PRODUCTIVITY OF *ACROPORA PALMATA* (Lamarck), MACROSCOPIC ALGAE, AND ALGAL TURF FROM TAGUE BAY REEF, ST. CROIX, U.S. VIRGIN ISLANDS

Caroline S. Rogers
West Indies Laboratory
Fairleigh Dickinson University
Christiansted, St. Croix, VI 00820, U.S.A.

and

Norman H. Salesky
Department of Conservation and Cultural Affairs
Division of Natural Resources Management
Christiansted, St. Croix, VI 00820, U.S.A.

PRODUCTIVITY OF *ACROPORA PALMATA* (Lamarck), MACROSCOPIC ALGAE, AND ALGAL TURF FROM TAGUE BAY REEF, ST. CROIX, U.S. VIRGIN ISLANDS[1]

CAROLINE S. ROGERS

West Indies Laboratory, Fairleigh Dickinson University, Christiansted, St. Croix, VI 00820, U.S.A.

and

NORMAN H. SALESKY

Department of Conservation and Cultural Affairs, Division of Natural Resources Management, Christiansted, St. Croix, VI 00820, U.S.A.

Abstract: Net primary productivity and respiration of *Acropora palmata* (Lamarck) and of the algal turf and macroscopic algae growing on dead coral from Tague Bay Reef, St. Croix, were measured inside an experimental chamber. Mean productivity rates differed significantly, with macroscopic algae producing more oxygen than algal turf and turf production exceeding that of the live coral. Mean respiration of macroscopic algae was significantly higher than that for *A. palmata* and for algal turf, while *A. palmata* respiration significantly exceeded turf respiration. Net primary productivity for macroscopic algae ranged from 1.16 to 8.98 $gO_2 \cdot m^{-2} \cdot h^{-1}$ ($\bar{x} = 3.13 \pm 2.26$ SD, $n = 31$), and respiration varied from 0.19 to 0.64 ($\bar{x} = 0.44 \pm 0.13$ SD, $n = 18$). Net primary production of *A. palmata* branches ranged from 0.15 to 0.54 $gO_2 \cdot m^{-2} \cdot h^{-1}$ ($\bar{x} = 0.30 \pm 0.10$ SD, $n = 27$), while respiration ranged from 0.22 to 0.53 $gO_2 \cdot m^{-2} \cdot h^{-1}$ ($\bar{x} = 0.32 \pm 0.08$ SD, $n = 12$). Net primary productivity and respiration of algal turf was 0.23 to 0.93 $gO_2 \cdot m^{-2} \cdot h^{-1}$ ($\bar{x} = 0.50 \pm 0.16$ SD, $n = 28$) and 0.13 to 0.40 ($\bar{x} = 0.23 \pm 0.08$ SD, $n = 16$), respectively. Although less conspicuous in some reef areas than live or turf-covered *A. palmata*, macroscopic algae may represent a major part of the total primary productivity of some coral reefs.

INTRODUCTION

The shallow reefs of St. Croix, U.S. Virgin Islands, are dominated by impressive living and dead stands of *Acropora palmata* (Lamarck). The branching morphology of this coral maximizes the amount of potentially productive surface area. Dead colonies support extensive and diverse communities of benthic algae, both macroscopic and fine filamentous species. Previous studies have emphasized either the corals (Kanwisher & Wainwright, 1967; Roffman, 1968; Franzisket, 1969; Gladfelter *et al.*, 1977; Davies, 1977; McCloskey *et al.*, 1978) or the reef algae (Marsh, 1970; Doty, 1971; Littler, 1973; Wanders, 1976a,b). The present research focused on the oxygen production and respiration of all three of the major reef components, living *A. palmata*, macroscopic algae, and turf algae, from Tague Bay Reef off the north coast of St. Croix ($17°46'N : 64°36'W$). The objective was to

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quantify the relative contributions of these primary producers to total reef productivity (see Marsh, 1976).

