HIGHLY PRODUCTIVE EASTERN CARIBBEAN REEFS: SYNERGISTIC EFFECTS OF BIOLOGICAL, CHEMICAL, PHYSICAL, AND GEOLOGICAL FACTORS

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ABSTRACT

Studies of reef productivity and community structure were conducted on three bank barrier reefs along the south shore of St. Croix, U.S. Virgin Islands. Primary productivity (rate of organic carbon fixation) was measured using upstream/downstream flow respirometry techniques. Mean annual gross primary productivity of the St. Croix reef ranged between 17-33 g $C/m^2/d$. These are among the highest values reported for reefs or for any biological community.

Reef productivity corresponds with the distribution and abundance of turf algae. These algae are minute filamentous forms which are highly diverse, productive, and abundant. Algal turf productivity is limited primarily by available solar energy and is influenced by wave surge and water flow (which enhance metabolite exchange). Turf cover is limited by the total surface area of standing dead coral. Nitrogen availability is increased by in situ nitrogen fixing blue-green algae, as evidenced by increased concentrations of inorganic nitrogen in water flowing over the most productive reef zones. Phosphorus availability is enhanced by wave surge and maintained by inflowing water from the open ocean.

Over geological time, reefs grow toward sea level. The three reefs we studied represent three stages in reef development. Younger reefs to the east are deeper, with considerable live branching coral (Acropora palmata) and with a low abundance of turf algae. The reverse is true for the older reefs to the west, where live coral is minimal but the dominant algal turfs occupy a rather smooth pavement of limited surface area. Intermediate between these two types of reefs, the abundance of live coral is low but biomass of algal turf is very high due to the large surface area left by the dead branching coral. The greatest reef productivity was measured under the latter conditions because of the synergistic effects of large surface area with abundant algal turf cover in shallow, strongly lighted, and turbulent water. It is clear that, given optimum conditions, coral reef algal turfs can develop primary productivities that reach and perhaps exceed the accepted theoretical maximum for primary production in the sea.

INTRODUCTION

Coral reefs have attracted interest over the last 30 yr in part because they are among the most productive biological communities in the world. Early studies of reef productivity (Sargent and Austin, 1949; Odum and Odum, 1955) focused on determining the productivity of individual reefs. There is little agreement in these and subsequent studies as to how productive reefs can be, and there is even less agreement concerning why high levels of production are attained or why reefs differ from each other so much (Lewis, 1977; Sournia, 1977; Mann, 1982). Smith (1981) considered some of these problems in an examination of the Houtman Abrolhos Islands off western Australia. We address these questions in some detail in our study of the reefs of St. Croix.

In an examination of the "Potential Productivity of the Sea," Ryther (1959) concluded that (net) "primary productivity of organic matter of some 10-20 g (dry)/m^2/d may be expected," with a maximum of 25 g (dry)/m^2/d under ideal conditions of maximum radiation and no nutrient limitation. Expected gross primary production (GPP) levels of up to 23-38 g (dry)/m^2/d (50-80% higher than the net values) also were cited. Ryther suggested that, while planktonic open ocean production (particularly in tropical/subtropical areas) is limited by nutrients, such limitation in benthic communities is not likely because nutrients "are continually being replenished as the water moves over the plants [and] probably prevents their ever being [nutrient] limited."

Recent reviews of coral reef primary productivity by Lewis (1977) and Sournia (1977), integrating 30 yr of research, reveal a range in GPP of nearly an order of magnitude (3.4 - 20 g C/m^2/d). The mean of these cited reef values is about 10 g C/m^2/d, but only a few points are above 13 g C/m^2/d. The mode is 7 g C/m^2/d, which, using a typical conversion ratio, would convert to a net biomass production of about 15 g (dry)/m^2/d. Overall, these values are much less than the theoretical maximum suggested by Ryther (1959). Significantly, all but one of the 17 coral reefs cited by these authors were located in the Indo-Pacific.

Despite Ryther's (1959) suggestion to the contrary, nutrient limitation of reef productivity has been the focus of numerous studies. Many of these have focused on explanations of how highly productive reef ecosystems can thrive in nutrient deserts (Odum and Odum, 1955; Stoddart, 1969; Johannes, et al., 1972; D'Elia, et al., 1981; Andrews and Muller, 1983). Recently, the role of major nutrients was questioned due to the finding that benthic algae have lower nutrient requirements than once thought (Atkinson and Smith, 1983). Also, some reefs are known to have a surplus of nitrogen (Webb, et al., 1975; Wiebe, et al., 1975) due to the in situ nitrogen fixation by cyanobacteria (blue-green algae) (Mague and Holm-Hansen, 1975; Capone, et al., 1977; Hatcher and Hatcher, 1981; Wilkinson and Sammarco, 1983). The benthic algal turf of reef communities usually is dominated by cyanobacteria (Sammarco, 1983; Van den Hoek, et al., 1975).

Phosphorus concentrations over reefs generally have been thought to change little (Pilson and Betzer, 1973), and some authors have suggested that a "tight recycling" or retention of phosphorus occurs (Pomeroy, et al., 1974; Pomeroy and Kuenzler, 1969). Atkinson (1982), on the other hand, has shown reactive phosphate depletion over broad reef flats.

Our study examines the productivity of three reef environments in tropical, oligotrophic seas. Large-scale temporal and spatial variations in their primary productivity with respect to potentially important biological, chemical, physical, and geological differences between the reefs are explored.

MATERIALS, METHODS, AND STUDY SITES

Our study was conducted on the southeastern bank barrier reef of St. Croix from October 1977 to November 1978. It extends 35 km along most of the windward shore of the island and is the most extensive reef system on the Puerto Rican-Virgin Island shelf. St. Croix is a small island which is unaffected by neighboring islands. Temperature, salinity, and wind direction and intensity are all remarkably constant. The south shore is relatively unpopulated, and it has no natural rivers affecting salinity or ambient nutrients. The south shore of St. Croix is ideal for examining the factors that affect reef productivity. The two major factors that change from east to west are water motion (decreasing) and geological reef development (increasing).

The western reefs of St. Croix lie on a shallower limestone basement than do the eastern reefs; they were the first to grow to sea level (Adey, 1975; 1978a), and they developed broader, more continuous reef flats. Several of these reefs have become so shallow that the abundance of live coral is reduced due to the negative effects of intense sunlight (including ultraviolet), temperature fluctuations, and desiccation during periods of extraordinarily low tides.

We studied three reefs on the south shore of St. Croix intensely and several others to a lesser extent (fig. 1). The following is a description of the morphology of the reefs from east to west. Isaac Bay Reef is a "young" reef with a high coral cover, rapid reef growth rates, and a crest that is just reaching sea level today. Mean depths are 6.3 m for the fore reef and 0.9 m for the back reef. The reef structure is open (many channels and breaks in the reef crest), and there is no continuous reef flat. Robin Bay Reef is more mature, with a nearly continuous crest and a moderately deep and broad reef flat. Mean depths are 5.1 m for the fore reef and 0.7 m for the back reef. Halfpenny Bay Reef is mature, with a continuous, broad, and shallow reef flat. Mean depths are 5.1 m for the fore reef and 0.3 m for the back reef. We selected these reefs because they fall along a gradient of reef maturity and because they are particularly well suited for the upstream/downstream method. All of these reefs have a continuous unidirection water flow inward across the reef to the lagoon.

