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Calcification by crustose coralline algae on the northern Great Barrier Reef, Australia

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Abstract

Calcification by four species of crustose coralline algae was estimated on the windward reef at Lizard Island, northern Great Barrier Reef, Australia, by combining measurements of O_2, pH, and total alkalinity with equations describing the seawater carbonate equilibrium. Calcification (C) was regressed against irradiance (I) and modeled using a general exponential function. C–I models yielded estimates of gross calcification that ranged from 9.6 mmol $CaCO_3$ m^{-2} h^{-1} at 0 m to 2.0 mmol $CaCO_3$ m^{-2} h^{-1} at 18 m. A significant proportion of all samples exhibited $CaCO_3$ dissolution in the dark. Integration of C–I models with half sine-curve approximations of whole-day irradiance yielded estimated net deposition rates of 0.82 to 9.1 g $CaCO_3$ m^{-2} d^{-1}. Net 24-h calcification was linearly correlated with noontime irradiance. Daily $CaCO_3$ deposition as a function of reef surface relief (3.1 for the crest and 5.0 for the slope) indicated potential contributions to reef accretion of 4.1 to 28.1 g m^{-2} d^{-1}, assuming 100% coralline cover. These estimates predict annual deposition rates of 1.5 to 10.3 kg $CaCO_3$ m^{-2} yr^{-1}, provided that measurements made between late summer and mid-winter are representative of calcification throughout the year. Since observed accretion falls far short of the quantities predicted by these measurements, erosive agencies must remove much of the $CaCO_3$ deposited annually by crustose coralline algae on windward reef margins.

Calcification by crustose coralline algae is crucial to the formation and maintenance of coral reefs (Wray 1971; Littler 1972). Coralline algae bind adjacent substrata and provide a calcified tissue barrier against erosion (Bak 1976). Coralline algae also serve as food for grazers—notably parrot fish, urchins, and starfish—and provide hard substrata for settlement of invertebrate larvae (Adey 1998).

Few data describe specific rates of calcification by coralline algae, although coarse estimates can be derived from metabolic studies of reef communities in which coralline algae were dominant components (e.g., Kinsey 1985). Long-term studies of growth rates have provided information on net accretion but not on losses due to chemical and mechanical erosion. Most data based on measurements of ^{45}Ca incorporation by calcareous algae are thought to be unreliable (Barnes and Chalker 1990). In particular, non–biologically mediated isotopic exchange has, on occasion, caused more ^{45}Ca to be incorporated into dead algal controls than actively growing samples (*see* Chisholm and Gattuso [1991] for references).

A significant body of research has shown that biological precipitation of $CaCO_3$ can be estimated from changes in seawater total alkalinity (*see* Kinsey 1985; Chisholm and Gattuso 1991). This technique has not been widely applied, however, in studies of algal calcification, perhaps because it has been perceived that prohibitively large quantities of biological material are needed to produce measurable changes in total alkalinity (Borowitzka 1977). Chisholm et al. (1990) demonstrated that this need not be the case if the ratio of seawater volume to algal biomass is suitably adjusted. Measurements of total alkalinity change (ΔA_T) can then be made in concert with measurements of O_2 concentration and pH change to derive values for the photosynthetic and respiratory quotients (PQ and RQ, respectively). Armed with reliable estimates for the metabolic quotients, calcification can be followed without recourse to laborious determinations of total alkalinity using oxygen and pH sensors (Barnes 1983; Barnes and Devereux 1984).

This study reports rates of calcification by four species of coralline algae, species that contribute significantly to reef development in the Indo-Pacific (Adey et al. 1982, and *see* taxonomic amendments by Woelkerling 1987, 1988; Penrose and Woelkerling 1992; Woelkerling et al. 1993). Measurements of O_2 concentration and pH, together with irradiance and temperature, were made over continuous 24-h cycles using a submersible respirometer. Water samples were taken from the sample chamber during certain incubations for determination of ΔA_T to permit calculation of the metabolic quotients.

Methods

Site—Measurement of crustose coralline calcification was undertaken between March and July of 1986 on the windward, southeast-facing margin of the reef at Lizard Island, northern Great Barrier Reef (GBR), Australia (14°40′S, 145°28′E).

Samples—Replicate, in situ, circular samples were produced on the reef by cutting through coralline crusts to a depth of 10–15 mm with a diamond-tipped core-barrel (36-

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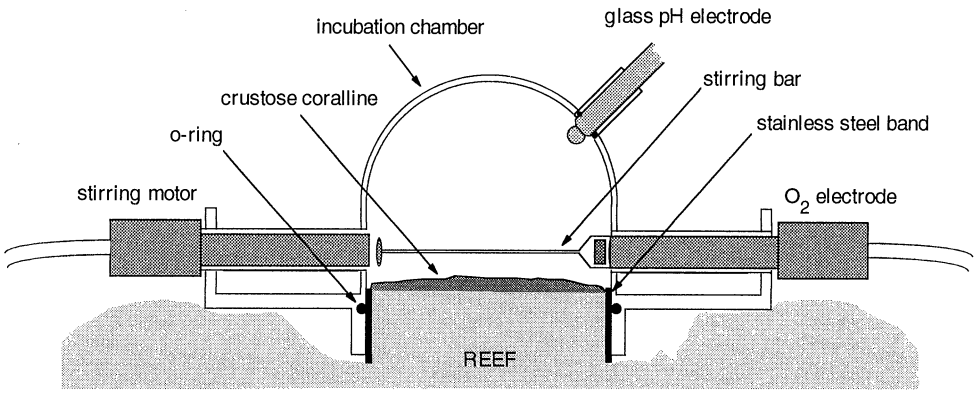

Fig. 1. Simplified cross-sectional diagram of experimental set-up used for in situ measurement of crustose coralline calcification (*see* Chisholm et al. [1990] for full details).

