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Received: 8 April 1998

Accepted: 4 December 1998

Amended: 18 January 1999

## Bicarbonate addition promotes coral growth

**Abstract**—The addition of 2 mM bicarbonate to aquaria containing tropical ocean water and branches of *Porites porites* caused a doubling of the skeletal growth rate of the coral. Nitrate or ammonium addition (20  $\mu$ M) to oligotrophic seawater caused a significant reduction in coral growth, but when seawater containing the extra bicarbonate was supplemented with combined nitrogen, no depression of the higher growth rate was evident. We infer that (1) the present dissolved inorganic carbon (DIC) content of the ocean limits coral growth, (2) this limitation is exacerbated by nitrate and ammonium, and (3) adding DIC increases coral calcification rates and confers protection against nutrient enrichment.

Dissolved inorganic carbon (DIC) is used by all hard corals for growth of CaCO<sub>3</sub> skeletons. Hermatypic corals (reef-

building corals that harbor zooxanthellae) also require DIC for photosynthesis. Until recently, the general view has been that, at concentrations greater than 2 mM, DIC in seawater is in ample supply compared with other essential solutes such as nitrate and phosphate and trace elements such as iron, zinc, and silicon. There is, however, a growing awareness (Raven 1993) that the supply of DIC limits photosynthesis in planktonic algae, seagrasses (Beer and Rehnberg 1997), coccolithophores (Merrett et al. 1993; Israel and Gonzales 1996), and macroalgae (Johnston et al. 1992). Several authors (Muscatine et al. 1989b; Weis et al. 1989; Dubinsky et al. 1990; Lesser et al. 1994) have speculated on DIC limitation in coral. The only study that tested experimentally the effect of adding DIC (Burris et al. 1983) focused only on photosynthesis and was inconclusive.

Table 1. Legend and chemical characteristics for each experimental treatment. Analytical grade  $\text{NaHCO}_3$ ,  $\text{KNO}_3$ , and  $\text{NH}_4\text{Cl}$  were used.

Nitrogen	Dissolved inorganic carbon	
	Seawater	+2 mM
Seawater	Control	Control + DIC
+20 $\mu\text{M}$ $\text{NO}_3^-$ -N	$\text{NO}_3^-$	$\text{NO}_3^-$ + DIC
+20 $\mu\text{M}$ $\text{NH}_4^+$ -N	$\text{NH}_4^+$	$\text{NH}_4^+$ + DIC

Our principal aim was to test the hypothesis that the supply of DIC in seawater limits calcification. To achieve this end, we compared the growth rate of nubbins of the hermatypic coral *Porites porites* cultured in seawater with that of nubbins of the same coral cultured in DIC-enriched (+2 mM) seawater. Long-term exposure to elevated levels (5–20  $\mu\text{M}$ ) of nitrate causes an increase in biomass of zooxanthellae and coral photosynthesis and a reduction in calcification (Marubini and Davies 1996). Competition for carbon between photosynthesis and calcification (Stambler et al. 1991) may explain these results. Calcification and photosynthesis are two processes dependent upon DIC availability: as the total biomass of zooxanthellae is increased by N enrichment, more DIC is used in photosynthesis (Dubinsky et al. 1990; Dubinsky and Jokiel 1994). This in turn decreases the amount of DIC available to the calcicoblastic cells for calcification.

Our second aim was to test if limitation of calcification by nitrogen can be compensated for by DIC enrichment. Branches of *P. porites* of similar shape and diameter were collected from adjacent colonies on a fringing reef off of the

Table 2. Details of the total  $\text{CO}_2$  system in the treatment chambers. pH and total alkalinity (averages with standard deviation) were used to compute  $\text{CO}_2$  speciation using the constants of Mehrbach et al. (1973).