A profile of Robin Reef along a permanent transect line established at the beginning of our study is shown in figure 2. Comparisons with Isaacs and Halfpenny Reefs are given in the accompanying table. The transects were parallel to the predominant current flow and were established using drogues to indicate the exact current flow. We omitted breaker zones due to logistic and scientific problems created by the turbulence (accelerated diffusion). The outer (seaward) limit to the fore reef was defined by the first appearance of the dominant reef-building coral, Acropora palmata. The inner fore reef and outer back reef zone were adjacent to the breaker zone. The inner (landward) limit of the back reef was defined by the abrupt transition between the reef and sandy lagoon. Our fore and back reef zones are consistent with other published studies (Adey, 1975; Adey and Burke, 1976).
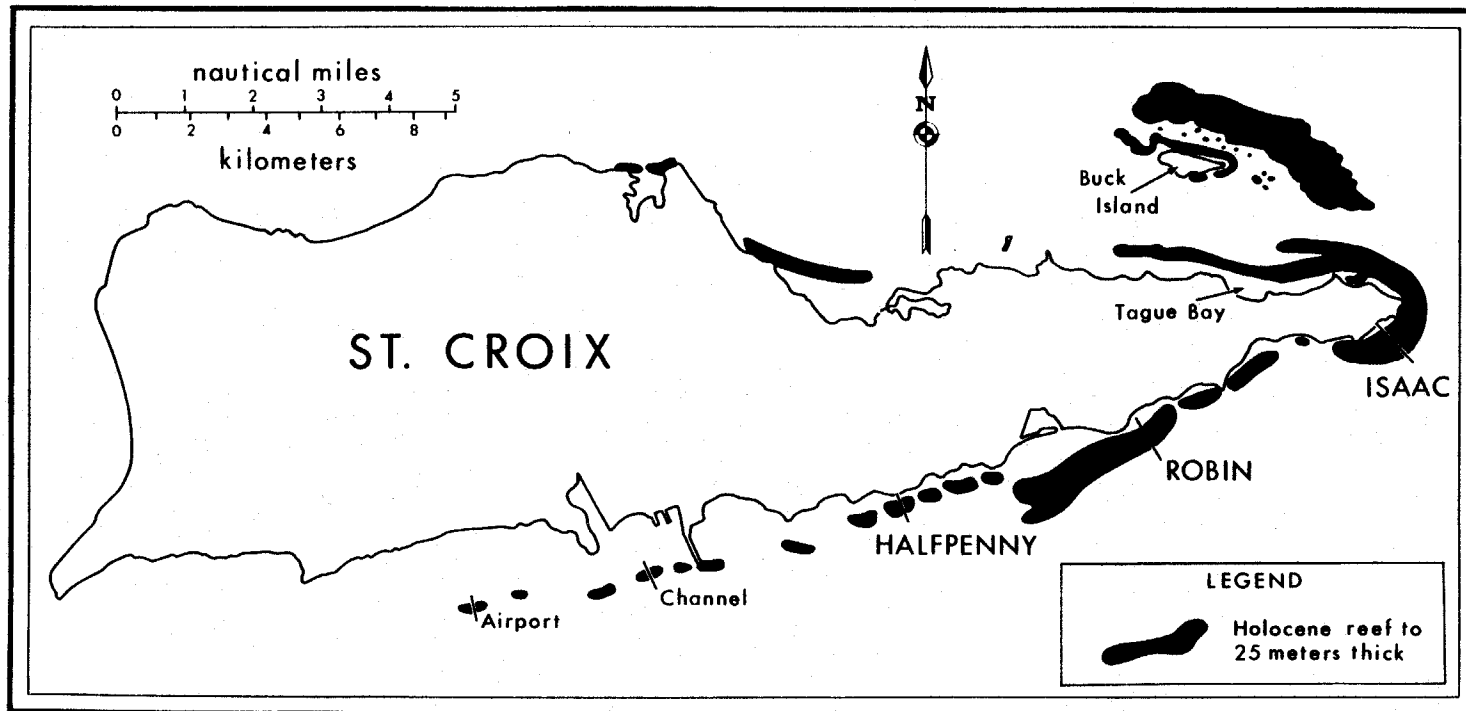
Figure 1.--Locations of transects across bank barrier reefs studied on the south shore of St. Croix, U.S. Virgin Islands, northeastern Caribbean.

BACK REEF

CREST

FORE REEF

4   3   2   1

DEPTH IN METERS

0

2

4

6

8

10

REEF	ZONES		
	4-3	3-2	2-1
ISAAC	48	125	287
ROBIN	47	70	203
HALFPENNY	62	95	138

Millepora

Acropora palmata
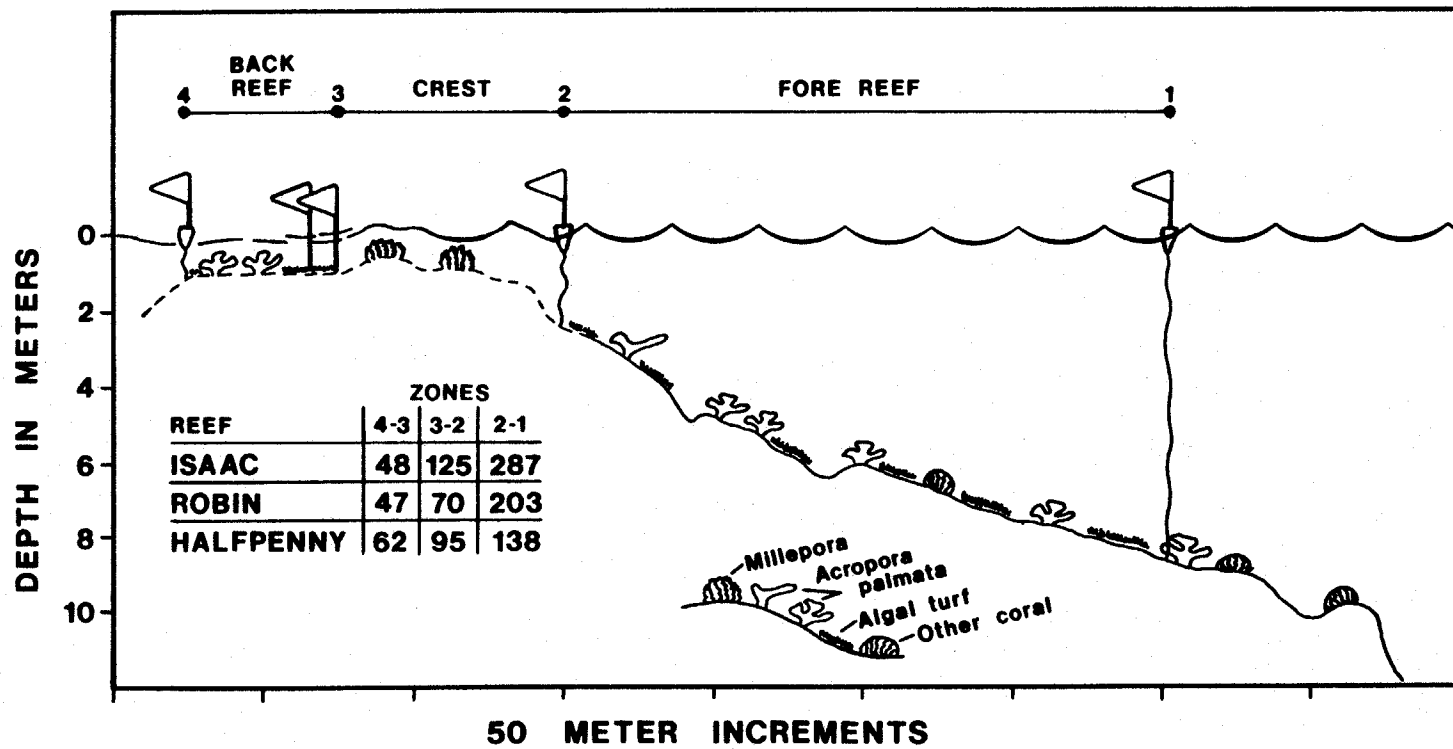
Algal turf

Other coral

50 METER INCREMENTS

Figure 2.--Typical reef transects (Robin Reef).

Diurnal measurements of changes in oxygen concentration and water flow were taken in all seasons of the year and were used to derive rates of community oxygen production (which reflect net or apparent productivity) and consumption (respiration). Accurate measurements of discharge rates (rate of water volume flow) are crucial to this upstream/downstream method. For this, we used a Marsh-McBirney model 527 electromagnetic, x-y current meter. Water samples were taken at each transect every 2 hr over a 2- to 3-day period during each season. Particular care was taken to maximize the level of precision at every step of analysis (see Adey, et al., 1981). A plot of a typical diurnal cycle of oxygen concentration at the Robin Bay site is shown in figure 3. Standard methods of calculating production in upstream-downstream methods were employed (Marsh and Smith, 1978). Computer plotting and integration of the area under the curve above the zero oxygen production level provided net daytime primary productivity values. The area below the zero line provided respiration values.

The biotic composition (percent cover) and surface area of these reefs were determined with chain transects (methods detailed in Rogers, et al., 1982). We measured all surfaces along each transect that we could reach, except for truly cryptic habitats (nearly devoid of light). This method also gave a measure of surface area per projected square meter of bottom [m^2/m^2, called a surface area ratio (SAR)].