mm internal diameter). The core-barrel was driven by a compressed-air drill connected to a SCUBA tank. Specimens smaller than the diameter of the core-barrel, specimens growing in locations that were too confined for deployment of the incubation chamber (135-mm base diameter), and specimens whose surfaces had been perforated by boring organisms were not investigated. In other respects, samples were selected at random at specific depth intervals. The sides of the cores were smeared with dental wax (Orthodonthic Tray, Sybron Kerr), and premium-grade (316) stainless-steel bands were fitted to provide smooth, corrosion-free surfaces. At least four replicates of each species were prepared in this manner at each selected depth interval. Samples of *Hydrolithon onkodes* (Heydrich) Penrose & Woelkerling (formerly *Porolithon onkodes*) were cored at 0 and 2 m; samples of *Neogoniolithon brassica-florida* (Harvey) Setchell & Mason (formerly *Neogoniolithon fosliei*) were cored at 0, 3, and 6 m; samples of *Hydrolithon reinboldii* (Weber van Bosse & Foslie in Foslie) were cored at 3 and 6 m; and samples of *Neogoniolithon conicum* (Dawson) Gordon, Masaki & Akioka (formerly *Paragoniolithon conicum*) were cored at 0, 6, and 18 m. These depths encompassed the limits of the species' vertical distributions at Lizard Island.

Respirometry—Once new tissue growth was visible at the periphery of the core samples, measurements were made of inorganic carbon metabolism over 24-h periods using a submersible respirometer (*see* Chisholm et al. [1990] for full description of equipment and procedures). A small-volume (120-ml), ultraviolet-transparent, acrylic incubation chamber was slid over the core sample until it seated against the encircling stainless-steel band, thereby isolating the specimen (Fig. 1). Oxygen (Kent EIL), temperature (Analog Devices AC2626K4), and pH (Radiometer GK2401) sensors were inserted through cylindrical acrylic fittings bonded to the sidewall of the incubation chamber. All sensors were sealed within their mounting fittings with O-rings. An underwater quantum sensor (Li-192SB) was placed inside a second replica chamber, similarly orientated, and mounted in an adjacent location.

Oxygen and pH sensors were calibrated before each 24-h incubation. The O_2 sensor was calibrated first against a saturated solution of Na_2SO_3 (zero O_2) and second against air-saturated seawater, which had been bubbled overnight with humidified air and maintained at ambient seawater temperature. The pH electrode was calibrated against Radiometer Precision Buffer Solutions S1500 (pH = 6.865 ± 0.005 at 25°C) and S1510 (pH = 7.410 ± 0.005 at 25°C). The temperature sensor was precalibrated against a quartz thermometer (Hewlett-Packard, 0.05°C accuracy traceable to National Bureau of Standards) and subsequently checked at regular intervals against a similarly calibrated glass mercury thermometer (O.1°C accuracy). The quantum sensor (Li-192SB) was calibrated against a second factory-calibrated Li-192SB sensor connected to a light meter (Li-188B).

All sensors with the exception of the pH sensor were connected by underwater electrical cable to a data logger (RCA microboard—CDP18S607, 32-KB RAM memory module, Australian Institute of Marine Science A/D converter and analogue interface control board, 6 × 1.5-V alkaline cell power supply), which was protected within a watertight housing. The pH electrode was connected to the data logger by passing the manufacturer's electrical cable through a flexible pressure-resistant conduit. Sensors were interrogated every 6 s. Sensor readings were integrated over 1-min intervals, stored in RAM, and later downloaded to a personal computer using custom-written data-communication software.

During incubations, seawater was continuously mixed within the sample chamber by a twin-paddle stirring bar (Kent Eil) attached to the tip of the O_2 sensor (*see Fig. 1*). The free end of the stirring bar coupled magnetically with a motor-driven rotating magnet contained within a stainless-steel casing; this magnet was mounted on the opposite side of the incubation chamber. Fresh seawater was flushed through the specimen chamber for 3 min during every 18–30-min period by a small centrifugal pump connected by Tygon hose to a spring-loaded Teflon ball-valve that was mounted on the sidewall of the incubation chamber. The pump was powered by a 12-V gel-cell battery (Yuasa NP6) contained within a separate compartment of the data-logger housing. Seawater exited the incubation chamber via a second self-sealing Teflon ball-valve.

Total alkalinity measurements—Two sets of water samples were collected from the specimen chamber (*see* Chisholm et al. [1990] for apparatus and operation) in 14 experiments that were timed to finish shortly after the sun had reached its zenith. The first sample was taken at the beginning of the final incubation phase (i.e., immediately after the last flush cycle). The second water sample was taken at the end of the final incubation phase (i.e., prior to removal of the specimen chamber). Water samples were collected at these times to bridge the daylight period over which the coralline samples would be as close as possible to "light saturated" with respect to photosynthesis. The 14 experiments were performed on three to five samples of each species. Pre- and postincubation water samples (100 ml) were filtered (0.45 μm; Millipore), stored without air in foil-wrapped, HCl-washed, seawater-conditioned glass bottles (at 4°C), and subsequently titrated against 0.005 N HCl for determination of ΔA_T (*see* Chisholm et al. 1990).

Postincubation procedures—The coralline specimen was chipped from the reef surface and taken to the laboratory in a seawater-filled container. The specimen was repositioned in the access port of the chamber, the sensors and stirrer motor were replaced, and the chamber was filled with fresh seawater. The pH sensor was removed, allowing the water to flow into a measuring cylinder, thereby enabling determination of incubation volume. Samples were then snap-frozen in a vapor stream of dry ice (CO_2 at −32°C) and stored in aluminum-foil wrappings at −20°C pending measurement of surface area. Surface area was estimated by molding and trimming aluminum foil of known surface area : weight ratio to fit the contours and boundaries of the specimen (Marsh 1970).

