Limnol. Oceanogr., 48(4), 2003, 1376–1387

Primary productivity of reef-building crustose coralline algae

John R. M. Chisholm[1]
School of Biological Sciences, James Cook University of North Queensland, Townsville, Queensland 4811, Australia; Australian Institute of Marine Science, Cape Ferguson, Townsville, Queensland 4810, Australia

Abstract

The primary productivity of four species of crustose coralline algae was measured as a function of depth (0–18 m) and irradiance on samples collected from and growing upon the windward coral reef at Lizard Island, northern Great Barrier Reef, Australia. Significantly higher productivities were measured in the field than in the laboratory. Maximum gross oxygen production in situ varied from 12.8 to 22.8 mmol m^{-2} h^{-1}; dark respiration consumed between 2.7 and 4.5 mmol O_2 m^{-2} h^{-1}. Integration of photosynthesis–irradiance models with half sine curve approximations of whole-day irradiance yielded estimated in situ net productivities of 15–132 mmol O_2 m^{-2} d^{-1}. When multiplied by previously determined photosynthetic quotients, in situ net carbon fixation was estimated to vary from 0.2 to 1.3 g m^{-2} d^{-1}. Multiplying these rates by measured surface relief factors of 3.1 for the reef crest and 5.0 for the windward slope yielded estimated contributions to reef organic production of ~0.9–5 g C (net) planar m^{-2} d^{-1} over the depth interval 0–18 m, given 100% cover. These data suggest that crustose coralline algae make a larger contribution to organic production on coral reefs than has been thought to this time. A curvilinear model is presented that enables their primary productivity to be estimated from measurements of in situ irradiance at the solar zenith.

Although it is recognized that crustose coralline algae may make a significant overall contribution to coral reef primary production by virtue of their high abundance, they are regarded as low rate producers of organic carbon (Larkum 1983). If this is true, it is surprising that some species are able to calcify their tissues at rates of up to 9.1 g $CaCO_3$ m^{-2} d^{-1} (Chisholm 2000), since this would require significant concomitant production of organic carbon. Given that specific rates of photosynthesis by crustose coralline algae have seldom been measured in the field and only once in a high-energy environment where conditions favor their development (Chisholm et al. 1990), it is possible that their organic productivity has been underestimated.

The organic productivity of crustose coralline algae is no less important to the maintenance of coral reefs than is their inorganic production, as the latter depends on the former. Calcification occurs within the cells walls of coralline algae and not externally, as in corals and other invertebrates; thus, photosynthesis creates the organic environment in which the calcite crystals are deposited. The rate at which coralline algae are able to bind loose substrata and provide protective barriers to erosion is therefore a function of their primary productivity.

Coralline algae are ubiquitous and often dominant components of coral reef communities (e.g., Littler 1973*a;* Stearn et al. 1977; Glynn et al. 1996; Keats et al. 1997), and their abundance in cryptic and shaded environments can be greatly underestimated (Littler 1973*a*). They also provide food for herbivores with hardened mouthparts (e.g., Steneck and Dethier 1994; Steneck 1997 and references given therein) and surfaces for settlement of invertebrate larvae (Adey 1998).

Analysis of how reefs will respond to major changes in the environment, such as increased ocean temperature or UV penetration, cannot be achieved without comprehensive data on their sources and sinks for organic carbon (Crossland et al. 1991 and references given therein). Estimation of the contributions made by different reef communities to whole-reef production and of coral reefs to global ocean production is compromised by a lack of data on the metabolic activity of outer reef slopes, which are thought to be zones of elevated production (Kinsey 1985; Crossland et al. 1991). Since productivity measurements cannot be accomplished on reef slopes using flow respirometry or open-top enclosures, the target organisms or communities must either be sampled and measured in the laboratory or examined in situ using incubation chambers (Chisholm 2000).

In order to estimate the organic productivity of crustose coralline algae on an outer reef slope, I measured their rates of oxygen production and consumption using laboratory- and field-based respirometers and converted the data into equivalent units of carbon using simultaneously determined metabolic quotients (Chisholm 2000). I selected four important reef-building species for study whose vertical distributions overlap on the windward reef at Lizard Island, northern Great Barrier Reef (GBR), Australia (14°40′S; 145°27′E) to encompass a total depth range of 0–18 m. I measured their laboratory productivities in late August through September 1985 and their in situ productivities between late March and early July 1986, thus 4–5 months before and 2–6 months after the sun passed overhead.

Methods

Samples—The samples selected for study comprised: *Hydrolithon onkodes* (Heydrich) Penrose and Woelkerling (for-

[1] Present address: 22A Rose Street, North Ward, Queensland 4810, Australia (j.chisholm@libertysurf.fr).

Acknowledgments

I could not have accomplished this work without the considerable help of D. J. Barnes, B. E. Chalker, J.-C. Collingwood, T. Cox, M. J. Devereux, W. C. Dunlap, E. F. Gill, B. Goldman, P. Pini, R. Pitcher, I. R. Price, G. Smith, and L. A. Wilson. The Lizard Island Research Station and its Doctoral Fellowship Scheme, James Cook University of North Queensland, and the Australian Institute of Marine Science supported the work.

merly *Porolithon onkodes*) at depths of 0 and 2 m; *Neogoniolithon brassica-florida* (Harvey) Setchell and Mason (formerly *Neogoniolithon fosliei*) at depths of 0, 3, and 6 m; *Hydrolithon reinboldii* (Weber van Bosse and Foslie) Foslie at depths of 3 and 6 m; and *Neogoniolithon conicum* (Dawson) Gordon, Masaki, and Akioka (formerly *Paragoniolithon conicum*) at depths of 0, 6, and 18 m. Crusts were selected at random at the given depth intervals, except when they were growing in locations too confined to sample or to measure in situ. Thus, crusts growing in cryptic or shaded environments were examined along with crusts on exposed reef surfaces.

Laboratory respirometry—Target crusts were located on the reef and tagged with colored ribbons to facilitate retrieval. The percentages of sea surface irradiance incident upon their upper surfaces at noon were determined under cloudless conditions using a pair of intercalibrated quantum sensors (Li-Cor 190SB and 192SB) connected to a light meter (Li-Cor 188B).

Crusts were bored to a depth of approximately 5 mm using a 17-mm internal diameter (ID) diamond-tipped core drill, driven by compressed air supplied from a SCUBA tank. The cores were left attached to the reef for at least 7 d to ensure repair of tissues cut by the core drill. Crusts were dislodged from the reef with a small chisel and carefully cleaned of noncoralline basal substratum using a grinding stone. Finally, the samples were transported to the laboratory and immersed for 30 min in filtered seawater (0.45-μm Millipore) containing 60 μg ml^{-1} penicillin G and 100 μg ml^{-1} streptomycin N (Commonwealth Serum Laboratories, Australia). The decision to pretreat with antibiotics resulted from pilot experiments that revealed a significant rise in respiration over the course of incubations. Extended tests revealed no significant alterations in the rates of photosynthesis or respiration after addition of the antibiotics.

Rates of O_2 production and consumption were determined in a clear acrylic, purpose-built incubation chamber (15-ml volume; Fig. 1a). The chamber possessed a circumferential jacket, through which water of constant temperature (25°C $\pm$ 0.1°C) was circulated. It also contained a port that traversed the water jacket for insertion of a sample holder or Li-190 SB quantum sensor. The sample holder was filled with soft wax (Tray Wax, Sybron Kerr) into which the sample was pressed and thus held stable in the path of a horizontal light beam in a manner that simulated attachment to the reef surface. The chamber was built to mate with an acrylic base-plate, containing a central polarographic O_2 electrode (Rank Bros. Pty. Ltd.). The electrode was connected via a signal amplifier to a chart recorder (Shimadzu R-112M) and calibrated daily in a saturated solution of Na_2SO_3 (zero O_2) and air-saturated seawater. The O_2 content of the air-saturated seawater was interpolated from the solubility tables of Carpenter (1966) under measured conditions of atmospheric pressure, salinity, and temperature and constant stirring.

Samples were irradiated with a 300 W quartz-halogen slide projector lamp. The lamp was fitted with a glass infrared heat filter to reduce heat output and to adjust the spectral distribution of the artificial illumination to better approximate that of sunlight in the shallow ocean. Irradiance was varied during experiments using neutral density filters. The irradiance transmitted by each of the filters was measured by inserting a Li-Cor 190SB sensor in place of the sample holder.