METHODS

The net primary productivity and respiration of three major reef components, live *A. palmata*, macroscopic algae, and turf algae were studied in Tague Bay using a Plexiglas cylinder with fitted ends (Fig. 1). An 0-ring at each end created a complete
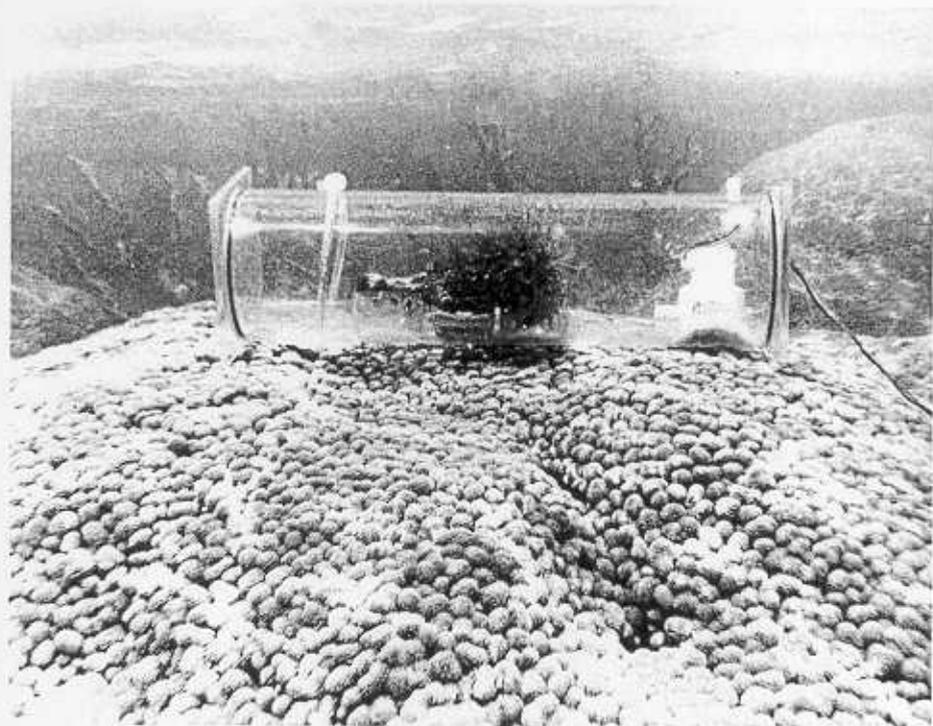
Fig. 1. Experimental chamber.

seal. The chamber had a volume of 13.5 l. A Jabsco bilge pump at one end of the chamber circulated water at the rate of 950 l/h. Gentle rocking of the chamber in the surge also produced some water movement inside the chamber. With closed chamber experiments, it is essential to have adequate circulation, high light intensities, and a small volume of water relative to the size of the sample so that detectable changes in oxygen occur within a short time interval. In this study, intervals of 5 to 15 min were short enough to prevent excessive changes in temperature and to avoid bubble formation. Over a 10-min interval, the temperature increase was 0.2 °C.

For all experiments, the chamber was placed in about 1 m of water in the backreef, usually on a mound of *Porites porites*. Oxygen consumption and production over 5- to 15-min intervals were measured using large syringes to fill BOD bottles on the boat. These samples were fixed immediately using the Winkler method (Strickland & Parsons, 1972). Initial duplicate samples were taken inside the chamber, immediately after placing the coral sample inside and snapping the ends in place, by inserting tygon tubing from the end of each syringe into a small hole in the cylinder. The hole was than stoppered. This procedure is preferable to assuming that initial O_2 concentration inside the chamber is identical to that of the surrounding water because the oxygen concentration changes very rapidly after insertion of the test sample. At the end of each run, duplicate syringe samples were taken. Duplicate water samples from the chamber were identical or within the limits of error for the Winkler method indicating that mixing with outside water did not occur.