Factor	Seawater	+2 mM dissolved inorganic carbon
pH	8.097 (0.054)	8.266 (0.039)
Total alkalinity (meq $\text{kg}^{-1}$ )	1.97 (0.294)	4.04 (0.436)
$\text{TCO}_2$ (mM)	1.722	3.473
$\text{pCO}_2$ (ppmV)	461	605
$\text{CO}_2$ (mM)	0.012	0.016
$\text{HCO}_3^-$ (mM)	1.556	3.017
$\text{CO}_3^{2-}$ (mM)	0.153	0.442

west coast of Barbados. These branches were made into nubbins (Davies 1995) by grinding the bases flat and gluing them onto 30 mm  $\times$  30 mm perspex tiles. The nubbins were secured to a rack and returned to the reef for 2 weeks until the experiment began. Experimental chambers consisted of 5-liter glass aquaria equipped with an air line system that produced strong, turbulent water motion; each aquarium was designed to hold 12 nubbins. Six chambers were contained in a constant temperature bath ( $27 \pm 0.5^\circ\text{C}$ ) and illuminated for 12 h  $\text{d}^{-1}$  by metal halide lamps ( $200 \pm 50 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ). Chambers were moved systematically around the water bath every 3 d to minimize position effects.

Low nutrient seawater ( $<0.05 \mu\text{M PO}_4^-$ -P,  $<0.2 \mu\text{M NO}_3^-$ -N) collected 3 km offshore was supplied independently to each chamber at a rate of 4  $\text{ml min}^{-1}$  from 18-liter reservoirs. The experimental design is shown in Table 1. Analytical grade  $\text{NaHCO}_3$ ,  $\text{KNO}_3$ , and  $\text{NH}_4\text{Cl}$  were used to in-

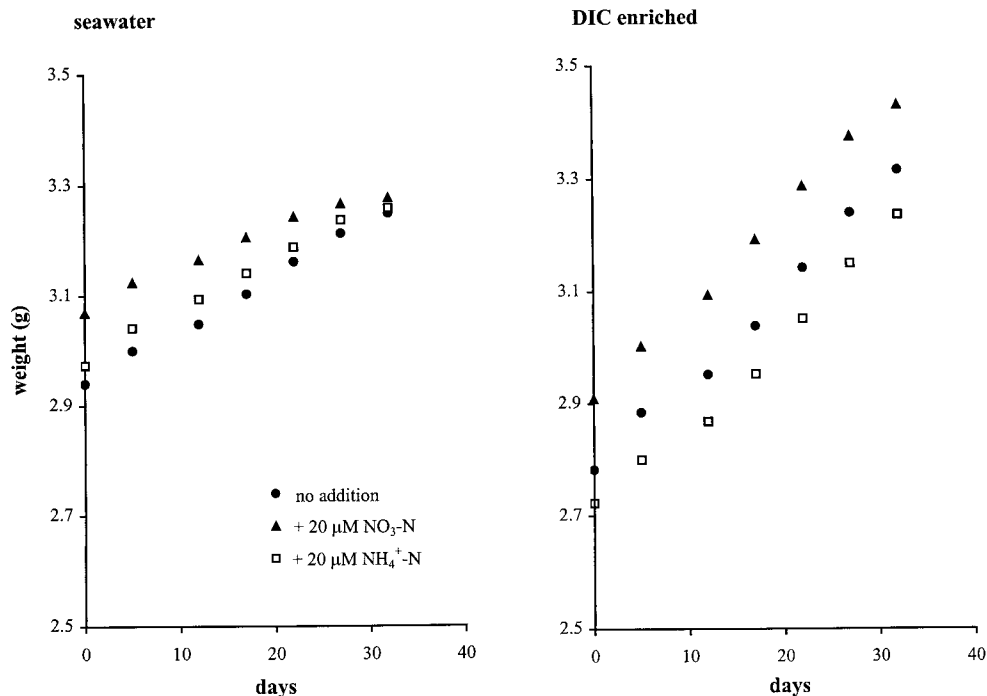


Fig. 1. Mean weight of nubbins of *P. porites* throughout the experiment. Corals were exposed to different nitrogen treatments in seawater and with the addition of 2 mM DIC.