To examine community structure of algal covered surfaces, random Acropora palmata substrate samples were collected from both fore and back reef zones. Algal cover and distribution on the surface were mapped using grids with 1 cm squares placed over the top and bottom surfaces. Algal turfs were subsampled by scraping from 3-12 visually representative, but distinct, 1 cm^2 microquadrats. Each sample included the upper millimeter of calcium carbonate in order to sample endolithic, crustose, and tightly adherent algae. Solutions of 5% HCl and 5% formalin were used to decalcify and fix the samples. A representative subsample of the scraped algal turf samples was spread in a monolayer over a microscope slide. Species composition of algal turf communities was quantified using a "point count" technique. This involved counting the number of times identifiable algae crossed points of intersection on an ocular grid placed within a compound microscope.

At each of the reef study sites, water samples were collected and analyzed for nutrients at the beginning and end of each field session, between 1000 and 1400 hr. Standard precision handling techniques were employed at every stage, and analyses for nitrate, nitrite, phosphate, and total dissolved phosphorus were accomplished with a Beckman DU spectrophotometer. Extensive descriptions of methods and data taken during the course of this study appear in Adey, et al. (1981).

RESULTS AND DISCUSSION

Reef Productivity

The reefs studied were highly productive. Community metabolism, as shown by mean diel oxygen production at each station, and seasonal metabolism at all stations is given in figures 4 and 5. Gross primary productivity (GPP), net
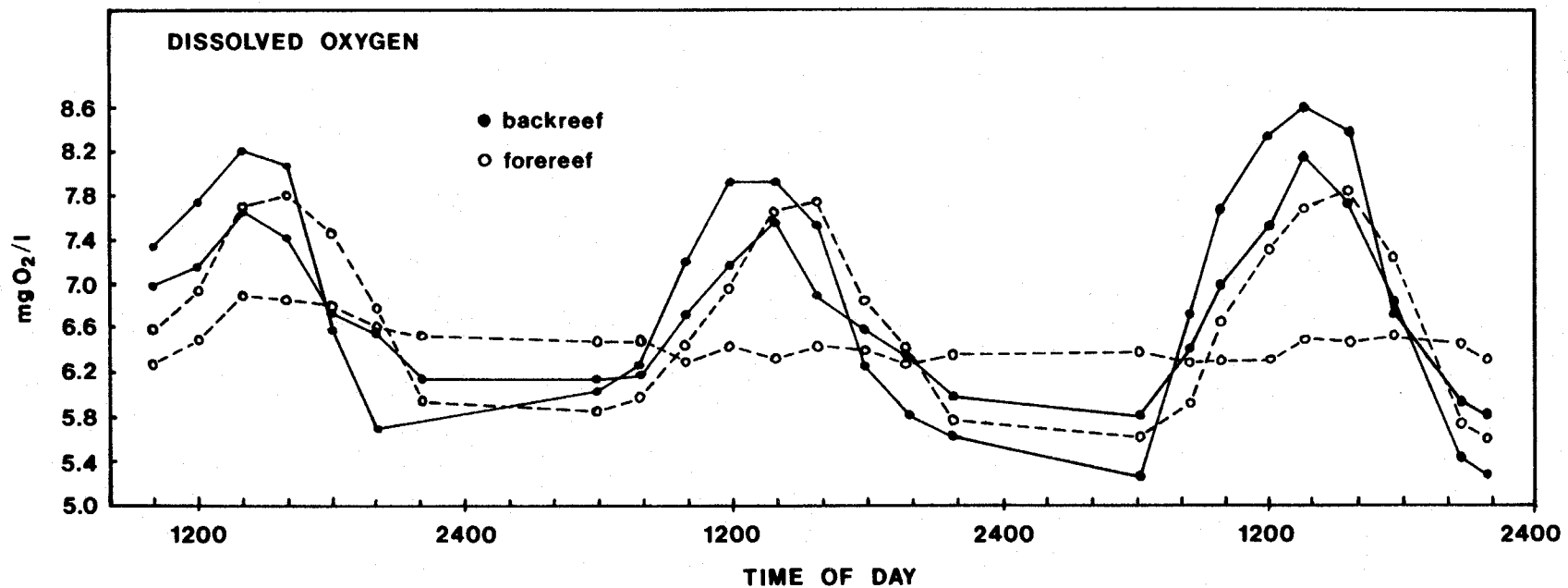
Figure 3.--Dissolved oxygen concentration across Robin Reef from 1/21/78 to 1/23/78. Numbers on individual plots refer to standard reef sites.
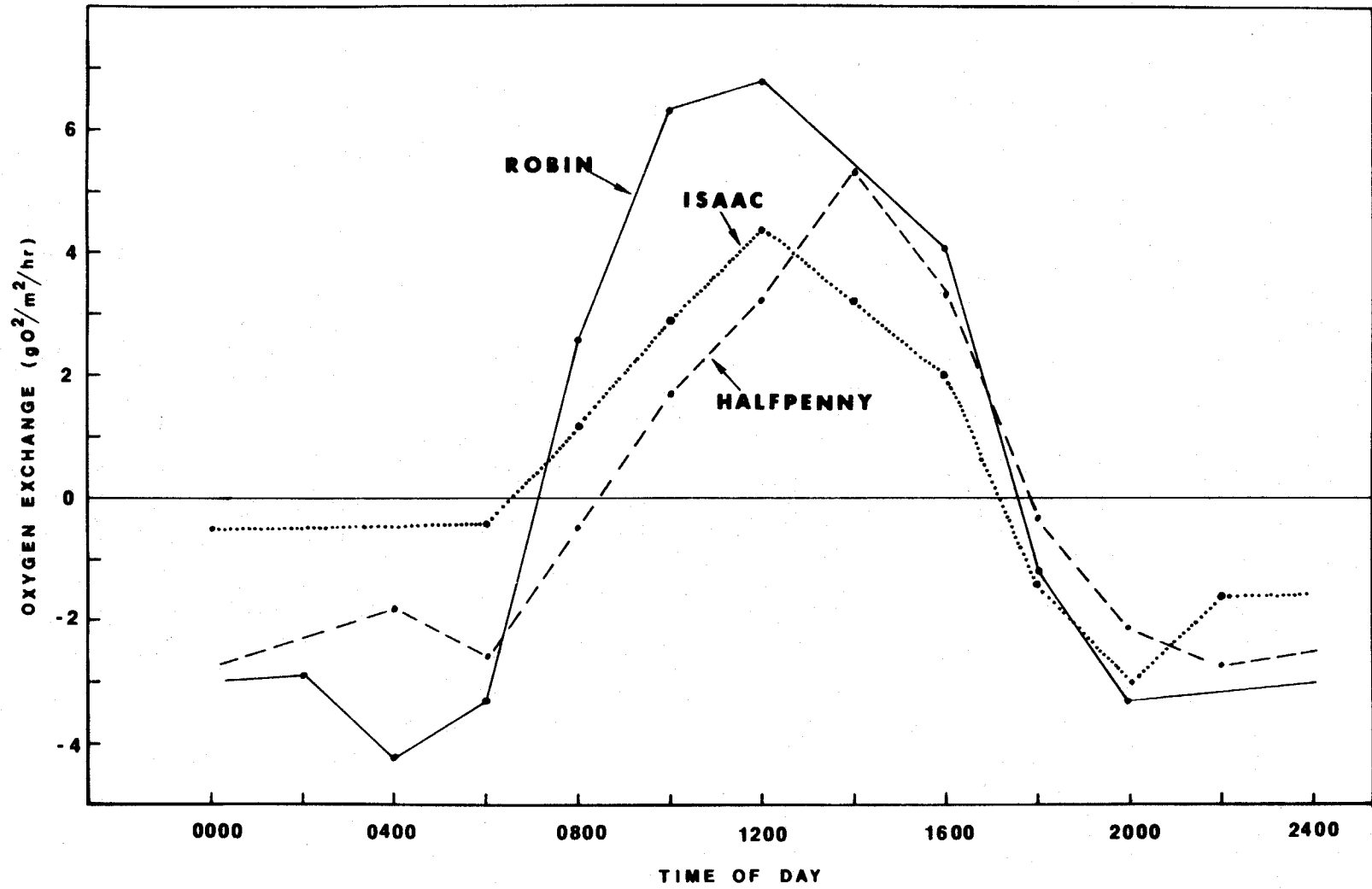
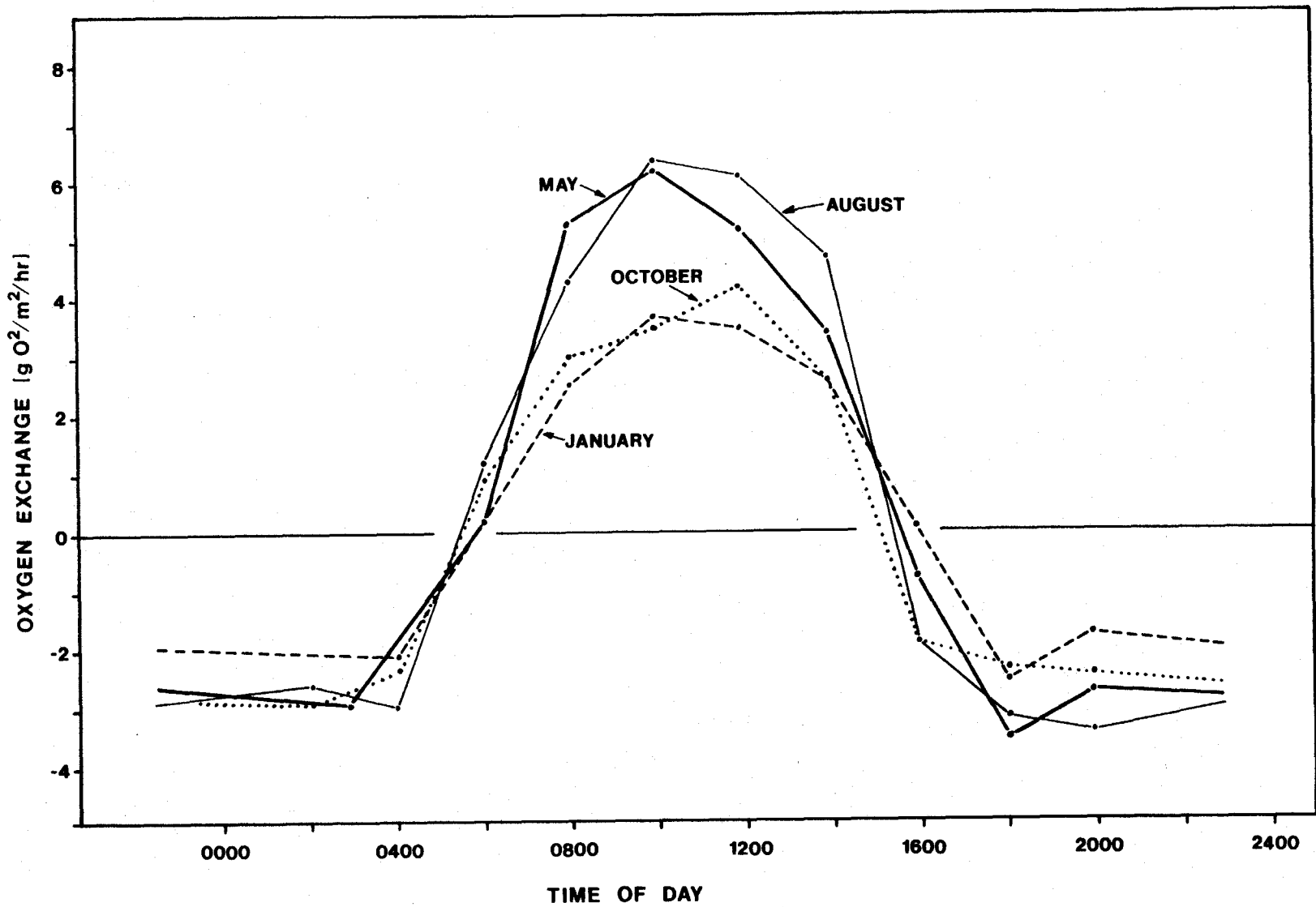Figure 4.--Mean yearly diurnal oxygen exchange for the reef transects.