All of the algal and coral samples were supported off the chamber bottom by short perforated sections of a Plexiglas tube. The net primary productivity and respiration measurements occurred between 1000 and 1500 h. Three to 12 replicate runs were done for each specimen.

Light was measured with a Lambda Instruments LI-185 quantum meter with the underwater sensor stationed near the chamber at the same depth. The chamber was enclosed in layers of black plastic for respiration measurements during the day. The quantum meter indicated that the black plastic eliminated all photosynthetically active radiation.

The area of live coral or of the dead coral supporting the algae was estimated by wrapping tin foil around each sample, weighing the foil, and comparing the weight to that of a standard piece of foil of known area (Marsh, 1970). Sample sizes ranged from about 775 to 2000 cm² for dead coral with turf, 80 to 650 cm² for dead coral with macroscopic algae, and 630 to 900 cm² for live *Acropora palmata*. In most cases, *A. palmata* branches were only used if they had dead bases. Some samples were broken-off live branches. Mucus secretion was not noticeable. Rates for branches with dead or live bases did not appear to differ. Flushing of the syringes between samples and of the chamber between runs was critical. All samples came from 1.5 m or less on the Tague Bay Reef and were transported under water a short distance to the chamber.

Rates for the turf and macroscopic algae samples actually represent the metabolic rates for small communities of organisms living on or inside the dead coral, although the algae are the dominant organisms in terms of cover and biomass. Algal turf genera included the following: *Giffordia*, *Sphacelaria*, *Polysiphonia*, *Ceramium*, *Taenioma*, *Amphiroa*, and *Derbesia*. The predominant macroscopic algae in the backreef were *Acanthophora*, *Padina*, *Ernodesmis*, and *Sargassum*. Dead *Acropora* is the primary substratum for turf and macroscopic algae on the Tague Bay Reef. Macroscopic algae and turf species were scraped off the dead coral and placed

in 5% formalin and dilute HCl. After drying, the samples were weighed for biomass determinations. In this way, rates of oxygen production and consumption could be calculated on a biomass or an area basis.

RESULTS

Net primary productivity (NPP) for turf on dead coral ranged from 0.23 to 0.93 $gO_2 \cdot m^{-2} \cdot h^{-1}$ ($\bar{x} = 0.50 \pm 0.16$ SD, $n = 28$), while respiration (R) varied from 0.13 to 0.40 ($\bar{x} = 0.23 \pm 0.08$ SD, $n = 16$). Gross primary productivity (GPP) was 0.89 and 0.76 $gO_2 \cdot m^{-2} \cdot h^{-1}$ for two turf samples. NPP for the macroscopic algal community ranged from 1.16 to 8.98 $gO_2 \cdot m^{-2} \cdot h^{-1}$ ($\bar{x} = 3.13 \pm 2.26$ SD, $n = 31$) and R varied from 0.19 to 0.64 ($\bar{x} = 0.44 \pm 0.13$ SD, $n = 18$). GPP for one sample was 2 $gO_2 \cdot m^{-2} \cdot h^{-1}$. NPP for *A. palmata* branches was 0.15 to 0.54 $gO_2 \cdot m^{-2} \cdot h^{-1}$ ($\bar{x} = 0.30 \pm 0.10$ SD, $n = 27$) and R was 0.22 to 0.53 $gO_2 \cdot m^{-2} \cdot h^{-1}$ ($\bar{x} = 0.32 \pm 0.08$ SD, $n = 12$). GPP for three samples was 0.52, 0.76, and 0.61 $gO_2 \cdot m^{-2} \cdot h^{-1}$.

Analysis of variance indicated significant differences between the mean NPP rates for live *A. palmata*, macroscopic algae, and algal turf ($F = 39.85$, $P < 0.01$), with macroscopic algae having higher production than algal turf and turf production exceeding that of the live coral. Mean respiration of macroscopic algae was significantly higher than that for algal turf ($F = 32.53$, $P < 0.01$) and for live *A. palmata* ($F = 8.10$, $P < 0.01$). Algal turf and *A. palmata* respiration rates differed significantly at $P < 0.01$, with higher rates for the coral ($F = 9.72$).