Estimates of the surface relief of the crest and windward slope of the reef at Lizard Island were obtained at 3-m depth intervals by comparing linear and topographical distances in horizontal and vertical planes. A steel stake was driven into the reef. One end of a 3-m–long tape measure was attached to the stake. The tape measure was then molded over projections and depressions in the reef surface. The straight-line distance between the stake and the termination point was measured after pulling the tape taut against the stake (n = five sets of comparative measurements in both horizontal and vertical planes at each depth interval).

Determination of calcification or dissolution—It was assumed that measured changes in seawater CO_2 concentration were the product of CO_2 removal by photosynthesis and calcification and CO_2 addition by respiration and $CaCO_3$ dissolution (Smith and Kinsey 1978). The change in total CO_2 concentration ($\Delta\Sigma CO_2$) was calculated by converting measured changes in pH into equivalent units of CO_2 using the first and second dissociation constants for carbonic acid (Skirrow 1975). The change in CO_2 concentration due to calcification and dissolution (ΔCO_{2C-D}) was estimated by subtracting the change in CO_2 due to photosynthesis and respiration (ΔCO_{2P-R}) from $\Delta\Sigma CO_2$. ΔCO_{2P-R} was estimated by dividing measured ΔO_{2P-R} by net PQ ($\Delta O_{2P-R}/\Delta CO_{2P-R}$). Net PQ was determined by simultaneous measurement of ΔO_2, ΔpH, and ΔA_T under saturating irradiance. ΔpH provided an estimate of $\Delta\Sigma CO_2$. ΔA_T provided an estimate of ΔCO_{2C-D} ($=\frac{1}{2}\Delta A_T$). Measured ΔO_{2P-R} divided by $\Delta\Sigma CO_2 - \Delta CO_{2C-D}$ yielded an estimate of net PQ. Net PQ was assumed to approximate true PQ, because all measurements were made under saturating or near-saturating irradiance (Barnes 1983). RQ was assumed to be the reciprocal of PQ.

Data analysis—Hourly rates of calcification, normalized to crust surface area, were plotted against irradiance and modeled using a general exponential function, thus:

$$C = C_m^{light}\left(\frac{e^{(\epsilon+1)(I/I_k)} - 1}{e^{(\epsilon+1)(I/I_k)} + \epsilon}\right) + C^{dark} \quad (1)$$

(Chalker 1980). This exponential function was modeled using the least-squares method (JMP v3 Statistics Made Visual, SAS Institute); note that when $\epsilon = 1$, 0, and −1, the differential form of Eq. 1 integrates to the hyperbolic tangent function, a simple exponential function, and the right-rectangular hyperbola function, respectively. When light saturation of calcification was not observed, data were modeled by linear regression.

Daily rates of calcification were estimated (using Simpson's Rule) by numerically integrating the C–I models with half sine-curve approximations of the change in irradiance between civil dawn and civil dusk (times obtained from the 1986 Nautical Almanac, Her Majesty's Stationery Office, London; *see* Chalker et al. 1984). The peak amplitude of the half sine-curve was determined by the maximum irradiance recorded during each incubation when the sun was near its zenith (I_{max}). Net 24-h calcification was plotted against I_{max} and analyzed by linear regression.

Results

Seawater temperature inside the specimen chamber varied from 30 to 23°C over the course of experiments (March–July) and by up to ±0.7°C during any single incubation. Maximum noontime irradiance varied from 30 μmol m^{-2} s^{-1} at 18 m to 1,516 μmol m^{-2} s^{-1} at 0 m. Samples at given depths on the reef slope experienced widely varying irradiance as a function of differential shading and orientation with respect to the sun (Table 1).

Experimentally determined values for PQ ranged from 1.05 to 1.48. The mean PQ of *N. conicum* was 1.07 (±0.04, 95% confidence limits; n = 3), which indicated production of carbon compounds predominantly at the reduction level of carbohydrate. The mean PQs of the other three species were in excess of 1.2: *H. onkodes* = 1.21 (±0.11, n = 5); *N. brassica-florida* = 1.27 (±0.45, n = 3); *H. reinboldii* = 1.33 (±0.27, n = 3); these measurements indicate synthesis of structural or storage compounds.

Curves or straight lines were fitted to C–I data with coefficients of determination (r^2) that ranged from 0.53 to 0.99. Maximum hourly rates of gross calcification ($C_m^{light} + C^{dark}$) ranged from 2.0 to 9.6 mmol m^{-2} h^{-1} (Table 1). Mean hourly rates of calcification in the dark varied from −1.8 to 1.1 mmol m^{-2} h^{-1} (Table 1). Full light saturation of calcification was rarely observed (Fig. 2). Samples existing in deep shade

Table 1. Gross calcification capacity in the light (C_m^{gross}) and calcification or dissolution in the dark (C^{dark}) of crustose coralline algae on the windward crest and slope of the reef at Lizard Island; rates are means of *n* samples ±95% confidence intervals; italicized numbers in parentheses indicate the number of samples that became sufficiently light-saturated to obtain reasonable estimates of C_m^{gross}; differences between these numbers and *n* indicate the number of samples that exhibited linear or nearly linear *C–I* relationships.

Species	Depth (m)	*n*	C_m^{gross}	C^{dark}
			mmol $CaCO_3$ m^{-2} h^{-1}	
Hydrolithon onkodes	0	5	9.57±4.96 (*5*)	−0.35±1.97
Neogoniolithon brassica-florida	0	4	8.49±1.04 (*3*)	−0.57±1.36
Neogoniolithon conicum	0	4	3.45±1.98 (*4*)	0.26±0.63
Hydrolithon onkodes	2	4	(*0*)	−0.07±0.56
Neogoniolithon brassica-florida	3	4	7.51 ± 1.08 (*2*)	1.13±1.36
Hydrolithon reinboldii	3	4	7.81 ± 1.88 (*4*)	−1.79±1.81
Neogoniolithon brassica-florida	6	4	3.14±1.48 (*2*)	0.37±1.65
Neogoniolithon conicum	6	4	2.07±4.08 (*2*)	0.20±0.77
Hydrolithon reinboldii	6	4	7.65±3.91 (*4*)	−0.77±0.60
Neogoniolithon conicum	18	4	1.95 (*1*)	−0.31±0.36

or close to their species' lower depth limits frequently exhibited nearly linear *C–I* profiles (Fig. 2).