Figure 5.--Mean seasonal diurnal oxygen exchange: summary of all transects.

Table 1.--Summaries of daily metabolism.

		Gross Primary Productivity (gO$_2$/m^2/day)			Net Community Primary Productivity (gO$_2$/m^2/day)				Respiration (-) (gO$_2$/m^2/hr)	
		Fore	Back	Means	Fore	Means	Back	Means	Fore	Back
Isaacs	Jan.	10.02	36.5		6.1		23.0		0.4	1.4
	May	17.4	48.9		9.3		32.7		0.8	1.6
	Aug.	12.4	57.6	46.7	6.6	8.4	29.1	27.5	0.6	2.8
	Oct.	13.8	43.7		11.5		25.2		0.2	1.8
Robin	Jan.	14.3	56.2		9.2		28.7		0.5	2.8
	May	15.2	109.0		10.6		72.4		0.5	3.7
	Aug.	18.3	115.3	88.4	15.0	10.5	78.9	55.7	0.3	3.6
	Oct.	14.6	72.9		7.2		41.0		0.7	3.2
Halfpenny	Jan.	17.3	40.2		10.9		22.0		0.6	1.8
	May	20.4	59.8		8.1		32.0		1.2	2.8
	Aug.	17.6	64.7	50.9	3.6	7.9	32.7	26.3	1.4	3.2
	Oct.	17.5	38.8		9.2		18.5		0.8	2.02

daytime primary productivity (NPP), and respiration (R) for each reef at each season appear in table 1. Back reefs are more productive than fore reefs. A mean annual GPP of about 17.5 g C/m^2/d is recorded at Isaac Reef, 19 g C/m^2/d at Halfpenny Reef, and 33 g C/m^2/d at Robin Reef (with a mean maximum value of 43.2 g C/m^2/d recorded in August and a mean all-reef productivity of 8500 g C/m^2/yr). These values are based on a conversion ratio of 0.375 g C/gO$_2$ with a metabolic quotient for reefs of 1.1 (Marsh and Smith, 1978) applied to the means in table

1. They are derived from the molecular weight difference and the ratio of oxygen to carbon dioxide exchange (the metabolic quotient) for reefs (Marsh and Smith, 1978). Higher GPP have been reported (Helfrich and Townsley, 1963; Connor and Adey, 1977), but such high levels of productivity have been subject to question. Because of this, great care was taken in data collection, and every potentially error-producing factor has been carefuly considered (see Adey, et al., 1981). The patterns we observed are not surprising once the processes affecting reef productivity are examined.

Processes Affecting Reef Productivity

Rates of carbon fixation on reefs reflect a complex interaction of environmental factors. Slight variations in some of these factors (water depth, biotic composition, substrate availability, or solar radiation) will affect these values. In the remaining sections of this paper, we will describe the results of our studies of biological, chemical, physical, and geological factors as they affect overall reef productivity.

Biological Components: The Role of Algal Turfs

Benthic algae, as both free-living forms and endosymbionts in coral and other invertebrates, are the primary producers on reefs. The focus of our study was on free-living benthic algae because it was the most abundant biological component of the reefs we studied (see table 2). Large-scale and small-scale data were integrated to determine community structure. Large-scale cover was based on chain transects and is presented as a measure of reef complexity (SAR) for the fore and back reef of each transect in table 2. Small-scale cover is based on point counts of prepared microscope slides (table 3).

To test the hypothesis that algal turfs are the most important primary producers of the St. Croix reefs, we compared rates of turf biomass production with rates of flow respiratory production. To make such a comparison, several conversions are necessary to obtain common units of measure. All conversions involve values from either table 1 or 2, or from published literature for a similar environment. Values for each back reef will be reported in east to west order (i.e., Isaac, Robin, and Halfpenny Reefs, respectively). Algal NPP was calculated from community GPP values (table 1) by multiplying by 0.24, which is the mean NPP/GPP ratio derived from chamber studies of algae by Wanders and Wanders-Faber (1974) and Rogers and Salesky (1981). The resulting algal NPP values for back reefs are 11.2, 21.2, and 12.2 g $O_2/m^2/d$. To equate our projected m^2 of a complex reef to a surface rather than a projected area, we divided by the SAR (table 2). This gave values of 4.1, 7.1, and 9.9 g $O_2/(surface)/m^2/d$. Assuming that all productivity was from algal turfs, we divided the surface production values by the proportion of turf in the back reef (table 2) (values of 15.8, 19.7, and 18.5 g $O_2/(planar)$ m^2/d. Oxygen production was converted to carbon production by multiplying by the difference in molecular weight (0.375) and dividing by the photosynthetic quotient for reefs (1.1) (Smith and Marsh, 1978), giving values of 5.4, 6.7, and 6.3 g $C/(surface)$ m^2/d. The conversion of carbon to organic matter involves the ratio of 2.2 dry wt/g C (Westlake, 1963, and confirmed by our carbon analysis of

Table 2.--Mean depth, major benthic components (% cover), and surface area ratio on chain transects.