Light during the NPP measurements varied between 134 and 2144 μEinstein $\cdot m^{-2} \cdot s^{-1}$ with most values around 1600 to 1800. Occasionally, clouds would pass overhead during a measurement interval, but net production did not decrease, presumably because of a physiological lag in the photosynthetic process or because the lowered light intensity still exceeded the saturation value. It appears that light intensities are at saturation for shallow corals for ≈ 10 h a day (Wanders, 1976a; Davies, 1977). In experiments on individual corals, Franzisket (1969) found that "daily changes in light intensity have essentially no effect on photosynthesis" after attainment of the light intensity necessary for the maximum rate of oxygen production. He states that "corals produce maximum oxygen at light intensities lower than maximum light in the reef".

In one experiment with macroscopic algae, the bilge pump was turned off and the chamber stabilized to minimize water circulation. The mean O_2 production was 5.69 $gO_2 \cdot m^{-2} \cdot h^{-1}$ with circulation and 1.96 without, representing a 66% decrease and indicating the importance of adequate circulation during closed chamber experiments.

DISCUSSION

Rates of production and respiration for *A. palmata*, macroscopic algae, and algal turf from Tague Bay Reef are in the same general range as those reported previously (Tables I, II). The only other available study of the productivity of *A. palmata* is that by Gladfelter *et al.* (1977); they found mean NPP rates for backreef colonies on Buck Island Reef, St. Croix, of 0.51 $gO_2 \cdot m^{-2} \cdot h^{-1}$ in the fall and 0.42 $gO_2 \cdot m^{-2} \cdot h^{-1}$ in the spring when the water temperature was lower. Mean R was 0.33 $gO_2 \cdot m^{-2} \cdot h^{-1}$ in the fall and 0.27 $gO_2 \cdot m^{-2} \cdot h^{-1}$ in the spring. These rates are similar to the mean R of 0.32 and the mean NPP of 0.30 for the Tague Bay corals which were examined periodically between July and November.

TABLE I

Productivity, respiration, and productivity to respiration ratios for scleractinian corals: GPP, gross primary productivity; R, respiration; NPP, net primary productivity.

Study	GPP/R	NPP/R	Productivity or respiration ($gO_2 \cdot m^{-2} \cdot h^{-1}$)	Species
Kanwisher & Wainwright, 1967	1.9–5.0		0.61–2.3 (GPP)	10 Atlantic spp.
Roffman, 1968	1.7–5.0			8 Pacific spp.
Franzisket, 1969		2.9–4.3		4 Pacific spp.
Wells *et al.*, 1973		0.79–2.90		6 Atlantic spp.
Gladfelter *et al.*, 1977	2.2–2.9		0.51 (mean NPP–fall)	*Acropora palmata*
			0.42 (mean NPP–spring)	
			0.33 (mean R–fall)	
			0.27 (mean R–spring)	
Davies, 1977	2.5		0.13–0.66 (GPP)	*M. annularis*
			0.14–0.25 (R)	
	2.8		0.07–0.27 (GPP)	*M. cavernosa*
			0.07–0.13 (R)	
This study	1.9–2.1	0.89–1.11	0.15–0.54 (NPP)	*Acropora palmata*
			0.22–0.53 (R)	

Note: This table includes only selected references. See review by McCloskey *et al.*, 1978.