Total $CaCO_3$ precipitation over the hours of daylight ranged from 1.2 to 9.2 g $CaCO_3$ m^{-2}; precipitation at night varied from −2.2 to 1.4 g $CaCO_{crust}^{-2}$ (Table 2). Over 24 h, net calcification ranged from 0.8 g $CaCO_3$ m^{-2} for samples of *N. conicum* at 18 m to 9.1 g $CaCO_3$ m^{-2} for samples of *H. onkodes* at 0 m (Table 2). Net 24-h calcification varied linearly with noontime irradiance (Fig. 3). Nighttime rates of calcification were highly variable and could be either positive (indicating calcification) or negative (indicating dissolution). Multiplication of net 24-h calcification by 365 yielded estimates of annual calcification that ranged from 0.3 to 3.3 kg $CaCO_3$ m^{-2} (Table 2).

The surface relief factors of the reef crest and windward slope were estimated to be 3.1 and 5.0, respectively. Mul-

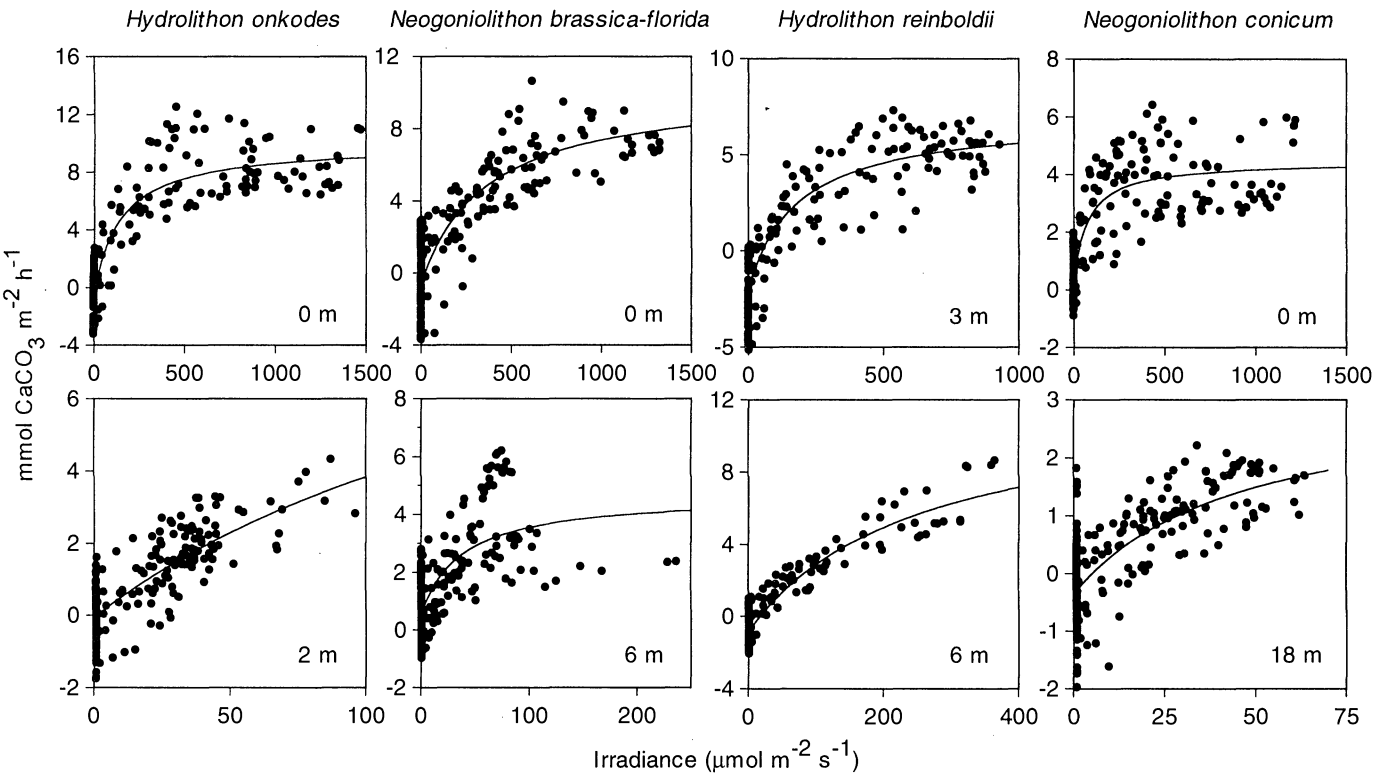

Fig. 2. Mean calcification versus irradiance curves for *Hydrolithon onkodes, Neogoniolithon brassica-florida, Hydrolithon reinboldii,* and *Neogoniolithon conicum* at indicated depths on the windward crest and slope of the reef at Lizard Island, northern GBR.

Table 2. Estimated precipitation or dissolution of $CaCO_3$ by crustose coralline algae over the day, the night, and 24 h on the windward crest and slope of the reef at Lizard Island; rates are the means of n samples ± 95% confidence intervals; I_{max}, the irradiance incident upon the coralline samples at noon.