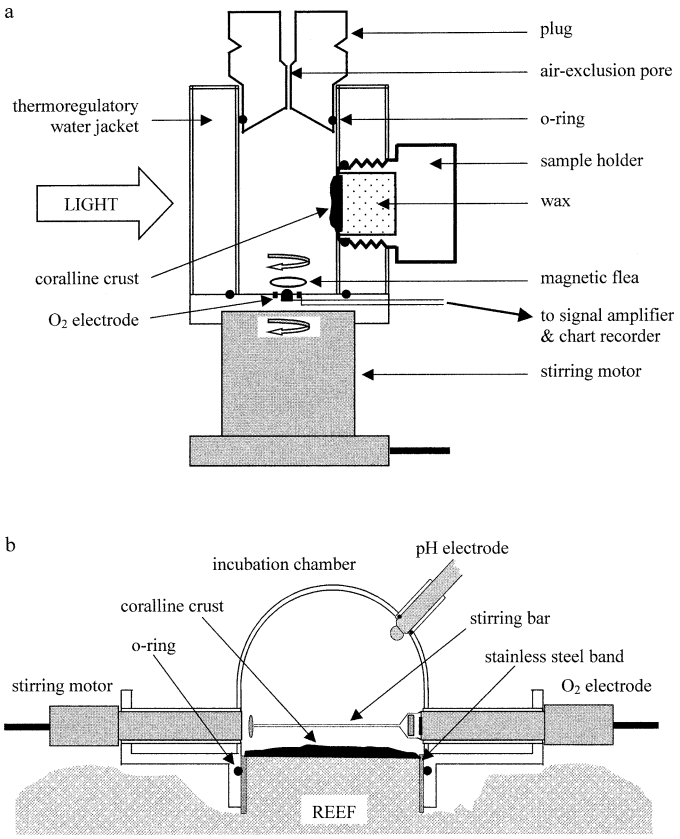

Fig. 1. Longitudinal section diagrams of (a) the laboratory incubation chamber and (b) the in situ incubation chamber; in the diagrams, the inlet and outlet water hoses for (a) thermoregulation and (b) flushing lie perpendicular to the sections and are therefore not shown.

All measurements of photosynthesis were made between 0730 and 1800 h. Dark respiration was measured at the beginning, middle, and end of the light incubations. Incubation water volume was measured by tipping the contents of the chamber into a volumetric cylinder before removing the sample.

In situ respirometry—In situ samples were prepared by boring through crusts to a depth of 10–15 mm with a 36-mm ID diamond-tipped core drill. Small amounts of surrounding substratum were removed with a hammer and chisel to render the cores marginally proud of the surrounding reef surface. Tray Wax was smeared around their sides and stainless steel bands (316 Grade) were fitted so that their uppermost edges lay just beneath the pigmented layers of the crusts (*see* Chisholm et al. 1990; or Chisholm 2000). Crusts were then left undisturbed for 7–10 d.

A small, domed, UV-transparent, acrylic incubation chamber was fitted over the stainless steel band surrounding each coralline sample, and sensors were inserted through acrylic

fixtures bonded to the sidewall of the chamber (*see Fig. 1b* and Chisholm et al. 1990 for specifications). Rates of net photosynthesis and dark respiration were measured over 24 h with a galvanic oxygen electrode fitted with a long stirrer bar attachment (50 mm, Kent EIL). The stirrer bar attachment traversed the chamber and coupled magnetically with a motor-driven magnet that rotated in a stainless steel housing positioned diametrically opposite. Seawater temperature was measured to ±0.1°C with a thermistor encased in a stainless steel tube (Analog Devices AC2626K4). Irradiance was measured with an underwater quantum sensor (Li-192SB, Li-Cor, Ltd.), fitted inside a replica chamber mounted adjacent.

The O_2 electrode was calibrated at the temperature of the ocean before each experiment in air-saturated seawater and zeroed against a saturated solution of Na_2SO_3. The temperature sensor was calibrated against a quartz thermometer (±0.01°C, traceable to the National Bureau of Standards). The quantum sensor was calibrated underwater against a second, manufacturer-calibrated, Li-192SB sensor, connected to a light meter (Li-188B). A data logger, protected within a pressure-resistant housing, interrogated the sensors every 6 s and recorded their mean outputs at 1-min intervals. A centrifugal pump periodically pumped fresh seawater through the chamber for 3 min in every 18–30-min period.

After incubation, the sample was chipped from the reef and taken to the laboratory. Incubation water volume was determined by refilling the chamber with seawater, refitting the coralline sample and sensors, and then withdrawing one sensor to allow the seawater to run into a volumetric cylinder.

Data normalization—The surface areas of the samples were estimated using the foil skin technique of Marsh (1970).

Samples were then frozen in a vapor stream of dry ice (CO_2 at −32°C), crushed in a stainless steel percussion press that had been chilled to 4°C, and finally ground to a fine powder on ice. Non–water soluble pigments were extracted successively into three volumes (5 ml) of 20% tetrahydrofuran (THF) in methanol (MeOH). During extraction, samples were partially immersed in beakers containing ice-water slurry (0°C) and ultrasonicated for 5 min to assist release of membrane-bound pigment fractions. The extracts were centrifuged at 3,000 × g for 10 min at 4°C to separate solid and liquid phases. Absorbances of the liquid phases at 665 nm were determined immediately in a spectrophotometer (Hitachi U-3200). Chlorophyll *a* (Chl *a*) was quantified according to the method of Chalker and Dunlap (1982) using an extinction coefficient for Chl *a* at 665 nm ($\xi_{\text{Chl}\,a@665}$) in 20% THF/MeOH of 77.015 L g^{-1} cm^{-1} (B. E. Chalker, Australian Institute of Marine Science, unpubl. data). The reliability of the resulting estimates of Chl *a* was checked by freeze-drying three THF/MeOH extracts, redissolving the residues in equivalent volumes of 90% acetone in water, and requantifying Chl *a* using the equation of Jeffrey and Humphrey (1975).

Examination of the quantities of Chl *a* extracted into successive volumes of THF/MeOH indicated contributions from at least two different sources. That is, Chl *a* did not extract exponentially, as in single-phase systems. Inspection of the samples revealed variable quantities of endolithic algae, predominantly cyanobacteria, in the skeletal carbonate below the living coralline layer.

Effort was made to quantify the amount of Chl *a* derived from endolithic algae by searching for specific accessory pigments that could be used as proxies for the associated Chl *a*. Pigments were extracted from samples of pure coralline tissue and pure endolithic algal tissue into 20% THF/MeOH. Pure coralline tissue was obtained by scraping the upper surfaces of coralline crusts with a scalpel in a cold room at −20°C. Pure endolithic algal samples were obtained by continuing this procedure after microscopic examination revealed no further traces of the red, phycoerythrin-containing cell layers of the coralline crusts. The two fractions were then crushed, ground, and extracted as before to remove Chl *a* and accessory pigments. Aliquots of the extracts were injected onto an RP-18 (Spheri-5, 25 cm) column and separated by solvent gradient HPLC using a Waters liquid chromatograph (ALC/GPC 204). Pigment fractions were detected by visible wavelength absorption at 436 nm (0.01 units full scale) using a Waters data module (730).

Data analysis—Rates of O_2 flux were plotted against irradiance and modeled using the general exponential function of Chalker (1980):

$$\frac{\partial P}{\partial I} = \alpha(P_m^g - P)\left(1 + \frac{\varepsilon P}{P_m^g}\right) + R \tag{1}$$

where P_m^g is the maximal rate of gross photosynthesis; R (negative in sign) is the absolute rate of dark respiration; I_k is the irradiance at which the initial slope intercepts the horizontal asymptote; and ε is the rate of transition from light-limited to light-saturated photosynthesis (i.e., the degree of curve inflexion). When $\varepsilon = -1$, Eq. 1 integrates to the right-rectangular hyperbola:

$$P = P_m^g \frac{I}{I + I_k} + R \tag{2}$$

When $\varepsilon = 0$, Eq. 1 integrates to a simple exponential function:

$$P = P_m^g(1 - e^{-I/I_k}) + R \tag{3}$$

When $\varepsilon = 1$, Eq. 1 integrates to the hyperbolic tangent function:

$$P = P_m^g \tanh\frac{I}{I_k} + R \tag{4}$$

For limits $-1 < \varepsilon < 1$ and $\varepsilon \neq 0$, Eq. 1 integrates to a general exponential function:

$$P = P_m^g\left[\frac{e^{(\varepsilon+1)(I/I_k)} - 1}{e^{(\varepsilon+1)(I/I_k)} + \varepsilon}\right] + R \tag{5}$$

which can define any rate of curvature intermediate to those of the right-rectangular hyperbola and the hyperbolic tangent. Curves were fitted by the method of least squares (JMP v3 Statistics Made Visual, SAS Institute). When ε converged upon an integer value characterizing Eqs. 2, 3, or 4 (−1, 0,

Table 1. Percent coefficients of variation (=SD/mean × 100) for maximal rates of gross and net photosynthesis by coralline algae under laboratory and field conditions after normalization to different parameters.