For the Tague Bay macroscopic algal communities, NPP ranged from 0.8 to 8.0 $mgO_2 \cdot g^{-1} \cdot h^{-1}$. These rates fall within the range reported by Doty (1971) for 39 species of benthic algae from a Hawaiian reef flat. Some of Doty's (1971) rates are higher, possibly because the samples were incubated in water with a very low oxygen content and a lower temperature than at their collection site. The Tague Bay samples were incubated in situ in saturated or supersaturated water. Downtown *et al.* (1976) observed inhibition of photosynthesis in zooxanthellae and several algal species when sea water was 65 to 90% of oxygen saturation. Also, all of the Hawaiian measurements were from small portions of the algae rather than the entire thallus. Presumably, rates from actively growing portions of the plants would be higher.

Previous research on metabolism of algal turf communities in closed chambers includes that by Sournia (1976) and Wanders (1976a). Sournia (1976) reported mean productivity and respiration rates that fell within the range presented here for algal turf communities. Wanders (1976a) found that "dense" algal turf vegetation had a mean NPP almost twice that of "sparse" algal turf, while mean R for dense and sparse turf were almost identical. The dense turf community, comprised of *Sphacelaria tribuloides* Menegh, *Herposiphonia tenella* (C. Ag.) Ambr., *Polysiphonia subtilissima* Mont., *Pterocladia americana* Taylor, *Taenioma nanum* Kütz,

Table II

Productivity, respiration, and productivity to respiration ratios for algal turfs and macroscopic algae: GPP, gross primary productivity; R, respiration; NPP, net primary productivity; *calculated from mean values for all experiments.

Study	GPP/R	NPP/R	Productivity and respiration	Species
Doty, 1971			0.16–43.2 mgO$_2$·g^{-1}·h^{-1}	39 Hawaiian spp.
Sournia, 1976			0.26 gO$_2$·m^{-2}·h^{-1} (mean R)	Algal community with
			0.82 gO$_2$·m^{-2}·h^{-1} (mean NPP)	*Wurdemannia, Jania, Gelidium, Valonia*
Wanders, 1976a	2.6		0.64 gO$_2$·m^{-2}·h^{-1} (mean NPP)	Dense algal turf
			0.11 gO$_2$·m^{-2}·h^{-1} (mean R)	
	3.1		0.30 gO$_2$·m^{-2}·h^{-1} (mean NPP)	Sparse algal turf
			0.08 gO$_2$·m^{-2}·h^{-1} (mean R)	
Wanders, 1976b	11.0	10.0	10.88, 11.96 mgO$_2$·g^{-1}·h^{-1} (GPP)	*Dictyota dentata*
	6.2	5.2	6.60, 7.27 mgO$_2$·g^{-1}·h^{-1} (GPP)	*Sargassum platycarpum*
	4.2	3.2	4.29, 5.21 mgO$_2$·g^{-1}·h^{-1} (GPP)	*Dictyopteris justii*
Connor & Adey, 1977	2.4	1.4	4.0–5.9 gO$_2$·m^{-2}·h^{-1} (NPP)	Algal communities with
			2.3–4.6 gO$_2$·m^{-2}·h^{-1} (R)	*Hypnea, Laurencia,*
			6.3–10.5 gO$_2$·m^{-2}·h^{-1} (GPP)	*Gracilaria, Pterocladia, Jania*
This study	8.1*	7.6*	1.16–8.98 gO$_2$·m^{-2}·h^{-1} (NPP)	Macroscopic algal
			0.19–0.64 gO$_2$·m^{-2}·h^{-1} (R)	community
			0.8–8.0 mgO$_2$·g^{-1}·h^{-1} (NPP)	
	3.2*	2.2*	0.23–0.93 gO$_2$·m^{-2}·h^{-1} (NPP)	Algal turf community
			0.13–0.40 gO$_2$·m^{-2}·h^{-1} (R)	

and *Wurdemannia miniata* (Drap.) Feldm. & Hamel, resembled the Tague Bay communities which had similar rates of net productivity and respiration. However, Wanders' (1976a) methods seem suspect because samples were cut into very small pieces, incubation periods were excessive, circulation was probably inadequate, and water samples were not fixed chemically until after they had been transported back to the laboratory.