Species	Depth (m)	n	C_{day}	C_{night}	$C_{24\ h}$	C_{annual}	I_{max}
			g m^{-2}			kg m^{-2}	μmol m^{-2} s^{-1}
Hydrolithon onkodes	0	5	9.20±2.56	−0.81±1.40	9.08±1.66	3.31±0.61	1,441–1,516
Neogoniolithon brassica-florida	0	4	6.35±1.17	−0.68±1.46	5.67±1.80	2.07±0.66	1,347–1,359
Neogoniolithon conicum	0	4	4.26±1.07	0.31±0.68	4.25±1.35	1.55±0.49	1,250–1,257
Hydrolithon onkodes	2	4	2.33±0.67	−0.08±0.60	2.25±1.25	0.82±0.46	50–120
Neogoniolithon brassica-florida	3	4	5.64±2.17	1.36±1.46	7.00±3.29	2.55±1.20	650–1,130
Hydrolithon reinboldii	3	4	4.63±0.90	−2.15±1.94	2.48±2.77	0.91±1.01	615–1,000
Neogoniolithon brassica-florida	6	4	2.83±0.87	0.44±0.84	3.28±1.71	1.20±0.62	70–390
Neogoniolithon conicum	6	4	2.47±0.61	0.24±0.83	2.72±1.73	0.99±0.45	130–550
Hydrolithon reinboldii	6	4	4.33±1.98	−0.93±0.65	3.40±2.01	1.24±0.73	54–355
Neogoniolithon conicum	18	4	1.19±0.32	−0.37±0.38	0.82±0.69	0.30±0.25	30–80

tiplication of the estimated annual rates of calcification by these relief factors indicated potential contributions to reef calcification that ranged from 10.3 kg $CaCO_3$ m^{-2} for *H. onkodes* at 0 m to 1.5 kg $CaCO_3$ m^{-2} for *N. conicum* at 18 m, assuming 100% coverage of the reef.

Discussion

Perceptions of "normal" reef metabolic activity have been derived almost exclusively from community-level studies using slack-water field enclosures or open-water flow techniques (Kinsey 1985). Although invaluable for characterizing certain reef zones (e.g., Barnes 1983; Barnes and Devereux 1984; Kinsey 1985; Barnes and Lazar 1993; Gattuso et al. 1993), both slack-water field enclosures and open-water flow techniques are constrained by requirements for work in shallow water: in the first case, to enable isolation of the chemical environment; in the second case, to ensure unidirectional flow, homogeneous mixing, and sufficient signal strength. Most estimates of community metabolism therefore pertain to reef-flat or shallow lagoonal environments, which are rarely sites of significant carbonate accretion. Net carbonate accretion occurs predominantly around the outer peripheral margins of reefs once they have reached sea level. These margins are not amenable to open-water flow techniques because of hydrodynamic uncertainties and loss of signal strength and are too deep to permit partitioning using open-top field enclosures. Out of necessity, then, measurement of reef slope metabolism must be achieved by isolating benthic communities or their component organisms within incubation chambers or other operationally equivalent structures.

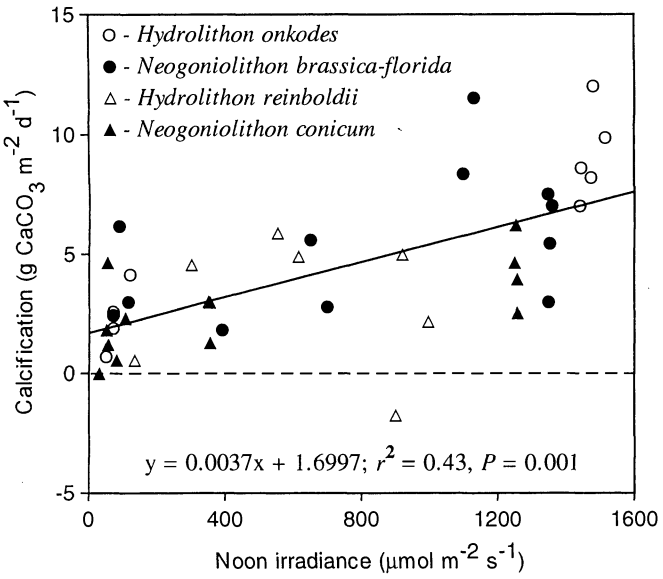

Fig. 3. First-order relationship between net 24-h calcification by the crustose coralline algae *Hydrolithon onkodes, Neogoniolithon brassica-florida, Hydrolithon reinboldii,* and *Neogoniolithon conicum* and irradiance incident upon their surfaces at noon on the windward reef at Lizard Island, northern GBR.

Logistical difficulties associated with work on windward reef margins have provided the greatest impediment to determination of the in situ metabolism of crustose coralline algae. For this reason, the contribution of coralline communities to reef growth has tended to be viewed as functionally important but quantitatively subordinate to corals. Data reported here do not support such a perception. When calcification rates are adjusted for surface relief to provide projected reef area estimates, shallow-water coralline algae can deposit $CaCO_3$ at rates that equate with Kinsey's (1983) and Smith's (1981) fast-rate category of 10 kg $CaCO_3$ m^{-2} yr^{-1} (hereafter all discussion of calcification rates pertains to projected area estimates). Recent work has further shown that elevation of seawater pH by turf algal photosynthesis can drive open-reef calcification faster than may be indicated by measurements made on organisms isolated within incubation chambers (Small and Adey 2000).

If *H. onkodes* covers 90–100% (e.g., Atkinson and Grigg 1984; Glynn et al. 1996) of a reef crest with a similar surface relief to that measured here, data indicate that it should deposit on the order of 9.2–10.3 kg $CaCO_3$ m^{-2} yr^{-1}. In less energetic environments, where the cover of coralline species declines to, for example, 41% (Stearn et al. 1977), the contribution of coralline communities to calcification on a reef

slope with similar physical characteristics to those of Lizard Island should vary between 0.6 and 5.2 kg $CaCO_3$ m^{-2} yr^{-1}.