	Mean Depth	Acropora palmata	Other Corals	Millepora	Corallines	Algal Turf	Macro-Algae	Sand	# (m)	Surface Area Ratio
Fore Reefs										
Isaacs	6.3	18.9	7.2	5.1	8.4	40.1	10.1	8.2	16	1.87
Robin	5.1	16.2	1.5	0	8.2	65.1	0	0	13	2.36
Halfpenny	4.5	10.3	9.2	11.2	16.2	9.9	8.6	35.0	14	2.51
Back Reefs										
Isaacs	0.9	65.9	0.8	0	1.9	25.9	5.7	0	6	2.70
Robin	0.7	19.7	0	0.6	6.5	36.1	10.1	26.7	10	2.98
Halfpenny	0.3	0	8.2	0	0	53.5	8.4	29.9	25	1.23

St. Croix turfs). This means that the rates of organic matter production of 10.0, 14.7, and 13.9 g (dry)/m^2/d on actual reef surfaces (rather than projected area) are necessary to produce the rate of oxygen production we observed in the water flowing over reefs.

Tests of these theoretical rates of biomass production were supported in a recent study in similar lagoon and back reef environments of Mayaguana in the Bahamas (Adey and Goertemiller, in ms.). By harvesting algal turfs grown on screens, actual biomass production was found to be 6-18 g (dry)/m^2/d. A mean rate of 12 g (dry)/m^2/d, under a nutrient regime of 0.10-0.13 microgram-at N/1 (NO_2 + NO_3) (D'Elia, in prep.), was achieved. A similar and more recent study at Grand Turk, Turk, and Caicos Islands (Peyton, et al., in prep.) gave rates of algal turf production of up to 31.8 g (dry)/m^2/d at nutrient concentrations (as measured by NO_2 + NO_3 nitrogen) of less than 0.2 microgram-at N/l. Steneck and Porter (in prep.) used a similar harvest technique for turfs growing on slabs of coral substrata at a depth of 10 m and found a production rate of 6.0 g (dry)/m^2/d. These harvest production rates are minimal since they do not include losses to micro-herbivores, abrasion, leaking of dissolved organics, or the release of reproductive structures. Thus, the values we obtained using upstream/downstream flow respirometry correspond well with measured rates of biomass produced by this "functional group" of algae (sensu Steneck and Watling, 1982) in the Caribbean. This also supports the pattern of high rates of production (per unit biomass) for turf algae that have a high surface area to volume ratio (Odum, et al., 1958; Littler, et al., 1983) and, perhaps equally important, live in a strong wave surge environment.

Table 3.--Dominant algal turf genera and abundance as determined by point counts (% mean abundance top and bottom of samples). Data were generated at the species level and are in Adey, et al. (1981).

		Mean	Isaac	Robin	Halfpenny
Fore Reef	Non-Heterocysted Blue Greens	10.7	9.5	12.7	10.1
	Heterocysted Blue Greens	7.3	14.6	5.1	2.2
	Sphacelaria spp.	7.2	7.3	11.8	2.7
	Endolithic algae	7.1	7.1	5.1	9.1
	Polysiphonia spp.	3.9	2.6	3.1	6.0
	Taenioma sp.	3.8	0.7	2.1	1.0
	Herposiphonia spp.	4.4	2.1	3.6	7.7
	Lobophora sp.	2.7	3.7	4.4	0
	Jania spp.	2.5	2.4	4.2	1.0
Back Reef	Non-Heterocysted Blue Greens	18.9	18.0	20.0	18.5
	Jania spp.	10.8	8.0	18.7	5.8
	Amphiroa spp.	10.3	13.4	14.5	3.2
	Endolithic algae	3.7	2.7	0	8.5
	Gelidiopsis sp.	2.1	3.8	2.0	0.4
	Asparagopsis (Falkenbergia stage)	1.6	0.6	3.9	0.2
	Heterocysted Blue Greens	1.5	3.7	0.3	0.5
	Sphacelaria spp.	0.8	2.2	0.4	0

We found over 100 species of algae (mostly in turfs) in the course of this study. Of these, only 30-50 species were common throughout the year, and fewer than 10 were common at any site in a given season (table 3). The most consistent elements on (and in) the upper surfaces of dead coral substrata were cyanobacteria, boring algae, and filamentous red and brown algae. A high

diversity of algae in low abundance was recorded on virtually every specimen regardless of season, reef, or zone.

Cyanobacteria of 6-8 species formed a large part of the turf biomass on both fore and back reefs. Heterocysted species (particularly Calothrix spp.) are far more abundant in fore reefs than back reefs, but nonheterocysted species (e.g., Oscillatoria) were most abundant overall. Of eukaryotic filamentous algae, the brown (Sphacelaria spp.) and red (Polysiphonia spp., Herposiphonia spp., and Taenioma macrourum) species dominate fore reef substrates. Boring filaments (usually green algae, e.g., Ostreobium) were also ubiquitous. The predominant macroalgae are calcareous, articulated red algae (e.g., Jania capillacea and Amphiroa fragilissima) which are found on bottom surfaces in the fore reef and on both top and bottom surfaces in back reefs. Crustose corallines (Porolithon pachydermum and Neogoniolithon megacarpum) were most abundant in the shallow fore reefs, particularly where grazing is intense. Of the fleshy macroalgae, Lobophora variegata and Acanthophora spicifera were found but they were not abundant compared to the turf community. Minute macrophytes such as Gelidiella trinitatensis and Gelidium pusillum commonly were found in the turfs of the back reef.

As shown in table 3, the differences between fore reef and back reef turf community structure along the St. Croix reef track are rather consistent. These numbers and the community structure of the turf species we found agree with that found on a reef in Curacao by Van den Hoek, et al. (1975). With the exception of Lobophora variegata (which does not appear in Van den Hoek, et al., 1975, for Curacao) and Dictyota dichotoma (which was common in Curacao but not in St. Croix), the floras for Curacao and St. Croix are quite similar. There are also floristic similarities for the same reef zones between the Caribbean and Indo-Pacific at the genus level (Hatcher and Larkum, 1983; Sammarco, 1983).

It is beyond the scope of this study to examine the myriad of factors maintaining turf algal community structure. Most studies indicate that intensive herbivory in productive environments is important for maintaining a turf community (Borowitzka, 1981; Carpenter, 1981; Littler, et al., 1983; Sammarco, 1983; Hatcher and Larkum, 1983).

Primary Production: Not Nutrient Limited

High primary productivity on reefs growing in nutrient poor water has received considerable scientific attention (reviewed by Mann, 1982). The resulting research has focused on the role of cyanobacteria as in situ nitrogen fixing organisms (Mague and Holm-Hansen, 1975; Capone, et al., 1977). Recently, Sammarco (1983) demonstrated that fish grazing on the Great Barrier Reef can cause a shift in the community structure of turf algae from filamentous reds (e.g., Polysiphonia) to minute filamentous cyanobacteria. Other studies have demonstrated that, as a result of this change in community structure, nitrogen fixation is significantly enhanced (Wilkinson and Sammarco, 1983). Our results support their conclusions.

Heterocysted (nostocacean) and nonheterocysted (hormogonalean) cyanobacteria are abundant in turfs growing on the upper surfaces of all reefs that we

Table 4.--Nutrient levels. Each value is a mean of two replicates taken on different days over approximately a 10-day period.

