea and Diploria are significantly higher than those for Acropora.

in evidence. Examination of the growth bands from cross-sections of dead coral colonies indicates that while many specimens died during dredging, others went through a period of decline before death occurred. Dryer and Logan (1978) found that the diverse community dominated by head corals on Bermuda patch reefs before dredging was replaced by a less diverse community dominated by small branching corals after dredging. These branching corals may be better adapted to handle the increased turbidity and sedimentation.

The integrated 24 P/R ratio of the control and sediment exposed corals were calculated. These net totals are highly dependent on the total amount of light the coral receives. Only under ideal, cloudless day irradiances will these totals reflect the organism's potential. These results (Table 1) show that all control corals were autotrophic (with respect to carbon) because their P/R are in excess of 1. Sediment-treated corals, without exception, however have P/R ratios less than 1. The high respiration rates measured during sediment rejection are not compensated for by adequate production. Sedimentation may also cause an interruption of the planktonic food supply to the polyps at night further reducing energy uptake.

Regarding the clearing rates for sediment by the three species, we found no significant differences between a species' clearing rate during the day and night (Table 3). There were, however significant differences between species (Fig. 4). Montastraea annularis and Diploria strigosa show similar clearing rates (Table 2). These rates are both significantly higher than that for Acropora palmata. A. palmata grows in shallow water, where water movement is high, but does not grow in deeper water, where water movement is less. In deep water its clearing effort may not be subsidized by wave energy.

Hemispherical corals with a small radius, such as Montastraea annularis in shallow waters and Diploria strigosa, have a higher chance of quickly removing particles; this may contribute to their broader depth range. Our results support the study of Rogers (1983) that showed that Acropora palmata, a species normally found in areas with strong wave action, was the least resistant to sediment application. Sediments accmulated on the flattened portion of A. palmata colonies, but not on the hemispherical colonies of M. annularis and D. strigosa. In the labortory, Hubbard & Pocock (1972) also found A. palmata to be less capable of rejecting sediment particles than M. annularis and D. strigosa. Lasker (1980) suggested that broad surfaces of A. palmata increase the probability that a sediment particle will lodge on the colony surface, and therefore increase the energetic cost of sediment rejection for this species.

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