	Planar area		Crust area		Chlorophyll *a*	
	P_m^g	P_m^n	P_m^g	P_m^n	P_m^g	P_m^n
Laboratory						
H. onkodes	15.2	17.4	11	14.4	29.6	29.1
N. brassica-florida	14.9	16.6	9.5	11.7	16.6	17.5
H. reinboldii	11.1	15.2	9	13.2	28.3	30.6
N. conicum	20.7	26.3	16.9	22.7	26.5	31.3
Mean	15.5	18.9	11.6	15.5	25.3	27.1
In situ						
H. onkodes	16.8	19.2	12.3	14.7	25	26
N. brassica-florida	13.7	18.3	9	13.8	13.3	16.2
H. reinboldii	11.1	15.7	9.7	14.7	21.7	35.9
N. conicum	11.7	15.8	7.7	11.5	41.5	43.8
Mean	13.3	17.3	9.7	13.7	25.4	30.5
Grand mean	14.4	18.1	10.6	14.6	25.3	28.8

and 1, respectively), the appropriate three-parameter model was substituted to eliminate the redundant variable, thereby reducing the confidence intervals surrounding the parameter estimates.

The *P-I* models were integrated with half sine curve approximations of the diurnal light profile at the sample surface. The length of the light period was considered to extend from civil dawn to civil dusk (data obtained from The Nautical Almanac, Her Majesty's Stationery Office, London). The amplitude of the half sine curve was set at the maximum irradiance measured at the crust surface at noon.

Organic C production was estimated by multiplying the measured rates of O_2 evolution by experimentally determined values for the photosynthetic quotients (*see* Chisholm 2000). Dark C consumption was estimated by multiplying rates of oxygen uptake by the reciprocals of the experimentally determined photosynthetic quotients.

The maximum potential contribution of each species to organic production on the windward reef (i.e., at 100% cover) was estimated by multiplying the rate of daily net C production per square meter of crust by the mean surface relief of the reef in the study area.

Results

Data normalization—The Chl *a* contents of samples calculated using the extinction coefficient of Chalker for Chl *a* in 20% THF/MeOH differed by less than 1% from the quantities calculated using the extinction coefficient and equation of Jeffrey and Humphrey (1975) for Chl *a* in 90% acetone, thus confirming the accuracy of Chalker's unpublished extinction coefficient.

Estimates of photosynthesis were least variable when data were normalized to crust surface area and most variable when normalized to Chl *a* (Table 1). The amount of Chl *a* extracted from the skeletal carbonate underlying the living coralline tissue represented a substantial proportion of the total Chl *a* (Table 2). Although extracts made from pure endolithic algal fractions contained several unidentified accessory pigments that did not occur in the coralline tissues, their concentrations relative to the associated Chl *a* were highly variable and thus could not be used to partition the chlorophyll sources (Fig. 2).

Table 2. Mean concentrations of chlorophyll *a*±95% confidence intervals in core samples taken through crusts of coralline algae, including contributions from endolithic algae, versus concentrations of chlorophyll *a* extracted exclusively from endolithic populations.

Species	*n*	Chlorophyll *a* (mg m^{-2})
H. onkodes	6	224±103
N. brassica-florida	4	434±81
H. reinboldii	5	163±47
N. conicum	5	334±89
Endolithic algae	4	188±116

Microscopic examination of endolithic algal populations present in the core samples after staining with 1% acridine orange indicated that much of their Chl *a* was inactive; that is, it fluoresced pale orange, not deep red. This is consistent

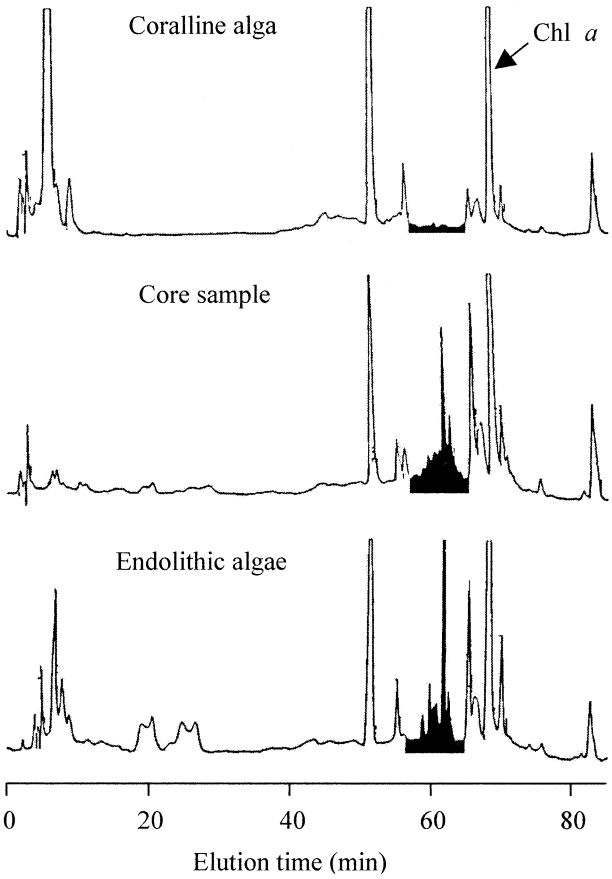

Fig. 2. Example chromatograms of photosynthetic pigments extracted from coralline algae, whole core samples, and endolithic algae into THF/MeOH (20 : 80, v : v) and separated by gradient flow HPLC; shaded regions identify accessory pigments unique to endolithic fractions.

with the very low rates of photosynthesis that have been reported for endolithic algae, in spite of their high Chl *a* contents (Hawkins and Lewis 1982). Indeed, rates of photosynthesis by endolithic algae present in cores from which the living coralline tissue had been removed were only just sufficient to compensate for respiratory consumption at the highest light levels applied during treatments. These data presumably explain why Chl *a* proved to be a poor standard for photosynthetic rate, and they indicate that assimilation numbers for coralline algae, if calculated, would be erroneously low. For this reason, rates of photosynthesis are not given per unit of Chl *a*.

Laboratory respirometry—P-I curves were fitted to individual sample data sets with coefficients of determination (r^2) of 0.99–1.00. Between the limits of −1 and 1, ε tended to become more positive with increasing depth and decreasing irradiance, indicating increased rates of transition from light-limited to light-saturated photosynthesis (Fig. 3). In two of the four species, ε varied inversely with the natural logarithms of the precollection percentages of surface irradiance incident at their surfaces when the sun was at its zenith (Fig. 4). Maximum noontime irradiance varied from 1,689 μmol m^{-2} s^{-1} at 0 m to 35 μmol m^{-2} s^{-1} at 18 m.

Mean rates of maximal gross oxygen production varied from 7.9 to 20 mmol m^{-2} h^{-1} (Table 3). Mean rates of dark oxygen consumption varied from 1.9 to 4.6 mmol m^{-2} h^{-1} (Table 3). Maximum net oxygen production varied from 6 to 15 mmol m^{-2} h^{-1} (Table 3). Mean ratios of maximal gross photosynthesis to dark respiration varied from 3.2 : 1 to 5.4 : 1 (Table 3).

Multiplication of daytime oxygen data by photosynthetic quotients of 1.21 for *H. onkodes*, 1.27 for *N. brassica-florida*, 1.33 for *H. reinboldii*, and 1.07 for *N. conicum* (*see* Chisholm 2000), and nighttime data by their reciprocals, provided mean estimates of maximal gross C fixation that ranged from 0.09 to 0.19 g m^{-2} h^{-1}, dark C consumption that ranged from 0.02 to 0.06 g m^{-2} h^{-1}, and maximal net C production that ranged from 0.07 to 0.15 g m^{-2} h^{-1}.

Integration of the *P-I* equations with half sine curve approximations of daily irradiance indicated that the coralline species could increase their organic C biomass by 0.12–1.2 g m^{-2} d^{-1}, on average (Table 4). Multiplying the rates given in Table 4 by surface relief factors of 3.1 for the reef crest and 5.0 for the reef slope at Lizard Island (Chisholm 2000) indicates planar area productivities of 2–4 g C m^{-2} d^{-1} on the crest and 0.6–4 g C m^{-2} d^{-1} on the slope, given 100% cover.