Nitrate + Nitrite (ug-at/1 - N as $NO_3 = NO_2$)

		Jan	May	Aug	Oct	Yearly Mean
Isaac	Fore	0.386	X	0.345	X	0.366
	Back	0.980	0.302	0.391	.772	0.611
Robin	Fore	0.294	0.175	0.549	.075	0.273
	Back	1.016	0.328	0.589	.220	0.538
Halfpenny	Fore	0.340	X	0.823	.107	0.423
	Back	0.650	0.629	0.816	.099	0.549
Channel	Fore			0.457	.150	
	Back			0.686	.130	
Airport	Fore	0.223	0.228	X	.050	0.167
	Back	0.466	0.350	X	.130	0.315
						Grand Mean
Means	Fore	0.311	0.134	.572	0.096	0.283
	Back	0.778	0.401	.599	0.270	0.512

Phosphate (ug-at/1 - P)

		Jan	May	Aug	Oct	Yearly Mean
Isaacs	Fore	0.024		0.118	0.032	0.058
	Back	0.046		0.020	0.038	0.035
Robin	Fore	0.010		0.055	0.187	0.084
	Back	0.037		X	0.047	0.042
Halfpenny	Fore	0.010		0.275	0.049	0.111
	Back	0.034		0.392	0.161	0.196
Channel	Fore				0.080	
	Back				0.030	
Airport	Fore	0.010		0.145	0.052	0.138
	Back	0.017		0.165	0.143	0.108
Means	Fore	0.013		0.148	0.080	
	Back	0.033		0.192	0.084	

studied, but particularly on fore reef and sand substratum habitats of Isaac
Reef. Results of nutrient analyses for nitrate plus nitrite and phosphate are
listed in table 4. The nitrite and nitrate concentration strongly increases in
the water as it flows over the three reefs studied. Ten of the twelve sets of
measurements showed a highly significant yearly increase of 0.35-0.57 microgram-
at/1 across the reef. With a mean yearly flow rate of 6.83 m^3/min/m for all
three transects (discussed below), this translates to a net "fertilization
rate" of 0.82 kg N/hectare/d (or 0.08 g N/m^2/d). While this is roughly half the
rate estimated by Wieb, et al. (1975) for Eniwetak, the maximum rates we
encountered on the south shore reef of St. Croix were three times the mean.

We assume that this fertilization is due to nitrogen fixation by cyanobacteria
(Wilkinson and Sammarco, 1983), but other possibilities exist. Regeneration of
nutrients from the internal cavity of a reef was demonstrated by Andrews and
Muller (1983). However, this is unlikely to occur on St. Croix reefs, since
the coral of these reefs grows on a pavement, below which the reef structure is
remarkably tight, with cavities usually sand filled (Adey, 1975; Adey and Burke,
1976). Empty cavities for nutrient regeneration are rare in St. Croix, which
is arid, devoid of rivers, and lacking in upwelling aquifers. Thus, nutrient
enrichment from ground water, such as that described in Jamaica (D'Elia, et
al., 1981) is unlikely. Nitrogen fixing algae may achieve a competitive advan-
tage in more oligotrophic waters, and thus nutrient availability probably has
some significance in determining community structure. Nevertheless, the
fact that this "excess" nitrogen escapes from the reef and flows over the highly
productive back reef suggests that primary production on the reef proper is
not nitrogen limited.

Phosphorus is more problematic, since an atmospheric source is not possible.
Reactive phosphorus as phosphate can be difficult to measure and, as briefly
discussed above, older work did not generally show any consistent pattern of
change in reef environments. A recent paper by Atkinson (1982) does show
significant upstream-downstream depletion of phosphate across 1000 m of reef
flat in Hawaii. However, in our St. Croix situation, with a mean incoming
concentration of 0.084 microgram-at/1 and a mean current flow of 6.83 m^3/min/m,
phosphorus as phosphate is delivered to a meter width transect of reef at a
rate of about 25 g/d. Even if all net primary productivity were to be exported
from these reefs, using a C/P of 430 (from Atkinson and Smith, 1983, for turfs),
only about 6.4 g P/d/meter width would be removed. Thus, phosphorus is present
in large quantities, though at low concentrations, from the constantly inflowing
waters of the North Equatorial Current as it impinges on St. Croix.

Epibenthic Water Flow and Discharge Rates

Nutrient availability, gas exchange, and metabolite release for aquatic
primary producers is facilitated by water flow past algal thalli. Water flow
over reef substrata (epibenthic water flow) is dependent upon the discharge
rate (movement rate per volume of water), water depth, and on the wave surge or
oscillation rate of the overflowing water. In St. Croix, water movement over
the reefs results primarily from wind-driven wave energy. Thus, measured rates
of epibenthic water flow have geologic (depth) and geographic (wind) components.

Epibenthic flow rates over reefs are variable in space and time. These
variations can affect both the productivity of the reef and the measurements of

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it. For these reasons, great care was taken in determining water flow and discharge rates (this information is provided in detail by Adey, et al., 1981). Our measurements of water motion demonstrate that water flowing over the reefs oscillates but has a net shoreward flow. Typically, we recorded a landward surge of 6-8 s duration (reaching speeds of about 0.3-0.6 m/s) and a reverse surge lasting 2-4 s (reaching 0.05-0.3 m/s). Net epibenthic water flow was determined from chart recordings of mean maximum currents in both directions (i.e., the peaks of spikes) integrated over 1 hr intervals from Marsh-McBirney current meter data. Reversing wave surges and accompanying turbulence produced by waves breaking over irregular reef surfaces mix the water flowing over the reef, particularly for back reef habitats where measured rates of production are the greatest. The turbulent effect of wave surges also significantly increases metabolite exchange and resulting photosynthesis and growth (Hackney, et al., in ms.).

Epibenthic flow rates increase dramatically from fore to back reef. Means for all reef transects were 1.2 + 0.066 m/min for fore reefs and 11.0 + 3.5 m/min for back reefs. This increased flow rate results from the progressive shallowing from fore reef (overall mean depth of 5.3 m) to back reef (overall mean depth of 0.6 m). With a constant discharge rate, flow rate varies with depth. Since depth changes daily with tidal changes, we recorded tidal heights during each sampling period.

Discharge rates are not constant because wind-induced water movements change geographically along the south shore of St. Croix due to the island's effect of diminishing the strength of easterly trade winds. Specifically, in the fore reef environments, Isaacs Reef to the east has the highest discharge rate (mean 8.1 m^3/min/m, range 2.5-12.1 m^3/min/m, N = 65 1 hr intervals). Robin Reef is intermediate (mean 6.2 m^3/min/m, range 2.8-9.8 m^3/min/m, N = 86 1 hr intervals), and Halfpenny Reef is the lowest (mean 5.3 m^3/min/m, range 1.4-9.8 m^3/min/m, N = 79 1 hr intervals). These discharge rates created mean back reef epibenthic flow rates of 9.2, 8.8, and 15 m/min/m, respectively. Although a geological pattern in exposure from east (most exposed) to west (least exposed) results in a similar pattern of decreased discharge rates, the magnitude is much less than the difference observed between back reef and fore reef at any one location.

There is little support for the hypothesis that reef productivity is controlled by water motion even though differences in flow rates between fore and back reefs roughly correspond with differences in rates of production. If reef productivity was primarily dependent upon water flow, diurnal reef productivity curves (figs. 4 and 5) would level off at the point where light saturation occurred rather than corresponding closely with variations in light intensity (discussed below). Also, for any given reef, productivity would correspond with data on water currents, which we did not observe. Water motion is an important factor, but the south shore of St. Croix is characterized by consistently high wind-induced wave energy year round (see Adey, 1978b); thus, water motion does not appear to limit productivity. Note that there is no relationship between reef productivity (table 1) and epibenthic flow rates.