Table 3. ANOVA results from the multiple regression models used to predict the weight of nubbins of *P. porites* exposed to different dissolved inorganic carbon and nitrogen treatments during the initial growth period and the established growth period.

ANOVA	Sum of squares	df	Mean square	F value	P
Initial growth*					
Regression	1,066	7	152	11.3	<0.0001
Residuals	792	59	13		
Established growth†					
Regression	2,608	7	373	16.5	<0.0001
Residuals	1,333	59	23		

\* Growth rate from day 0–17;  $R^2 = 0.76$ .

† Growth rate from day 17–32;  $R^2 = 0.81$ .

crease DIC by 2 mM and  $\text{NO}_3^-$ -N and  $\text{NH}_4^+$ -N by 20  $\mu\text{M}$ , respectively. Total alkalinity (TA, determined by titration; Barnes 1959) and pH (National Bureau of Standards scale) were measured biweekly. Table 2 shows the average pH and TA and the concentrations of constituents of total DIC in the chambers.

Nubbins were retrieved from the reef, their weight and size were measured, and 12 of them were randomly allocated to each chamber. The skeletal weight was measured by buoyant weighing (Davies 1989) at 5-d intervals. The height and mean diameter of each nubbin were measured with calipers at the beginning and at the end of the experiment, and surface area was estimated by assuming each nubbin to be a cylinder capped by a half sphere. Corals were scored daily for the presence of the mucus tunics characteristic of this genus (Coffroth 1991), because calcification is known to cease when tunics are present. The experiment lasted for 32 d but, because of air-supply problems, was interrupted after 9 d, and the nubbins were returned to the reef for 2 d. After day 32, all corals were freeze-dried and photosynthetic pigments extracted in 90% acetone; concentrations were assayed following the equations of Jeffrey and Humphrey (1975).

The response of corals cannot be assumed to be directly proportional to time, because any effect of N on calcification is expected to be dependent upon the increasing algal biomass and therefore indirect. Thus we chose to divide our data set into two parts: initial growth (from day 0 to day 17) and established growth (day 17 to day 32).

The analysis of growth rate in corals often suffers from inappropriate normalization (Marshall 1996), because no parameter can measure directly and precisely the surface area of the calciblastic epithelium upon which calcification is dependent. Weight and surface area are approximations and are thus subject to large errors. We chose a multiple regression model in which growth rate (calculated from the slope of the regression of the raw weight data on time) was the dependent variable. The independent variables included initial surface area, number of days with tunics, and five dummy variables. By using the initial surface area as a variable in the model, any effect of nubbin size can be properly accounted for and separated from any treatment effect. The five dummy variables were designed as contrasts (Draper

Table 4. Significance tests for individual regression coefficients used to predict the weight of nubbins of *P. porites* exposed to different DIC and nitrogen treatments during the initial growth period and established growth period.

	Coefficient	SE	t	P
Initial growth analysis*				
DIC	2.875	0.456	6.306	<0.0001
Initial surface area	1.643	0.338	4.861	<0.0001
Days in tunic	-1.385	0.595	2.328	<0.05
In seawater				
N	0.473	0.473	1.001	n.s.
$\text{NO}_3^-$ vs. $\text{NH}_4^+$	0.896	0.801	1.117	n.s.
In +2 mM DIC				
N	0.214	0.434	0.493	n.s.
$\text{NO}_3^-$ vs. $\text{NH}_4^+$	-1.286	0.751	1.713	n.s.
Established growth analysis†				
DIC	4.226	0.612	6.903	<0.0001
Initial surface area	1.851	0.415	4.454	<0.0001
Days in tunic	-2.037	0.398	5.123	<0.0001
In seawater				
N	-1.650	0.610	2.704	<0.01
$\text{NO}_3^-$ vs. $\text{NH}_4^+$	-0.599	1.114	0.537	n.s.
In +2 mM DIC				
N	-0.825	0.567	1.453	n.s.
$\text{NO}_3^-$ vs. $\text{NH}_4^+$	1.092	0.976	1.119	n.s.