In situ respirometry—Seawater temperature inside the specimen chamber varied from 30°C to 23°C over the course of experiments and by up to ±0.7°C during any single incubation. Maximum noontime irradiance varied from 1,516 μmol m^{-2} s^{-1} at 0 m to 30 μmol m^{-2} s^{-1} at 18 m.

P-I curves were fitted to individual sample data with coefficients of determination (r^2) of 0.92–1.00. Full light-saturation of photosynthesis was uncommon, even among reef crest samples, and the *P-I* responses of crusts in low-light environments were often nearly linear (Fig. 5). There was little difference in the fitting power of the various *P-I* models (Eqs. 2–5) due to variability in the data.

Mean rates of maximal gross oxygen production varied from 12 to 23 mmol m^{-2} h^{-1} (Table 3). Mean rates of dark oxygen consumption varied from 2.7 to 4.5 mmol m^{-2} h^{-1} (Table 3). Maximum net oxygen production varied from 9.1 to 20 mmol m^{-2} h^{-1} (Table 3). Mean ratios of maximal gross photosynthesis to dark respiration varied from 4.5 : 1 to 7 : 1 (Table 3).

Estimates of maximal gross and net oxygen production, dark respiration, and the irradiance required for the onset of saturation (I_k) were in almost all instances significantly higher in situ than in the laboratory (Table 5); the mean differences were 52%, 54%, 26%, and 37%, respectively (Table 3). The differences tended to be less pronounced among reef crest samples. Although in situ samples exhibited larger values for I_k, they were not necessarily acclimated to higher incident irradiance (Table 4). Lower rates of dark respiration in the laboratory were likely due, at least in part, to suppression of bacterial respiration by treatment with antibiotics.

Multiplication of daytime oxygen data by the photosynthetic quotients of the four species and nighttime data by their reciprocals provided mean estimates of maximal gross C fixation that ranged from 0.11 to 0.23 g m^{-2} h^{-1}, dark C consumption that ranged from 0.02 to 0.05 g m^{-2} h^{-1}, and net C production that ranged from 0.09 to 0.18 g m^{-2} h^{-1}.

Integration of the *P-I* equations with half sine curve approximations of daily irradiance indicated that the coralline species could increase their mean organic C biomass by 0.17–1.3 g m^{-2} d^{-1} (Table 4). Multiplying the rates given in Table 4 by surface relief factors of 3.1 for the reef crest and 5.0 for the reef slope indicates planar area productivities of 3–4 g C m^{-2} d^{-1} on the crest and 0.9–5 g C m^{-2} d^{-1} on the slope, given 100% cover. The rates of net 24-h C fixation for the four species varied curvilinearly with noontime irradiance (Fig. 6).

Discussion

Under tightly controlled irradiance and temperature, inverse relationships were observed in two of the four species between the rates of *P-I* curve inflexion and the natural logarithms of the percentages of surface irradiance upon the samples when the sun was at its zenith. Some species therefore reduce the optical thickness of their photosynthetic layers as the seawater column attenuates light, just as terrestrial plants adjust the thickness of their leaves beneath shade canopies (Arnold and Murray 1980; Littler 1980). The physical support provided by cell wall calcification presumably allows coralline algae to develop extremely thin tissues to complement their green light harvesting capacity, thus enabling them to live at extreme depths in the water column (Littler and Littler 1985).

Rates of photosynthesis were significantly lower in the laboratory than in situ. The differences were most likely due to either seasonal adjustment of the photosynthetic apparatus or to detachment of crusts from the reef matrix. It is unlikely that chance was responsible for the differences, as in situ

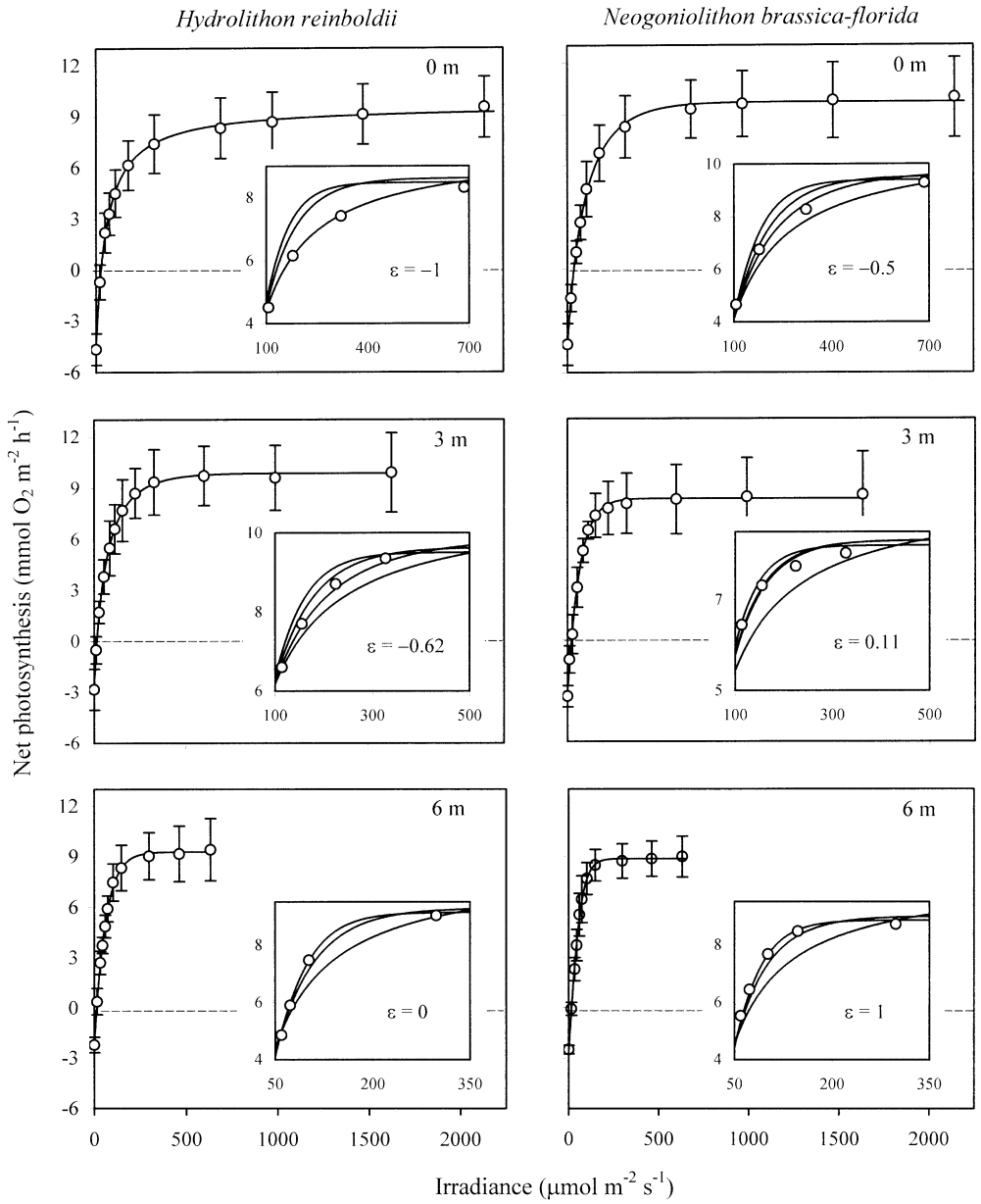

Fig. 3. Mean *P-I* curves for samples of *Hydrolithon reinboldii* and *Neogoniolithon brassica-florida* in the laboratory, modeled using the right-rectangular hyperbola ($\varepsilon = -1$); a simple exponential function ($\varepsilon = 0$); the hyperbolic tangent function ($\varepsilon = 1$); and a general exponential function (noninteger values between -1 and 1). Error bars are 95% confidence intervals. Inserts expand the regions of curve inflexion to illustrate differences in the fitting power of the models, whereby the hyperbolic tangent simulates the fastest rate of transition from light-limited to light-saturated photosynthesis, the right-rectangular hyperbola simulates the slowest, the simple exponential function simulates an intermediate rate, and the general exponential function simulates all other intervening rates. When only three curves are shown, the general exponential model was not fitted because ε converged upon an integer value characteristic of one of the three-parameter models. The value shown for ε in the insert indicates the model that most accurately described the data.

rates were higher in every comparable instance (Table 6). Suppression of cyanobacterial metabolism via antibiotic treatment also appears an unlikely explanation for the inferior rates of productivity in the laboratory, since tests demonstrated that core samples lacking coralline tissue exhibited maximum rates of photosynthesis that were only just sufficient to compensate for respiratory consumption. Equally, inadequate simulation of the spectral distribution of light to which samples had become adapted does not explain the lower photosynthetic capacities of laboratory samples, since