Light

Primary production on the reefs we studied is most likely controlled by light. Evidence for this comes from the correspondence between diurnal and seasonal cycles in light intensity (fig. 6) and measured rates of primary
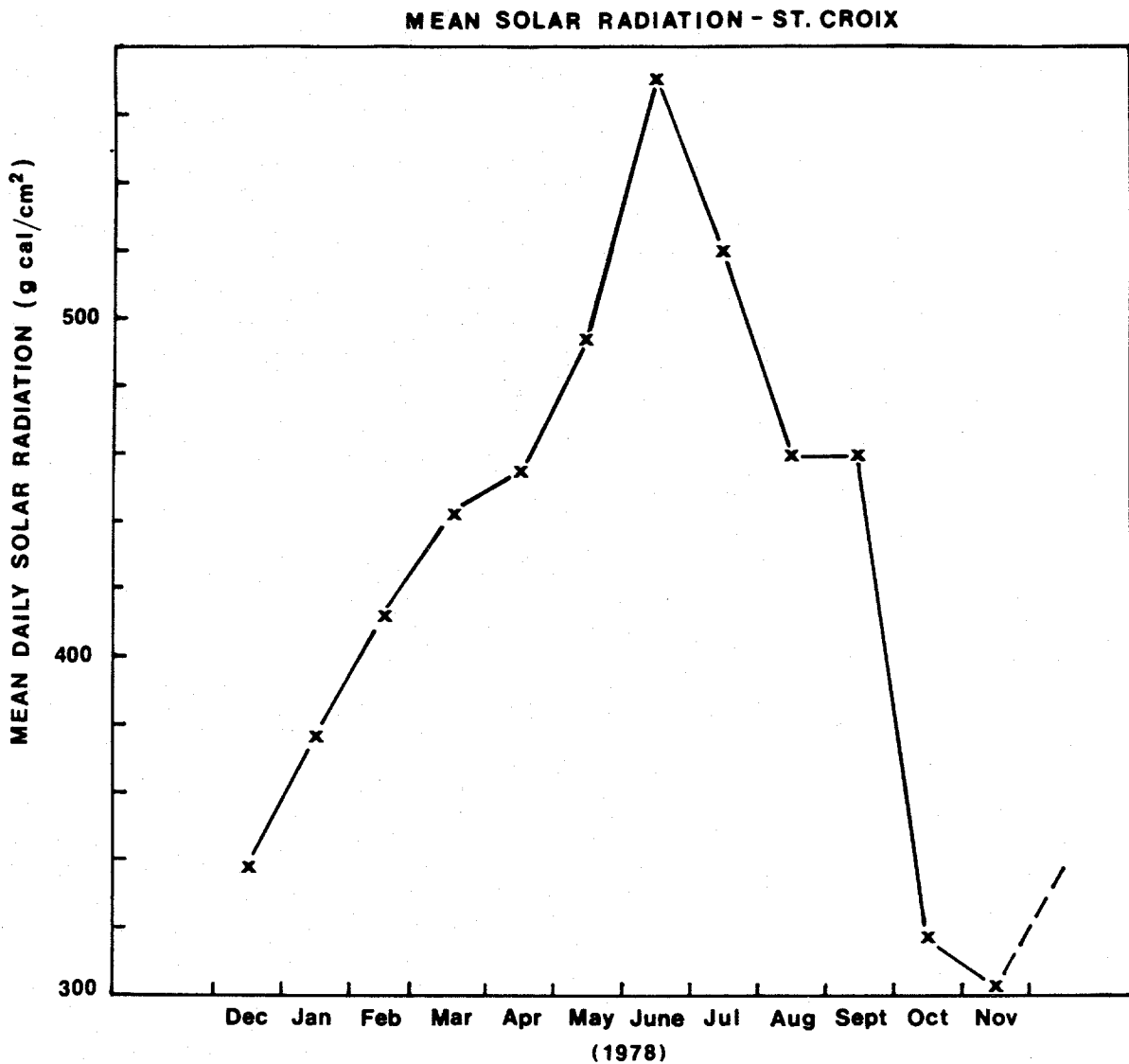
MEAN SOLAR RADIATION - ST. CROIX

Figure 6.--Monthly means of daily solar radiation.

production (figs. 3, 4, and 5). If any other environmental factor was limiting, the rate of oxygen production would level off, indicating light saturation. In contrast to our field measurements, most studies using enclosures, even with stirring, commonly report light saturation. This is likely an artifact of insufficient water motion. In more recent work with chambers (e.g., Carpenter, in ms.), where efforts have been made to simulate surge motion, this lack of light saturation for algal turfs is repeatedly demonstrated.

In this investigation, daily solar radiation levels were recorded with a pyroheliometer (see fig. 6 for monthly mean values). During our study we sampled two periods of high light intensity (May and August) and two periods of lower light intensity (January and October). Averaging hourly production rates

GROSS PRIMARY PRODUCTIVITY (ALGAE)
[gm O$_2$/m^2 · day]

100

80

60

40

20

0

May 520
430 annual mean (g cal/cm^2)
470 ROBIN
Aug
Jan 376
HALFPENNY
Oct 310
daily solar radiation – seasonal mean
ISAAC

Ⓧ annual mean – individual reef
● seasonal mean – all reefs

200   400   600   800   1000

TOTAL ALGAL BIOMASS [AREA x SAR. x BIOM.]
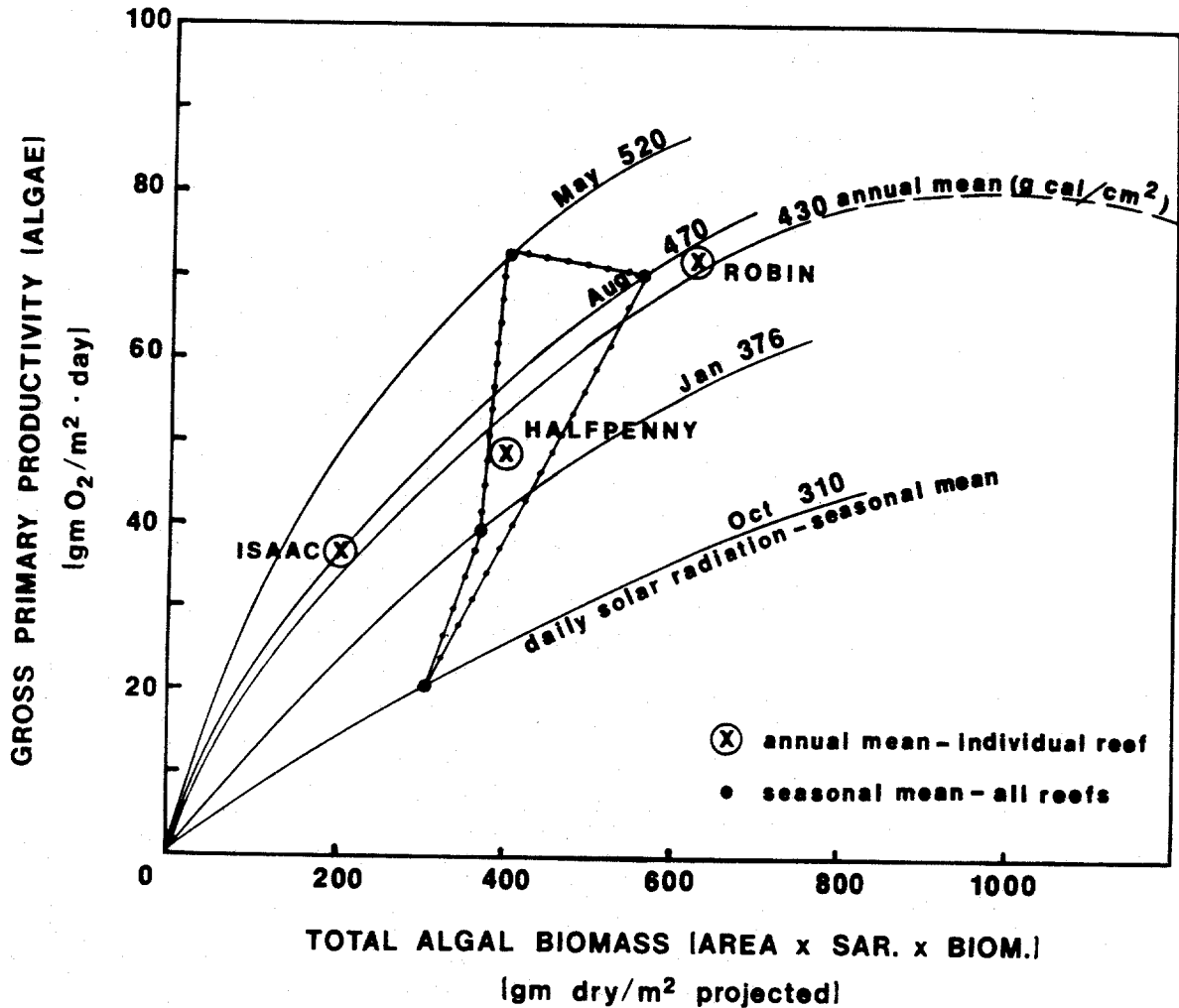
[gm dry/m^2 projected]

Figure 7.--Back reef: Gross primary productivity as a function of total algal
biomass and monthly solar radiation

for all reefs reveals a strong seasonal pattern in productivity corresponding
to these seasonal differences in light intensity (fig. 5). Although the seasonal
decrease in primary productivity roughly corresponds to a 40% reduction in
light during that period, the relationship is not exact, since the GPP in October
is reduced to only 30% of that value in May. A better correspondence exists
between the seasonality of primary production and the combination of algal
biomass and solar radiation. Loss of light in autumn is exacerbated on St.
Croix by a higher frequency of rainfall and cloudiness. Thus, incoming light
in October and November is considerably below that of December and January
(fig. 6).