\* Growth rate from day 0–17;  $R^2 = 0.76$ .

† Growth rate from day 17–32;  $R^2 = 0.81$ .

and Smith 1981) to study the effect of DIC treatment regardless of N, the effect of both forms of N with and without added DIC, and the effect of  $\text{NO}_3^-$ -N versus the effect of  $\text{NH}_4^+$ -N with and without added DIC.

Figure 1 shows the mean weight of nubbins in each treatment during the course of the whole experiment; all treatments in seawater with added DIC have a higher slope. This outcome is reflected in the results from the multiple regressions for initial and established growth (Tables 3, 4), where DIC is the best predictor of growth. In the initial growth phase, there is no significant effect of nitrogen treatment on the total amount of calcium carbonate deposited. This changes in the established growth phase, when the effect of N on calcification becomes significant among corals growing in seawater. Corals in enriched DIC did not show a decreased growth rate in response to increased N.

Data on the linear extension of nubbins and on photosynthetic pigment concentration are presented in Table 5. Similar multiple regression analyses with contrasts were carried out on these dependent variables. Regardless of nitrogen treatment, DIC addition had a highly significant effect ( $t = 5.29$ ,  $P < 0.0001$ ) on the linear extension of nubbins. Nitrogen addition had a highly significant effect on chlorophyll concentration in both seawater (Chl  $a$ :  $t = 4.23$ ,  $P < 0.001$ ; Chl  $c_2$ :  $t = 3.76$ ,  $P < 0.001$ ) and in enriched DIC (Chl  $a$ :  $t = 4.24$ ,  $P < 0.001$ ; Chl  $c_2$ :  $t = 3.74$ ,  $P < 0.001$ ).

This experiment has shown that an addition of sodium bicarbonate causes a dramatic increase in coral calcification. This response is fast and sustained: a significant difference

Table 5. Summary data for nubbins of *P. porites* exposed to different dissolved inorganic carbon and nitrogen treatments. Data are mean (SE);  $n = 10$  in each treatment.

Treatment	Initial weight (g)	Initial surface area (cm <sup>2</sup> )	Total linear extension (μm d <sup>-1</sup> )	Initial growth rate (mg d <sup>-1</sup> )	Established growth rate (mg d <sup>-1</sup> )	Chl <i>a</i> (μg cm <sup>-2</sup> )	Chl <i>c</i> <sub>2</sub> (μg cm <sup>-2</sup> )
Control	2.97 (0.199)	10.6 (0.51)	40.3 (8.5)	10.2 (1.3)	11.5 (1.6)	13.08 (0.34)	6.74 (0.58)
NO <sub>3</sub> <sup>-</sup>	3.05 (0.216)	10.8 (0.59)	30.4 (5.2)	8.2 (0.9)	5.5 (0.8)	22.20 (2.23)	10.10 (1.14)
NH <sub>4</sub> <sup>+</sup>	2.99 (0.206)	10.9 (0.55)	28.8 (5.8)	10.0 (1.2)	8.6 (0.9)	23.65 (2.14)	10.58 (0.92)
Control + DIC	2.78 (0.167)	10.3 (0.40)	62.6 (10.0)	14.3 (1.8)	18.6 (2.6)	12.98 (1.41)	6.78 (0.52)
NO <sub>3</sub> <sup>-</sup> + DIC	2.91 (0.151)	10.4 (0.32)	63.0 (5.1)	16.2 (1.5)	16.0 (1.8)	21.76 (1.74)	10.06 (0.60)
NH <sub>4</sub> <sup>+</sup> + DIC	2.72 (0.159)	10.2 (0.29)	80.9 (8.5)	13.0 (1.4)	19.0 (2.0)	22.45 (1.79)	9.87 (0.80)