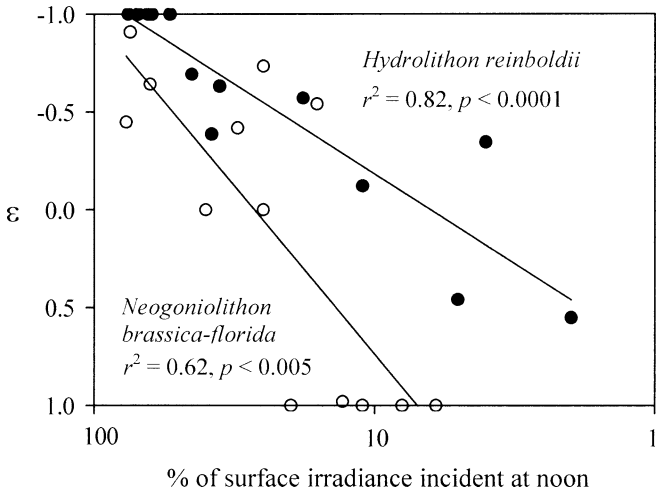

Fig. 4. Significant inverse relationships between the rate of transition from light-limited to light-saturated photosynthesis (ε) and the precollection percentages of sea surface irradiance incident upon samples of *Hydrolithon reinboldii* and *Neogoniolithon brassica-florida* at noon.

they received sufficient white light to fully saturate their photosynthetic apparatus (Fig. 3). The lower values for I_k among laboratory samples might, nonetheless, indicate differences in their seasonally adapted states relating to measurement before the austral summer, or they may have become light saturated at lower irradiance due to a supply of greater amounts of red light than are available at depth in the seawater column.

Seasonal considerations aside, it is significant that all species except for *Hydrolithon onkodes,* which shows a marked preference for high light and shallow water (e.g., Littler 1973*a;* Hawkins and Lewis 1982), exhibited higher rates of primary production in situ than have been reported in simulated in situ studies (Table 6). It would be interesting to investigate whether coralline production is supported by nutrients (and/or CO_2) diffusing out of reef pore waters (*see* Rougerie and Wauthy 1988) or fixed by cyanobacteria resident in the underlying reef carbonate, since the enhanced growth of coralline algae near sewage outlets suggests that they may be strongly nutrient limited in the open ocean (Littler 1973*a;* Kindig and Littler 1980; Littler et al. 1991).

The net productivities of coral reef plant communities have been estimated as follows: benthic fleshy algae 0.1–4 g C m^{-2} d^{-1}; phytoplankton 0.1–0.5 g C m^{-2} d^{-1}; sand algae 0.1–0.5 g C m^{-2} d^{-1}; sea grasses 1–7 g C m^{-2} d^{-1}; turf algae 1–6 g C m^{-2} d^{-1}; and zooxanthellae 0.6 g C m^{-2} d^{-1} (Larkum 1983). After adjustment for reef surface relief, the rates reported here for coralline algae of 0.9–5 g C m^{-2} d^{-1} equate with the rates given for fleshy and turf algae. Without adjustment for surface relief, coralline algae have similar net productivities (0.17–1.3 g C m^{-2} d^{-1}) to turf-dominated epilithic algal communities growing upon coral settlement plates in the central GBR (0.06–1.26 g C m^{-2} d^{-1}, Klumpp and McKinnon 1989).

It is estimated that highly productive coral reef flats fix C

Table 3. Parameters describing the *P-I* curves of crustose coralline samples in the laboratory and in situ. *N,* number of samples measured; *n,* number of samples that became sufficiently light saturated to obtain reasonable estimates of P_m^g, I_k, and $P_m^g/-R$; thus $N-n$ = the number of samples that exhibited linear or nearly linear *P-I* curves; mean estimates are based on *n*; half 95% confidence intervals in parentheses.

Species	Depth (m)	*N*	*n*	P_m^g	P_m^n	$-R$	I_k	$P_m^g/-R$
				(mmol O_2 m^{-2} h^{-1})			(μmol m^{-2} s^{-1})	
Laboratory								
H. onkodes	0	6	6	19.5 (4.9)	14.9 (4.1)	4.6 (1.2)	124	4.3
N. brassica-florida	0	4	4	14.4 (1.4)	10.1 (1.2)	4.5 (0.7)	85	3.2
N. conicum	0	5	5	13.2 (3.2)	10.1 (3.0)	3.1 (0.5)	84	4.2
H. reinboldii	0	5	5	14.2 (1.1)	9.7 (2.0)	4.5 (1.0)	59	3.2
H. onkodes	3	4	4	15.6 (0.6)	11.9 (0.7)	3.6 (0.5)	85	4.3
N. brassica-florida	3	4	4	11.9 (2.4)	8.5 (2.2)	3.4 (0.4)	57	3.5
H. reinboldii	3	4	4	12.5 (3.0)	9.9 (2.2)	2.6 (1.0)	59	4.8
N. brassica-florida	6	5	5	11.4 (1.3)	8.9 (1.2)	2.6 (0.3)	71	4.5
N. conicum	6	5	5	9.8 (3.0)	7.4 (3.0)	2.4 (0.4)	35	4.2
H. reinboldii	6	4	4	11.3 (0.9)	9.2 (1.3)	2.1 (0.5)	63	5.4
N. conicum	18	5	5	7.9 (1.1)	6.0 (1.3)	1.9 (0.3)	31	4.1
In situ								
H. onkodes	0	5	5	22.8 (2.7)	18.4 (2.7)	4.5 (0.4)	205	5.1
N. brassica-florida	0	4	4	18.4 (1.6)	14.6 (1.8)	3.9 (0.6)	157	4.8
N. conicum	0	4	4	19.6 (2.1)	15.3 (1.6)	4.3 (0.5)	85	4.6
H. onkodes	2	4	0			3.2 (0.4)		
N. brassica-florida	3	4	4	21.1 (3.6)	16.6 (3.2)	4.5 (0.5)	155	4.7
H. reinboldii	3	4	4	20.1 (2.7)	16.5 (3.1)	4.2 (0.8)	129	5.0
N. brassica-florida	6	4	4	12.1 (1.8)	9.1 (2.4)	2.7 (0.8)	68	4.5
N. conicum	6	4	2	16.7 (0.6)	13.8 (0.7)	2.9 (0.7)	65	5.8
H. reinboldii	6	4	4	22.8 (1.4)	19.6 (1.3)	3.3 (0.3)	117	7.0
N. conicum	18	4	2	12.8 (0.7)	10.0 (1.6)	2.7 (0.3)	52	4.7

Table 4. Estimated production and consumption of organic carbon by crustose coralline algae over 24 h based on laboratory and in situ measurements; rates are means of *n* samples; half 95% confidence intervals in parentheses; I_{max}, the irradiance incident upon the coralline samples at noon.

Species	Depth (m)	*n*	P^g	P^n	$-R$	I_{max} (μmol m^{-2} s^{-1})
			(g C m^{-2} d^{-1})			
Laboratory						
H. onkodes	0	6	2.31 (0.41)	1.21 (0.35)	1.1 (0.19)	1,689
N. brassica-florida	0	4	1.68 (0.1)	0.66 (0.12)	1.02 (0.1)	1,683
N. conicum	0	5	1.78 (0.27)	0.93 (0.22)	0.84 (0.08)	1,629–1,633
H. reinboldii	0	5	1.55 (0.07)	0.56 (0.21)	0.99 (0.14)	1,636–1,638
H. onkodes	3	4	1.69 (0.17)	0.82 (0.21)	0.86 (0.07)	281–1,037
N. brassica-florida	3	4	1.27 (0.26)	0.49 (0.24)	0.78 (0.06)	130–864
H. reinboldii	3	4	1.33 (0.19)	0.76 (0.12)	0.57 (0.14)	389–974
N. brassica-florida	6	5	1.25 (0.1)	0.67 (0.07)	0.58 (0.05)	170–535
N. conicum	6	5	0.73 (0.02)	0.12 (0.7)	0.64 (0.06)	43–107
H. reinboldii	6	4	0.77 (0.26)	0.32 (0.3)	0.45 (0.06)	43–234
N. conicum	18	5	0.69 (0.09)	0.16 (0.09)	0.53 (0.04)	35–129
In situ						
H. onkodes	0	5	2.37 (0.09)	1.31 (0.11)	1.06 (0.08)	1,441–1,516
N. brassica-florida	0	4	1.82 (0.14)	0.94 (0.25)	0.88 (0.15)	1,347–1,359
N. conicum	0	4	2.33 (0.22)	1.18 (0.09)	1.15 (0.15)	1,250–1,257
H. onkodes	2	4	1.12 (0.24)	0.35 (0.3)	0.77 (0.09)	50–120
N. brassica-florida	3	4	1.95 (0.45)	0.93 (0.42)	1.02 (0.11)	650–1,130
H. reinboldii	3	4	1.74 (0.09)	0.83 (0.24)	0.9 (0.17)	615–1,000
N. brassica-florida	6	4	1.0 (0.1)	0.43 (0.16)	0.57 (0.14)	70–390
N. conicum	6	4	1.44 (0.21)	0.66 (0.16)	0.78 (0.19)	130–550
H. reinboldii	6	4	1.58 (0.33)	0.87 (0.31)	0.71 (0.07)	54–355
N. conicum	18	4	0.9 (0.17)	0.17 (0.12)	0.73 (0.08)	30–80