Remarkably good correspondence between estimates of calcification on algal and coral reef flats at Enewetak Atoll, One Tree Island, and Lizard Island led Smith and Kinsey (1976) to propose that some unknown factor, one that is independent of community structure, sets an upper limit of around 4 kg $CaCO_3$ m^{-2} yr^{-1} on seaward reef-flat calcification. The data presented here indicate that such a result would be surprising on oceanic reef margins where the cover of *H. onkodes* frequently surpasses 70%. Rates of calcification obtained for *H. onkodes* in this study predict deposition rates that are more in keeping with the 15 kg $CaCO_3$ m^{-2} yr^{-1} reported by Stearn et al. (1977) for a rich coral-algal–covered fringing reef on the west coast of Barbados and Kinsey's (1983) forecasted 10 kg $CaCO_3$ m^{-2} yr^{-1} rate for "continuous coral-algal cover" on seaward slopes that are shallower than 5 m. Such a rate also fits better with the Barnes and Chalker (1990) evaluation that $CaCO_3$ precipitation on coral reefs varies between 1 and 35 kg m^{-2} yr^{-1}, with an average of around 10 kg m^{-2} yr^{-1}. These authors remark that this average is probably biased by a small number of high measurements, which, if eliminated, would result in a mean rate of 3–6 kg $CaCO_3$ m^{-2} yr^{-1}. The bias here may have more to do with overreliance on reef-flat estimates than with overestimation of $CaCO_3$ precipitation rates in particular studies.

Smith (1983) estimates that a deposition rate of 10 kg $CaCO_3$ m^{-2} yr^{-1} should translate to upward reef growth of around 7 mm yr^{-1}, assuming an average porosity of 50%. Indo-Pacific reefs have made little upward progress in recent geological history (Adey 1978*b*; Davies 1983), indicating that erosive forces (which are probably combined with stress-induced periods of little or no growth) must remove much of the $CaCO_3$ precipitated in the near-surface waters of coral reefs (Buddemeier et al. 1975). Davies (1983) reviewed in detail the rates of past and present reef growth and summarized much of what is known concerning the factors that affect them. Collated information on reef erosion indicates rates of 0.5–4 mm yr^{-1}, with greater reliability at the uppermost limit for lithified intertidal reef platforms at Aldabra. Adey and Vassar (1975) and Steneck and Adey (1976) reported vertical accretion rates of 1–5.2 mm yr^{-1} for coralline crusts of *Hydrolithon pachydermum* and *Lithophyllum congestum,* with the most rapid growth of the latter species occurring 10 cm above and below mean low water at St. Croix in the Virgin Islands. Analysis of core samples taken from Caribbean reefs led Adey (1978*a,b*) to conclude that rates of upward reef growth are generally more rapid when corals predominate but that the degree of consolidation is greater when coralline algae are the principal reef-building components.

Smith's (1983) estimate of upward reef growth of 7 mm yr^{-1} at a deposition rate of 10 kg $CaCO_3$ m^{-2} yr^{-1}, given 50% porosity, drops to 5 mm yr^{-1} if the reef rock is more heavily consolidated to a porosity of 25%. Metabolic measurements presented here for *H. onkodes* indicate potential upward growth of this order on oceanic reef margins, which accords well with estimates of algal ridge growth in the Caribbean (when not limited by sea level rise; ~6 mm; Adey and Burke 1976). Annual erosion on intertidal platforms at Aldabra, which experience a tidal range similar to that associated with many reefs on the GBR (mean high water springs − mean low water springs = 2.8 m), is estimated at 4 mm yr^{-1} (Trudgill 1976). Erosion at rates similar to those estimated by Trudgill at Aldabra could explain the apparent lack of significant coralline accumulation on windward reef margins in the GBR (Hopley 1977; Davies 1983).

A fundamental understanding of the major factors controlling the development of coralline (and other) algae on coral reefs has come from the work of Adey, Littler and Littler, Steneck, and their coworkers (*see* Steneck [1986], Steneck and Dethier [1994], and Adey [1998] for references). Commencing with analysis of the geological record (Adey and Macintyre 1973), this understanding was boosted by recognition of the importance of algal "functional form groups" (Littler and Littler 1980, 1984) and of their control by productivity versus disturbance gradients (Steneck and Dethier 1994; Steneck 1997 [and references given in both]). Crustose coralline algae benefit from and may even depend upon herbivores in shallow fore-reef environments to remove faster growing species of filamentous algae that foul their surfaces and impede extension of their peripheral margins (e.g., Steneck 1986; Steneck and Dethier 1994; Littler et al. 1995; Adey 1998). In lower energy environments (e.g., deeper water), coralline algae can exist beneath macroalgal or coral canopies in the absence of grazers because light levels are too low to support effective growth of more productive competitor species (Jackson and Kaufmann 1987; Steneck and Dethier 1994). Under such conditions, epithallial sloughing appears sufficient to keep their upper surfaces largely free of fouling epiphytes (Littler 1971; Keats et al. 1997; Steneck 1997).

Effective removal of fouling algae requires deep grazing by organisms that are capable of excavating carbonate: chitons, limpets, urchins, and herbivorous fishes (Steneck 1983, 1985). The primary ridge-building coralline algae—*H. onkodes* in the Indo-Pacific (Littler 1971) and *H. pachydermum* in the Caribbean (Steneck and Adey 1976)—are supremely well adapted to withstand and recover from the damage caused by excavating grazers (Steneck 1986). They are often thick (>10 mm) and crustose (i.e., lacking erect branches or protuberances). They possess embedded spore chambers that protect their reproductive propagules from surface grazers. They have subapical meristems, from which damaged upper cell layers can be regenerated. They possess fusion cells that operate in conjunction with primary and secondary pit connections, enabling vertical and lateral translocation of photosynthetic products to facilitate repair of deeply gouged perithallial (mid) and hypothallial (basal) tissues. These attributes explain the preponderance of thickly encrusting coralline forms on the intensively grazed, high-energy, windward margins of coral reefs (Steneck 1985).