Production to respiration ratios for turf, macroscopic algae, and *Acropora palmata* appear in Tables I and II along with previously reported ratios. A GPP/R ratio > 1 suggests that more oxygen is produced than is consumed during the measurement period. In general, GPP/R ratios for algae exceed those for corals. Using upstream–downstream methodology, Smith & Marsh (1973) and Kinsey (1977) found that a reef transect dominated by algae had a higher GPP/R ratio than a mixed coral-algal transect.

One of the objectives of the chamber experiments was to correlate the rates of respiration and production of the major primary producers on the reef to the rates observed in upstream–downstream studies. Rates of production reported previously for corals in the laboratory or in closed chambers in situ (Table I) appear low relative to some of the reported rates for entire reefs (e.g., Kohn & Helfrich, 1957; Odum *et al.*, 1959). This discrepancy arises partly from attempts to compare rates for individual corals to rates from entire reefs, particularly very shallow reef flats dominated by algae. Also, certain inaccuracies are inherent in both the chamber and the upstream-downstream method (Lewis, 1977). It is likely that chamber measurements are somewhat artificial and underestimate productivity and possibly respiration, although respiration could increase under stressed conditions. Although production by an entire reef is the sum of all individual population productivities, there should be a close correlation between total productivity of the reef and the combined productivity of the major primary producers.

When making a comparison between reef metabolism and metabolism of individual species, it is necessary to consider the topographical complexity of the reef bottom. Chamber rates are based on the area of the dead or live coral branch used, rather than, as in upstream–downstream studies, on the area of reef bottom. A single square meter of reef bottom can support 1 to ≈ 5 m^2 of productive surface area (Wanders, 1976a), largely because of the complex morphology of *A. palmata* colonies. This ratio of total surface area to area of reef bottom is referred to here as spatial heterogeneity.

The relative amount of benthic cover by each of the major primary producers must also be considered. Averaging of the relative percentage cover by *A. palmata*, macroscopic algae, and algal turf for two shallow St. Croix reefs (based on chain transects) gives an estimated 45% cover by *A. palmata*, 30% cover by turf, and 8% cover by macroscopic algae. Based on mean NPP rates from Tague Bay of 0.30 (*A. palmata*), 0.50 (turf), and 3.13 gO$_2$·m^{-2}·h^{-1} (macroscopic algae) and considering relative cover, one can calculate a weighted mean production of 0.54 gO$_2$·m^{-2}·h^{-1} and a weighted mean respiration of 0.25 gO$_2$·m^{-2}·h^{-1}. Multiplying by an average spatial heterogeneity of 2.84 gives a final hourly NPP of 1.53 gO$_2$·m^{-2} (18.4 gO$_2$·m^{-2}·12 h day^{-1}) and R of 0.71 gO$_2$·m^{-2} (8.5 gO$_2$·m^{-2}·12 h day^{-1}). The calculated gross production is 27 gO$_2$·m^{-2}·12 h day^{-1}. Previously reported rates for gross production (in gO$_2$·m^{-2}·day^{-1}) of coral–algal transects and shallow reef areas include 24.0 (Odum & Odum, 1955), 20.0, 28.4, 39.0, 44.0 (Odum *et al.*, 1959), 16.2 (Smith & Marsh, 1973) and 21.1 (Kinsey, 1977). Although the calculated rate for Tague Bay falls within this range, it is a maximum rate because multiplying by spatial heterogeneity overestimates productivity as not all surfaces on the reef are equally productive. There is, therefore, a reasonable correlation between reported

rates for reef productivity based on the upstream–downstream method and a derived rate based on the combined productivity of corals and algae from chamber experiments.

In conclusion, macroscopic algae have been shown to be more productive than turf-covered or living *A. palmata*. Although less conspicuous than these other primary producers in some areas, their high rates of production contribute more to reef metabolism than their abundance would indicate. Macroscopic algae may represent a major part of the total primary productivity of some coral reefs.

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