at gross rates of close to 7 g m^{-2} d^{-1} (Kinsey 1985), with whole reefs averaging around 3 g m^{-2} d^{-1} (Crossland et al. 1991). At a gross production rate of 6.9 g C m^{-2} d^{-1}, given 100% cover and a surface relief factor of 5, the coralline algae investigated here could substitute for the high rate category. At a more moderate cover of around 40% (e.g., Stearn et al. 1977), they could account for the average productivity of whole reefs.

Although coralline algae are often dominant components of Caribbean and Indian Ocean reefs and can attain surface

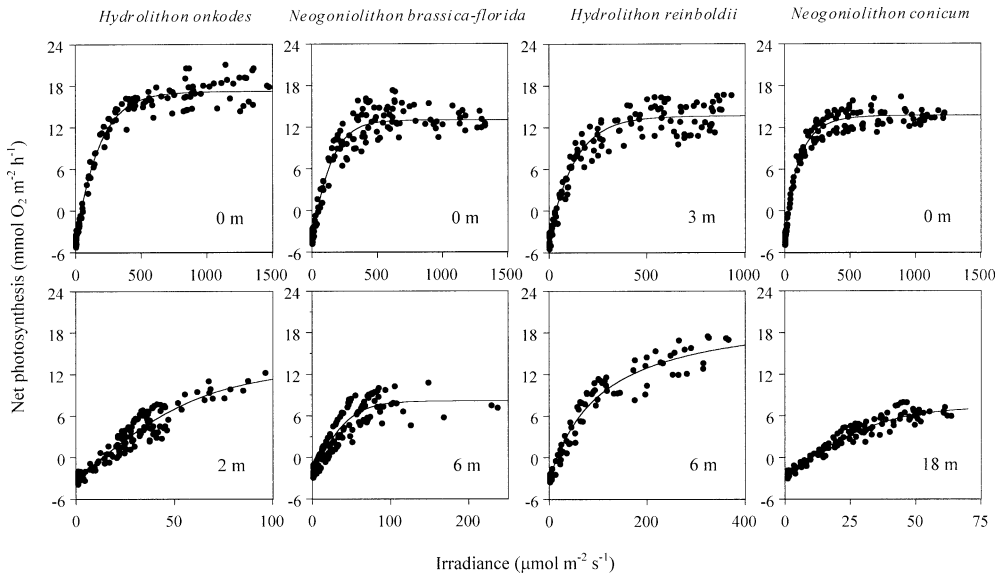

Fig. 5. Mean in situ *P-I* curves for *Hydrolithon onkodes, Neogoniolithon brassica-florida, Hydrolithon reinboldii,* and *Neogoniolithon conicum* at indicated depths on the windward crest and slope of the reef at Lizard Island, northern GBR.

Table 5. Statistical comparison of parameters describing the *P-I* curves of coralline algae in situ and in the laboratory (LSD test; $\alpha = 0.05$), after confirmation of normality and variance homogeneity and three-way ANOVA ($F_{1, 47} = 22.6$, $p < 0.00005$); probabilities are for differences between the group means for location × depth × species interactions; ns, nonsignificant.

Depth (m)	Species	P_m^g	P_m^n	$-R$	I_k
0	*H. onkodes*	<0.05	<0.05	ns	<0.000001
	N. brassica-florida	<0.05	<0.01	ns	<0.000001
	N. conicum	<0.0005	<0.005	<0.01	ns
3	*N. brassica-florida*	<0.000005	<0.00001	<0.05	<0.000001
	H. reinboldii	<0.00005	<0.0005	<0.001	<0.000005
6	*H. reinboldii*	<0.000001	<0.000001	<0.05	<0.0005
	N. conicum	<0.0005	<0.0005	ns	<0.05

covers approaching 100% on true algal crests and exposed oceanic reef margins, it would be unrealistic to suggest that their average global cover is anywhere near this level. Also, in areas when they do cover 90%–100% of the reef, surface relief factors of five are abnormal. Thus, when I have given estimates based on 100% cover, they represent what might be possible in exceptional instances. This assumes, however, that samples measured within continuously stirred incubation chambers perform similarly to samples in open water, and there are reasons that they might not. For example, much higher rates of productivity have been measured at times on both natural and artificial reefs using open-water techniques (Adey 1983; Adey and Steneck 1985; Small and Adey 2001), and turf algae have been shown to be more productive in chambers equipped with oscillating flow regimes (Carpenter et al. 1991). Since it is very difficult to generate flow regimes and rates that closely approximate reef waters, it would appear likely that chamber-bound specimens possess thicker boundary layers that inhibit nutrient delivery and gas exchange. Even with regular flushing, samples experience abnormal excursions from normal seawater [O_2], [CO_2], and pH, and when confined within chambers they are not continuously influenced, to their benefit or detriment, by chemical changes produced by the surrounding benthos (*see* McConnaughey et al. 2000; Small and Adey 2001). In spite of these deficiencies, rates greatly above those presented here do not appear to be the norm in open reef environments (Kinsey 1985) or in coral reef microcosms (Griffith et al. 1987; Atkinson et al. 1999).

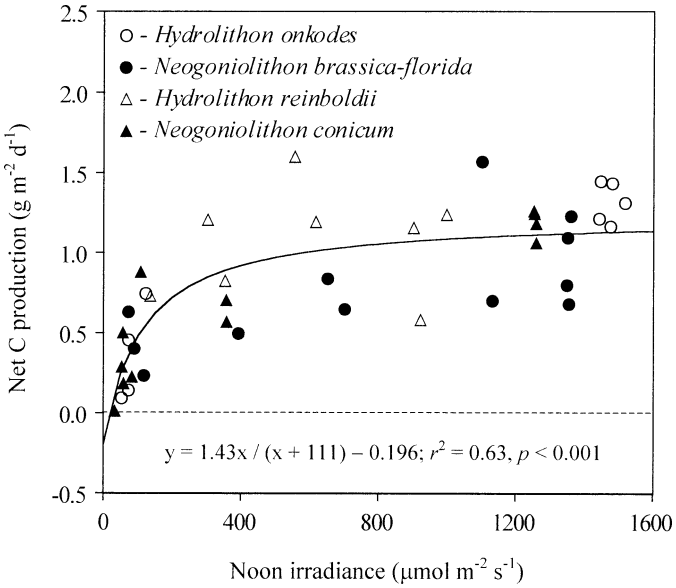

Fig. 6. Net 24-h carbon production by the crustose coralline algae *Hydrolithon onkodes, Neogoniolithon brassica-florida, Hydrolithon reinboldii,* and *Neogoniolithon conicum* as a function incident irradiance at noon on the windward reef at Lizard Island, northern GBR.

R. Steneck very generously provided me with recent and as yet unpublished estimates of crustose coralline cover on reefs in the GBR, Palau, and Guam; they vary from around 10% to 30% (pers. comm.). These estimates are higher than McClanahan (1997) obtained on a fringing reef in Kenya (0.1%–18.3%), lower than Littler (1971) reported for a fringing reef in Hawaii using line transect and photographimetric methods (mean estimates of 31.9% and 45.6% cover, respectively), and far below what can be observed on true algal ridges in the Caribbean and on Pacific atoll rims (e.g., Adey 1975; Steneck and Adey 1976; Andréfoüet et al. pers. comm.).

Steneck derived his estimates from line transects by measuring the uppermost species cover. Multiplying the mean gross production rate obtained here for the four species on the windward reef slope at Lizard Island of 1.4 g C m^{-2} d^{-1} (data for in situ samples in Table 4, averaged over the interval 2–18 m) by Steneck's estimates yields rates of 0.1–0.4 g C m^{-2} crust d^{-1} and 0.7–2 g C m^{-2} planar d^{-1}. The latter rates thus represent 23%–67% of the estimate of Crossland et al. (1991) for average whole-reef gross production.