Coanalysis of present-day grazing impacts and scars preserved in the geological record shows that herbivores have become not only more abundant but also significantly more effective at removing carbonate over the last several tens to hundreds of million years (Steneck 1983). In regions such as the GBR, where tidal oscillation normally limits windward reef height to at least a meter below high water, her-

bivorous fishes (overwhelmingly parrot fish) are most likely responsible for removing much of the carbonate that is deposited annually by coralline algae in shallow fore-reef environments. This conclusion is strongly supported by data and observations made on the growth of coralline species with branched morphologies (*see* Steneck [1985] for references). Erect, strongly branched species, such as *L. congestum,* are less susceptible to dessication, because the interstices formed between their branches aid in water retention. Their morphologies further deter limpets from grazing and ensure that a proportion of their photosynthetic surface remains above accumulating sediment. However, branched species can be grazed by fishes to the point of extinction (Steneck and Adey 1976) and thus tend only to occur in high-energy environments, where parrot fish are excluded, or in low-energy environments, where parrot fish are not abundant (*see* Steneck [1985] for discussion and references).

The data presented in this study again demonstrate the strong enhancement of calcification by irradiance. That many coralline algae exhibit measurable rates of $CaCO_3$ dissolution in the dark in fact indicates that light may be a prerequisite for calcification in coralline algae and that when calcification is observed at night, it results from processes that occurred when light was available. Although bioerosion may account for significant carbonate loss on the open reef, it is unlikely that bioerosion was responsible for the measured rates of nighttime carbonate dissolution. As samples were isolated within an incubation chamber, surface grazers were excluded during measurements. Chemical erosion might have been caused by boring organisms that were present in the underlying reef rock, but since noticeably bored crusts or their underlying substrata were not included in our experiments, this seems an unlikely explanation. More plausibly, nighttime carbonate dissolution resulted from respiratory acidification of the alga's tissues or from equivalent pH changes produced by microbial activity in the underlying reef rock.

At this time, it is impossible to determine whether decalcification serves a biological function or if coralline algae are often simply unable to maintain conditions that favor the precipitation of $CaCO_3$ at night. Processes such as the production of spore chambers (conceptacles) and the sloughing of epithallial cells presumably involve localized $CaCO_3$ dissolution and could contribute to variability in the direction and magnitude of carbonate flux in the dark. If localized decalcification were to occur in the light, the processes normally responsible for removal or neutralization of protons resulting from calcification (Barnes and Chalker 1990) would have to be reversed. Such a reversal of chemical action would not be required in the dark if acid resulting from respiratory CO_2 production were channeled to, concentrated at, or simply not removed from sites of decalcification.

In spite of the observed variability in carbonate flux in the dark, Fig. 3 demonstrates that it is possible to estimate net 24-h calcification by mixed populations of reef-building coralline algae on the basis of incident irradiance at noon ($P = 0.001$). Although there is clearly significant variation around the fitted line ($r^2 = 0.43$), the variability is appreciably less than the more than two orders of magnitude that has been observed in calcification rates that were determined using radioisotope techniques (*see* table 3 in Borowitzka [1983]). In an ecological context, it is probably not by chance that the data shown in Fig. 3 are more concentrated at the extremities of the irradiance axis. It is evident on mid-shelf reefs in the GBR that crustose corallines are proportionately more abundant in shallow water, where grazing activity and wave action serve to reduce turf algal biomass, and in deeper or cryptic environments, where light levels are too low to support vigorous growth of competitor species.

Given the current knowledge of surface cover and submarine irradiance, the model presented in Fig. 3 enables (1) calculation of the contribution made by crustose coralline algae to reef calcification and (2), in conjunction with data on accretion, the amount of consolidated carbonate converted into sediment or redissolved during reef maintenance. Figure 3 indicates that rates of calcification do not differ significantly among the four selected coralline species. Therefore, energy input and surface area available for crystal deposition appear to be the major controls on calcification.

Might it be that reef calcification, generally, is limited by the same parameters? That is, do unbranched organisms (e.g., crustose coralline algae, massive corals) and simply structured communities (e.g., reef flats) possess lower rates of calcification than do branched corals or complex reef communities (seaward slopes)—principally because they have lower relative surface areas for $CaCO_3$ deposition? Could this explain why reef calcification appears to fall into specific rate categories (Smith and Kinsey 1976)? Our inability to accurately measure the dimensions of the surfaces upon which new $CaCO_3$ crystals are deposited may obscure the role of skeletal surface geometry in determining calcification rate.

References

ADEY, W. H. 1978*a*. Coral reef morphogenesis: A multidimensional model. Science **15:** 831–837.

———. 1978*b*. Algal ridges of the Caribbean sea and West Indies. Phycologia **17:** 361–367.

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

———, AND R. BURKE. 1976. Holocene bioherms (algal ridges and bank barrier reefs) of the eastern Caribbean. Geol. Soc. Am. Bull. **87:** 95–109.

———, AND I. G. MACINTYRE. 1973. Crustose coralline algae: A re-evaluation in the geological sciences. Geol. Soc. Am. Bull. **84:** 883–904.

———, R. A. TOWNSEND, AND W. T. BOYKINS. 1982. The crustose coralline algae (Rhodophyta: Corallinaceae) of the Hawaiian Islands. Smithson. Contrib. Mar. Sci. **15:** 1–74.

———, AND J. M. VASSAR. 1975. Colonization, succession and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales). Phycologia **14:** 55–69.

ATKINSON, M. J., AND R. W. GRIGG. 1984. Model of a coral reef ecosystem. II. Gross and net benthic primary production at French Frigate Shoals, Hawaii. Coral Reefs **3:** 13–22.

BAK, R. P. M. 1976. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. Neth. J. Sea Res. **10:** 285–337.

BARNES, D. J. 1983. Profiling coral reef productivity and calcifi-

cation using pH and oxygen electrodes. J. Exp. Mar. Biol. Ecol. **66:** 149–161.

———, AND B. E. CHALKER. 1990. Calcification and photosynthesis in reef-building corals and algae, p. 109–131. *In* Z. Dubinsky [ed.], Ecosystems of the world, coral reefs 25. Elsevier.

———, AND M. J. DEVEREUX. 1984. Productivity and calcification on a coral reef: A survey using pH and oxygen electrode techniques. J. Exp. Mar. Biol. Ecol. **79:** 213–231.