The GPP data, when plotted directly against total algal biomass (per
projected m^2, fig. 7), suggests that a weak relationship between productivity
and total biomass exists on these reefs (note that this is not surface biomass
alone, but includes the effects of SAR and percent cover of algae). Also, the

plot of biomass as a function of seasonal productivity (line with closed circles, fig. 7) indicates a cyclic pattern. The sharp reduction in algal biomass recorded in the fall of 1978 (45% of that recorded in May) cannot be attributed to wave action, since that is generally a quiet season and no unusual conditions were experienced during the period of study. Data for nutrients (table 4) and suspended matter (Adey, et al., 1981) suggest very minimal effects of runoff on the reefs. We observed, but did not quantify, changes in the abundance of micrograzers (amphipods and worms). It is possible that during the spring and summer algal biomass and the resident micrograzers increase with higher levels of solar radiation. As light levels fall in autumn, grazing by the resident micrograzers exceeds rates of algal growth. Such overgrazing could result in a "crash" in both algal biomass and productivity.

Geological Control of Reef Productivity: Synergy of Multiple Factors

It is to be expected that those reefs which are less complex (lower SAR), deeper, with lower epibenthic water currents, and have a larger percentage of living stony coral (relative to algae) will be less productive than the shallow, complex, algae-dominated reefs of the south shore of St. Croix. All of these factors, however, are ultimately the result of the reef's geological history, and thus the relationship between reef morphogenesis and primary production should be considered.

The south shore bank barrier reef system of St. Croix "matured" (i.e., reached sea level) from west to east (see Adey, 1975; Adey and Burke, 1976, for a summary of the geological history of the reefs of St. Croix). Isaac Reef is relatively young and is just reaching sea level today. Its live Acropora palmata cover is high (table 2), but its reef flats are narrow and the crest is broken (forming numerous channels). Robin Reef is more mature, as evidenced by its nearly continuous crest and wide, relatively shallow back reef. While living Acropora palmata is still an important constituent, the percent cover of A. palmata on Robin back reef is less than a third of that found on Isaac back reef (table 2). Halfpenny Reef is older and has a continuous crest and a very shallow reef flat with very few living acroporids. The age difference between Isaacs and Halfpenny Reefs is about 500-1,000 yr.

Productivity on the young Isaac Reef is low, even though its SAR is quite high. This is because coral is less productive than algae per unit of surface area (Rogers and Salesky, 1981). At the other extreme, coral cover is low at Halfpenny Reef, and this shallow reef flat is dominated by turf algae. However, this reef is nearly planar (the SAR is half that of the other reefs), and thus the surface area available for turf photosynthesis is proportionately reduced.

Because carnivorous predators are so abundant on reefs, herbivores do not stray far from their refuge in the spaces within the reef (e.g., Ogden, et al., 1973; Talbot and Goldman, 1972). Thus, reefs with a high SAR are more heavily grazed because they have more habitat space for reef-dwelling herbivores. In this way, geological events that contribute to a high SAR on reefs also maintain herbivore populations that intensely graze the dead coral substrate, thereby maintaining the turf communities.

Light levels, depth, current velocity, and abundance of live Acropora palmata all increase with geological time as a reef grows toward sea level. As it reaches the surface, several of these trends reverse (i.e., coral dies and water flow decreases). Aspects of this complex relationship between reef morphogenesis and primary productivity can be seen along the south shore of St. Croix. For example, productivity was greatest for the mature Robin Reef and lower on the younger Isaacs and older Halfpenny Reefs (fig. 7). On Robin Reef, the SAR of primarily dead Acropora palmata is very high and algal cover is about 80% greater than that of Halfpenny. Thus, peak productivity probably occurs soon after the transition from a live, coral-dominated reef to one of equal surface area but dominated by algae. With time, productivity declines as destructive forces (e.g., bioeroding sea urchins or severe storms) reduce the standing dead coral to a pavement-like algal-dominated flat. This pattern of reef succession is characteristic of many reef systems. Adey, et al. (1977) described a similar history for the now largely planar algal dominated pavement in eastern Martinique. Over the past 500 yr the open Acropora palmata reef matured and lost its structure, possibly due to a catastrophic event such as a hurricane. It has remained an algal pavement, devoid of coral, ever since. In the case of Martinique, excess sediment and nutrient runoff from the island following the introduction of intense sugar cane farming in the 17th century undoubtedly was a major factor in transforming these reefs into macroalgal pavements. After the completion of this study in 1978, a similar event occurred at the south shore of St. Croix when a hurricane passed off the coast in 1979. Rogers, et al. (1982) documented the event and showed a significant reduction in SAR and live coral following the hurricane.

Differences in reef morphogenesis may be responsible for some of the reported differences in reef productivity. Holocene sea level characteristics for the Indo-Pacific differs from that of the Caribbean. Sea level rise stopped over 5,000 yr ago in the Indo-Pacific (reviewed by Adey, 1978a), resulting in the characteristic old reefs of the region having emergent, broad reef flats (many km wide), often with no epibenthic water flow during low tide and with a low SAR. This extreme "old age" condition of Indo-Pacific reef flats, developed under stable or dropping sea levels, contrasts with conditions in the Caribbean, where sea level has been slowly rising until the past several centuries (e.g., Adey, et al., 1978a). This geological characteristic of reefs could be responsible for the lower levels of primary production reported for the Indo-Pacific compared to results presented here for the St. Croix reefs.

CONCLUSIONS

Fundamentally, reef productivity is controlled by its geology (reef growth and morphogenesis). Coral reefs grow slowly towards sea level over time, thereby changing their physical, chemical, and biological environment. Primary productivity is maximal at the time when the reef surface is becoming too shallow to support a large cover of live coral but still deep enough for contin-uous water flow. Dead branching coral (Acropora palmata) in standing position provides a complex and convoluted substratum on which minute algal turfs can grow and herbivores can take refuge. The structurally complex reefs maintain a high biomass per projected area of reef, thereby increasing the total turf

biomass. The intense grazing maintains the algal community at the turf stage, wherein the productivity per unit biomass is very high.

Facilitating this high productivity are nitrogen fixing cyanobacteria that fix more nitrogen than is required by even the most productive reef zones. Other nutrient requirements, particularly phosphorus, are met by the combination of continuous and strongly flowing equatorial currents as well as by constant wave-driven currents. This, with the lower phosphorus requirements of algal turfs, results in a highly productive community that is not limited by nutrient availability.

Thus, synergy is attained by the interaction of factors that optimize reef productivity. If any factor is removed from this system (i.e., water depth, SAR, wave oscillation, water flow, or algal community structure), the primary productivity would be less than we found.

The back reefs we studied are among the most productive biological communities in the world. Using standard conversions, our measurements of a mean annual gross production of about 23 g $C/m^2/d$ and a net production of about 14 g $C/m^2/d$ exceed the theoretical maximum gross productivity hypothesized by Ryther (1959) of 17 g $C/m^2/d$ and the net productivity of 12.3 g $C/m^2/d$. On the other hand, this is not unreasonable, since maximum experimental rates of net production of 22-31 g (dry)/m^2/d (approximately 9-12 g $C/m^2/d$) have now been found in both laboratory and field environments. Limitations to primary production due to desiccation, nutrient availability or gas exchange (Lieth and Whittaker, 1975) are nonexistent or of reduced importance on the reefs of St. Croix. Thus, productivity of these reefs seems to be limited by the ultimate limiting source: incoming solar radiation.

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