However, coralline cover beneath coral canopies and in crevices was not included in Steneck's survey. This cover can be considerable on oceanic reef margins (pers. obs.). Although the average productivity of heavily shaded corallines will be lower, it will not be negligible. Also, as light is more strongly attenuated by the water column at Lizard Island, a midshelf reef system, than by the open ocean, the rates of production given here are likely lower than would be measured at equivalent depths on barrier and atoll reef systems. When all of these factors are taken into account, it would appear that crustose coralline algae are not low rate producers of organic carbon. Given their abundance on coral reefs, the conclusion of Larkum (1983) that coralline algae

Table 6. Reported mean rates of maximal gross and net photosynthesis by tropical coralline algae, including data given here (in situ rates in bold text), in descending order with priority given to net production. In this study, planar area rates are for planar areas of crust, rather than for planar areas of reef, since the rates were calculated by scaling up from the cross-sectional areas of the core samples (i.e., from πr^2), which exhibited comparatively little variation in surface topography (maximum real area : projected area ratio of 1.4 : 1). Empty cells indicate rates not provided or incalculable from the information given. Note that *Hydrolithon onkodes, Hydrolithon gardineri, Neogoniolithon brassica-florida,* and *Neogoniolithon conicum* may be better known by their former names of *Porolithon onkodes, Porolithon gardineri, Neogoniolithon fosliei,* and *Paragoniolithon conicum,* respectively (*see* Chisholm 2000 for references to taxonomic revisions).

Source	Species	Depth (m)	*n*	Max. photosynthesis ($mg\ O_2\ m^{-2}\ h^{-1}$) Net		Gross	
				Crust	Planar	Crust	Planar
In situ	***Hydrolithon reinboldii***	**6**	**4**	**627**	**739**	**730**	**860**
In situ	***Hydrolithon onkodes***	**0**	**4**	**589**	**636**	**730**	**788**
Littler (1973*a*)	*Hydrolithon onkodes*	0		563			
In situ	***Neogoniolithon brassica-florida***	**3**	**4**	**531**	**682**	**675**	**887**
In situ	***Hydrolithon reinboldii***	**3**	**4**	**528**	**567**	**643**	**691**
In situ	***Neogoniolithon conicum***	**0**	**4**	**490**	**574**	**627**	**734**
Laboratory	*Hydrolithon onkodes*	0	6	477	547	624	717
In situ	***Neogoniolithon brassica-florida***	**0**	**4**	**467**	**558**	**589**	**703**
In situ	***Neogoniolithon conicum***	**6**	**3**	**442**	**475**	**534**	**574**
Littler and Doty (1975)	*Hydrolithon gardineri*	0			533		
Littler (1973*b*)	*Hydrolithon gardineri*	0	2				600
Littler (1973*b*)	*Hydrolithon onkodes*	0	12				517
Littler and Doty (1975)	*Hydrolithon onkodes*	0			480		
Hawkins and Lewis (1982)	*Hydrolithon onkodes* (dominant species)	0	10	380		600	
Laboratory	*Hydrolithon onkodes*	3	4	381	422	499	554
Marsh (1970)	*Hydrolithon onkodes* (probable identity)	0	32	360		480	
Wanders (1976)	*Neogoniolithon solubile*	0.5–3	17	340		430	
Laboratory	*Neogoniolithon conicum*	0	5	323	362	422	474
Laboratory	*Neogoniolithon brassica-florida*	0	4	323	333	460	483
In situ	***Neogoniolithon conicum***	**18**	**2**	**320**	**344**	**410**	**441**
Laboratory	*Hydrolithon reinboldii*	3	4	317	358	400	454
Laboratory	*Hydrolithon reinboldii*	0	5	310	333	454	490
Laboratory	*Hydrolithon onkodes*	2	4	301	336	483	541
Laboratory	*Hydrolithon reinboldii*	6	4	294	320	362	390
In situ	***Neogoniolithon brassica-florida***	**6**	**2**	**291**	**339**	**387**	**450**
Laboratory	*Neogoniolithon brassica-florida*	6	5	285	317	365	410
Laboratory	*Neogoniolithon brassica-florida*	3	4	272	310	381	438
Littler (1973*b*)	*Sporolithon erythraeum*	0	9				360
Littler et al. (1986)	Unidentified sp.	81	4		267		
Laboratory	*Neogoniolithon conicum*	6	5	237	256	314	339
Wanders (1976)	*Hydrolithon pachydermum*	0.5–3	21	220		320	
Wanders (1976)	*Lithophyllum* sp. 3	0.5–3	25	200		280	
Laboratory	*Neogoniolithon conicum*	18	5	192	214	253	282
Wanders (1976)	*Lithophyllum intermedium*	0.5–3	18	190		280	
Wanders (1976)	*Lithophyllum* sp. 4	0.5–3	19	150		230	
Vooren (1981)	*Hydrolithon boergesenii*	11	2	120		220	
Vooren (1981)	*Hydrolithon boergesenii*	25	3	120		220	
Vooren (1981)	*Archaeolithothamnion dimotum*	25	7	110		210	

could make a significant contribution to overall production appears to be well supported.

Larkum (1983) proposes that 8 g C $m^{-2}\ d^{-1}$ is the maximum sustainable limit to net primary production on coral reefs, which is equivalent to a gross productivity of 12 g C $m^{-2}\ d^{-1}$ according to Kinsey (1985). Kinsey (1985) argues against Larkum's theoretical limit on the basis of a few higher rate measurements, made over extended periods: 17 g C $m^{-2}\ d^{-1}$ on a coral shoal in the Houtman Abrolhos reefs (Smith 1981) and 30 g C $m^{-2}\ d^{-1}$ on an inner reef flat at St. Croix (Adey 1983; Adey and Steneck 1985). Kinsey's arguments may be justified because data are almost entirely lacking for outer reef slopes, which frequently have high living cover, complex three-dimensional structures, and higher rates of water advection, mixing, and nutrient supply than other reef zones (Smith 1981; Kinsey 1985). The outer slopes of barrier reefs on the GBR regularly have high cover of coralline algae beneath canopies of branching corals; thus, total live cover can significantly exceed 100% on a projected area basis (pers. obs.). Coralline algae could contribute up to half of the suggested maximum sustainable gross production (12 g C $m^{-2}\ d^{-1}$) at 70%–85% cover on a reef slope with high surface relief. When combined with coral production, it would not be surprising to find rates in excess of the

suggested 12 g m^{-2} d^{-1} limit, although Larkum's arguments would appear to be reasonable in most other reef situations in the absence of eutrophication.

Eutrophication can favor the development of crustose and articulated coralline algae (Littler 1973*a;* Kindig and Littler 1980; Littler et al. 1991), and there is ample evidence that anthropogenic nutrient enrichment is affecting nearshore reefs in many parts of the world (Wilkinson 2000). An increase in the abundance of crustose coralline algae is much preferable to the development of large fleshy algae, since the latter make no contribution to carbonate production or reef consolidation and they deprive carbonate-secreting organisms of irradiance. However, coralline algae may not increase in abundance under nutrient enrichment if concomitant restructuring of the grazing community leads to arrestment of the algal successionary series at the stage of filamentous turf algae (McClanahan 1997).

While many coralline algae depend upon grazers to limit turf algal competition (e.g., Steneck and Dethier 1994; Adey 1998), grazers remove substantial amounts of their tissue and skeletal carbonate (e.g., Steneck 1983; Steneck 1985; Chisholm 2000). Although coralline algae shed tissue by epithallial sloughing (e.g., Keats et al. 1997; Steneck 1997), their generally slow rates of accretion indicate that they make important trophic contributions to coral reef development.

In conclusion, the primary productivity of reef-building coralline algae might have been underestimated because of the difficulties associated with making measurements in situ. The higher rates of productivity measured in situ raise the possibility that coralline crusts derive nutrients from the underlying reef matrix. In estimating the importance of coralline algae to reef organic production, their cover in shaded environments must be considered. The combination of relatively high instantaneous productivity and low rates of long-term accretion indicates that coralline algae make substantial contributions to the food supply within reef systems. Within broad limits, the data provided here enable the productivity of reef-building coralline algae to be estimated from measurements of in situ irradiance near the solar zenith (Fig. 6).

References

ADEY, W. H. 1975. The algal ridges and coral reefs of St. Croix. Atoll. Res. Bull. No. 187.