———, AND B. J. LAZAR. 1993. Metabolic performance of a shallow reef patch near Eilat on the Red Sea. Exp. Mar. Biol. Ecol. **174:** 1–13.

BOROWITZKA, M. A. 1977. Algal calcification. Oceanogr. Mar. Biol. Annu. Rev. **15:** 189–223.

———. 1983. Calcium carbonate deposition by reef algae: Morphological and physiological aspects, p. 16–28. *In* D. J. Barnes [ed.], Perspectives on coral reefs. Australian Institute of Marine Science.

BUDDEMEIER, R. W., S. V. SMITH, AND R. A. KINZIE, III. 1975. Holocene windward reef flat history, Enewetak Atoll. Geol. Soc. Am. Bull. **86:** 1581–1584.

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

———, T. COX, AND W. C. DUNLAP. 1984. Seasonal changes in primary production and photoadaptation by the reef-building coral *Acropora granulosa* on the Great Barrier Reef, p. 73–87. *In* O. Holm-Hansen, L. Bolis, and R. Gilles [eds.], Marine phytoplankton and productivity. Springer-Verlag.

CHISHOLM, J. R. M., 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.

———, AND J.-P. GATTUSO. 1991. Validation of the alkalinity anomaly technique for investigating calcification and photosynthesis in coral reef communities. Limnol. Oceanogr. **36:** 1232–1239.

DAVIES, P. J. 1983. Reef growth, p. 69–106. *In* D. J. Barnes [ed.], Perspectives on coral reefs. Australian Institute of Marine Science.

GATTUSO, J.-P., M. PICHON, B. DELESALLE, AND M. FRANKIGNOULLE. 1993. Community metabolism and air–sea CO_2 fluxes in a coral reef ecosystem (Moorea, French Polynesia). Mar. Ecol. Prog. Ser. **96:** 259–267.

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.

HOPLEY, D. 1977. The age of outer ribbon reef surface, Great Barrier Reef, Australia: Implications for hydro-isostatic models, p. 23–28. *In* D. L. Taylor [ed.], Proceedings of the third International Coral Reef Symposium of Miami. Univ. of Miami.

JACKSON, J. B. C., AND L. KAUFMANN. 1987. *Diadema antillarum* was not a keystone predator in cryptic environments. Science **235:** 687–689.

KEATS, D., 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.

KINSEY, D. W. 1983. Standards of performance in coral reef primary production and carbon turnover, p. 209–220. *In* D. J. Barnes [ed.], Perspectives on coral reefs. Australian Institute of Marine Science.

———. 1985. Metabolism, calcification and carbon production. I. System level studies, p. 505–526. *In* C. Gabrie and B. Salvat [eds.], Proceedings of the fifth International Coral Reef Congress, Tahiti. Antenne Museum-Ephe.

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

———. 1972. The crustose Corallinaceae. Oceanogr. Mar. Biol. Annu. Rev. **10:** 311–347.

———, AND D. S. LITTLER. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae. Am. Nat. **116:** 25–44.

———, AND ———. 1984. Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. J. Exp. Mar. Biol. Ecol. **74:** 13–34.

———, ———, AND P. R. TAYLOR. 1995. Selective herbivore increases biomass of its prey: A chiton–coralline reef-building association. Ecology **76:** 1666–1681.

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

PENROSE, D., AND W. J. WOELKERLING. 1992. A reappraisal of *Hydrolithon* and its relationship to *Spongites* (Corallinaceae, Rhodophyta). Phycologia **31:** 81–88.

SKIRROW, G. 1975. The dissolved gases—carbon dioxide, p. 1–192. *In* J. P. Riley and G. Skirrow [eds.], Chemical oceanography, v. 2. Academic Press.

SMALL, A., AND W. H. ADEY. 2000. Reef corals, zooxanthellae and free-living algae: a microcosm study that demonstrates synergy between calcification and primary production. Ecological Engineering. In press.

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

———. 1983. Coral reef calcification, p. 240–247. *In* D. J. Barnes [ed.], Perspectives on coral reefs. Australian Institute of Marine Science.

———, AND D. W. KINSEY. 1976. Calcium carbonate production, coral reef growth, and sea level change. Science **194:** 937–939.

———, AND ———. 1978. Calcification and organic carbon metabolism as indicated by carbon dioxide, p. 469–484. *In* D. R. Stoddart and R. E. Johannes [eds.], Coral reefs: Research methods. UNESCO.

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-Verlag.

———. 1986. The ecology of coralline algal crusts: Convergent patterns and adaptive strategies. Ann. Rev. Ecol. Syst. **17:** 273–303.

———. 1997. Crustose corallines, other algal functional groups, herbivores and sediments: Complex interactions along reef productivity gradients, p. 23–28. *In* H. A. Lessios and I. G. Macintyre [eds.], Proceedings of the eighth International Coral Reef Symposium 1, Panama. Smithsonian Tropical Research Institute.

———, AND W. H. ADEY. 1976. The role of environment in control of 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.

TRUDGILL, S. T. 1976. The marine erosion of limestones on Aldabra Atoll, Indian Ocean. Z. Geomorphol. (suppl.) **26:** 164–200.

WOELKERLING, W. J. 1987. The status and disposition of *Parago-*

niolithon (Corallinaceae, Rhodophyta). Phycologia **262:** 144–148.

———. 1988. The coralline red algae: An analysis of the genera and subfamilies of nongeniculate Corallinaceae. Oxford Univ. Press.

———, D. PENROSE, AND Y. M. CHAMBERLAIN. 1993. A reassessment of type collections of non-geniculate Corallinaceae (Corallinales, Rhodophyta) described by C. Montagne and L. Dufour, and of *Melobesia brassica-florida* Harvey. Phycologia **32:** 323–331.

WRAY, J. L. 1971. Algae in reefs through time, p. 1358–1373. Proceedings of the North American Palaeontological Convention, Part J.

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