between treatments was established within the initial growth phase and maintained over the established growth phase. Skeletal growth in corals involves at least two different processes (Barnes and Crossland 1980; Gladfelter 1982). At night, an organic matrix is laid down that deposits the CaCO<sub>3</sub> crystal framework, resulting in apical linear extension (Vago et al. 1997). This process is followed the next day by the nucleation of new crystals into the framework, resulting in increased skeletal density. Hence an increase in skeletal weight could be caused by a higher skeletal density and need not involve an increase in height. However, the linear extension of nubbins growing in enriched DIC was also found to be higher, confirming that both skeletal processes are directly influenced by the supply of DIC.

By adding 2 mM bicarbonate, we changed not only the total concentration of DIC but also the relative proportion of each carbon species as pH increased from 8.10 to 8.27. While CO<sub>2</sub> increased only by a third, HCO<sub>3</sub><sup>-</sup> doubled and CO<sub>3</sub><sup>=</sup> became three times as large. The role of each carbon species in calcification needs to be addressed in future research.

In hermatypic corals, it is commonly assumed that photosynthesis and calcification are tightly coupled (Goreau and Goreau 1959; Barnes and Chalker 1990). Under oligotrophic conditions, however, the addition of ammonium (Hoegh-Guldberg and Smith 1989; Muscatine et al. 1989a; Stimson and Kinzie 1991) or nitrate (Marubini and Davies 1996) results simultaneously in increased photosynthesis (due to higher zooxanthellae population density and photosynthetic pigment concentration) and in a reduction of calcification. Competition for carbon between calciblastic cells and a larger zooxanthellae population could explain this paradox. After a 32-d exposure to elevated N, the photosynthetic pigment concentration was twice as high as controls. Growth rate was reduced, but only in the established growth phase and only in seawater with no DIC addition. No difference was found between NO<sub>3</sub><sup>-</sup>-N- and NH<sub>4</sub><sup>+</sup>-N-enriched corals. Nitrogen does not affect calcification immediately; only after 2 weeks of elevated N is the symbiont biomass high enough to cause a reduction in calcification. The reduced growth rate is compensated for by DIC enrichment. These results fit the hypothesis that N affects calcification indirectly by enhancing the zooxanthellae biomass, which in turn limits the supply of DIC available for calcification (Stambler et al. 1991; Marubini and Davies 1996).

Our study has obvious practical consequences. The

growth rate of hermatypic corals can be readily enhanced by the addition of sodium bicarbonate. This could promote the development of coral farms to provide cultured specimens for the repopulation of damaged reefs, for experimental use, and for the growing aquarium trade. Small areas of damaged natural reef could, in some locations, be treated with bicarbonate, thus providing a kick-start for reef regeneration. Also, since the experimental results show that the low growth rate in the nitrogen-enriched corals is mitigated by adding DIC, such a treatment could produce the double benefit of increasing coral growth rates while also conferring protection against nutrient pollution.

In a wider context and in the longer term, the predicted increase in atmospheric CO<sub>2</sub> will result in a small increase in DIC. However, this increase will be offset by a much more significant decrease in pH. This decrease in pH will cause a significant decrease in CO<sub>3</sub><sup>=</sup> that, in turn, will result in a reduced aragonite saturation state and possibly a reduced global calcification (Gattuso et al. in press). The predicted rise in sea-surface temperature, however, would tend to counteract this effect. Clearly, a deeper understanding of the interaction of DIC, temperature, and pH on calcification is needed before accurate predictions of the effects of climate change on reefs can be made.

We conclude that in seawater, carbon limits coral growth and that this limitation is intensified by the combined addition of nitrogen.

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#### Acknowledgments

We wish warmly to thank P.S. Rainbow for his encouragement and support. The experimental work was carried out at the Bellairs Research Institute of McGill University in Barbados. We are grateful to W. Hunte and J. Marsden for use of the facilities.

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Received: 27 April 1998

Accepted: 25 November 1998

Amended: 31 December 1998