———. 1983. The microcosm: A new tool for reef research. Coral Reefs **1:** 193–201.

———. 1998. Coral reefs: Algal structured and mediated ecosystems in shallow, turbulent, alkaline waters. J. Phycol. **34:** 393–406.

———, AND R. S. STENECK. 1985. Highly productive eastern Caribbean reefs: Synergistic effects of biological, chemical, physical and geological factors, p. 163–187. *In* M. L. Reaka [ed.], The ecology of deep and shallow coral reefs, Symposia Series for Undersea Research 1. NOAA.

ARNOLD, K. E., AND S. N. MURRAY. 1980. Relationships between irradiance and photosynthesis for benthic marine green alga (Chlorophyta) of differing morphologies. J. Exp. Mar. Biol. Ecol. **43:** 183–192.

ATKINSON, M. J., AND OTHERS. 1999. The Biosphere 2 coral reef biome. Ecol. Eng. **13:** 147–171.

CARPENTER, J. H. 1966. New measurements of oxygen solubility in pure and natural water. Limnol. Oceanogr. **11:** 264–277.

CARPENTER, R. C., J. M. HACKNEY, AND W. H. ADEY. 1991. Measurements of primary productivity and nitrogenase activity of coral reef algae in a chamber incorporating oscillatory flow. Limnol. Oceanogr. **36:** 40–49.

CHALKER, B. E. 1980. Modelling light-saturation curves for photosynthesis: An exponential function. J. Theor. Biol. **84:** 205–215.

———, AND W. C. DUNLAP. 1982. Extraction and quantitation of endosymbiotic algal pigments from reef-building corals, p. 45–50. *In* Proceedings of the 4th International Coral Reef Symposium, v. 2.

CHISHOLM, J. R. M. 2000. Calcification by crustose coralline algae on the northern Great Barrier Reef, Australia. Limnol. Oceanogr. **45:** 1476–1484.

———, J.-C. COLLINGWOOD, AND E. F. GILL. 1990. A novel in situ respirometer for investigating photosynthesis and calcification in crustose coralline algae. J. Exp. Mar. Biol. Ecol. **141:** 15–29.

CROSSLAND, C. J., B. G. HATCHER, AND S. V. SMITH. 1991. Role of coral reefs in global ocean production. Coral Reefs **10:** 55–64.

GLYNN, P. W., J. E. N. VERON, AND G. M. WELLINGTON. 1996. Clipperton Atoll (eastern Pacific): Oceanography, geomorphology, reef-building coral ecology and biogeography. Coral Reefs **15:** 71–99.

GRIFFITH, P. C., J. D. CUBIT, W. H. ADEY, AND J. N. NORRIS. 1987. Computer-automated flow respirometry: Metabolism measurements on a Caribbean reef flat and in a microcosm. Limnol. Oceanogr. **32:** 442–451.

HAWKINS, C. M., AND J. B. LEWIS. 1982. Benthic primary production on a fringing coral reef in Barbados, West Indies. Aquat. Bot. **12:** 355–363.

JEFFREY, S. W., AND G. F. HUMPHREY. 1975. New spectrophotometric equations for determining chlorophylls *a, b,* c_1, and c_2 in higher plants, algae and natural phytoplankton. Biochem. Physiol. Pflanz. **167:** 191–194.

KEATS, D. W., M. KNIGHT, AND C. PUESCHEL. 1997. Antifouling effects of epithallial shedding in three crustose coralline algae (Rhodophyta, Coralinales) on a coral reef. J. Exp. Mar. Biol. Ecol. **213:** 281–293.

KINDIG, A. C., AND M. M. LITTLER. 1980. Growth and primary production of marine macrophytes exposed to domestic sewage effluents. Mar. Environ. Res. **3:** 81–100.

KINSEY, D. W. 1985. Metabolism, calcification and carbon production. I. System level studies, p. 505–526. *In* Proceedings of the 5th International Coral Reef Congress, v. 4.

KLUMPP, D. W., AND A. D. MCKINNON. 1989. Temporal and spatial patterns in primary productivity of a coral-reef epilithic algal community. J. Exp. Mar. Biol. Ecol. **131:** 1–22.

LARKUM, A. W. D. 1983. The primary productivity of plant communities on coral reefs, p. 221–230. *In* D. J. Barnes [ed.], Perspectives on coral reefs. Australian Institute of Marine Science.

LITTLER, M. M. 1971. Standing stock measurements of crustose coralline algae (Rhodophyta) and other saxicolous organisms. J. Exp. Mar. Biol. Ecol. **6:** 91–99.

———. 1973*a*. The population and community structure of Hawaiian fringing-reef crustose Corallinaceae (Rhodophyta, Cryptonemiales). J. Exp. Mar. Biol. Ecol. **11:** 103–120.

———. 1973*b*. The distribution, abundance, and communities of deep-water Hawaiian crustose Corallinaceae (Rhodophyta, Cryptonemiales). Pac. Sci. **27:** 281–289.

———. 1980. Morphological form and photosynthetic performanc-

es of marine macroalgae: Tests of a functional form hypothesis. Bot. Mar. **22:** 161–165.

———, AND M. DOTY. 1975. Ecological components structuring the seaward edges of tropical Pacific reefs: The distribution, communities and productivity of *Porolithon.* J. Ecol. **63:** 117–129.

———, AND D. S. LITTLER. 1985. Deepest known plant life discovered on an uncharted seamount. Science **227:** 57–59.

———, ———, S. M. BLAIR, AND J. N. NORRIS. 1986. Deep-water plant communities from an uncharted seamount off San Salvador Island, Bahamas: Distribution, abundance and primary productivity. Deep-Sea Res. **33:** 881–892.

———, ———, AND E. A. TITLYANOV. 1991. Comparisons of N- and P-limited productivity between high granitic islands versus low carbonate atolls in the Seychelles Archipelago: A test of the relative dominance paradigm. Coral Reefs **2:** 111–118.

MARSH, J. A., JR. 1970. Primary productivity of reef-building calcareous red algae. Ecology **51:** 255–263.

MCCLANAHAN, T. R. 1997. Primary succession of coral-reef algae: Differing patterns on fished versus unfished reefs. J. Exp. Mar. Biol. Ecol. **218:** 77–102.

MCCONNAUGHEY, T. A., W. H. ADEY, AND A. M. SMALL. 2000. Community and environmental influences on reef coral calcification. Limnol. Oceanogr. **45:** 1667–1671.

ROUGERIE, F., AND B. WAUTHY. 1988. The endo-upwelling concept: From geothermal convection to reef construction. Coral Reefs **12:** 19–30.

SMALL, A. M., AND W. H. ADEY. 2001. Reef corals, zooxanthellae and free-living algae: A microcosm study that demonstrates synergy between calcification and primary production. Ecol. Eng. **16:** 443–457.

SMITH, S. V. 1981. The Houtman Abrolhos Islands: Carbon metabolism of coral reefs at high latitude. Limnol. Oceanogr. **26:** 612–621.

STEARN, C. W., T. P. SCOFFIN, AND W. MARTINDALE. 1977. Calcium carbonate budget of a fringing reef on the west coast of Barbados. I. Zonation and productivity. Bull. Mar. Sci. **27:** 479–510.

STENECK, R. S. 1983. Escalating herbivory and resulting adaptive trends in calcareous algal crusts. Paleobiology **9:** 44–61.

———. 1985. Adaptations of crustose coralline algae to herbivory: Patterns in space and time, p. 352–366. *In* D. F. Toomey and M. H. Nitecki [eds.], Paleoalgology. Springer.

———. 1997. Crustose corallines, other algal functional groups, herbivores and sediments: Complex interactions along reef productivity gradients, p. 23–28. *In* Proceedings of the 8th International Coral Reef Symposium, v. 1.

———, AND W. H. ADEY. 1976. The role of environment in control or morphology in *Lithophyllum congestum,* a Caribbean algal ridge builder. Bot. Mar. **19:** 197–215.

———, AND M. N. DETHIER. 1994. A functional group approach to the structure of algal-dominated communities. Oikos **69:** 476–498.

VOOREN, C. M. 1981. Photosynthetic rates of benthic algae from the deep coral reef of Curacao. Aquat. Bot. **10:** 143–159.

WANDERS, J. B. W. 1976. The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles). I. Primary productivity in the coral reef. Aquat. Bot. **3:** 357–390.

WILKINSON, C. 2000. Status of coral reefs of the world: 2000. Australian Institute of Marine Science.

Received: 22 November 2002
Accepted: 18 February 2003
Amended: 4 March 2003