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Effect of nutrient enrichment and elevated CO_2 partial pressure on growth rate of Atlantic scleractinian coral *Acropora cervicornis*

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ABSTRACT: The growth rate of *Acropora cervicornis* branch tips maintained in the laboratory was measured before, during, and after exposure to elevated nitrate (5 and 10 µM NO_3^-), phosphate (2 and 4 µM P-PO_4^3) and/or pCO_2 (CO_2 ~700 to 800 µatm). The effect of increased pCO_2 was greater than that of nutrient enrichment alone. High concentrations of nitrate or phosphate resulted in significant decreases in growth rate, in both the presence and absence of increased pCO_2. The effect of nitrate and phosphate enrichment combined was additive or antagonistic relative to nutrient concentration and pCO_2 level. Growth rate recovery was greater after exposure to increased nutrients or CO_2 compared to increased nutrients and CO_2. If these results accurately predict coral response in the natural environment, it is reasonable to speculate that the survival and reef-building potential of this species will be significantly negatively impacted by continued coastal nutrification and projected pCO_2 increases.

KEY WORDS: *Acropora cervicornis* · Nutrient enrichment · pCO_2 · Growth rate

INTRODUCTION

Global climate change scenarios predict a rather unpleasant future for coral reefs worldwide (Buddemeier 2001, Knowlton 2001, Guinotte et al. 2003, Hughes et al. 2003), and particularly in the Caribbean. Projected increases in coastal population density, mean atmospheric temperatures and frequency of extreme weather events (such as hurricanes) are expected to result in increased coastal runoff and nutrient import into the coastal zone (Landsea 2000a,b, Goldenberg et al. 2001, Houghton et al. 2002, Cohen 2003, Karl & Trenberth 2003). Coral reefs generally occur in waters characterized by low levels of inorganic nutrients (0.2 to 0.5 µM ammonium, 0.1 to 0.5 µM nitrate, and <0.3 µM phosphate, Furnas 1991), and significant increases in nutrient concentrations (>1 µM inorganic nitrogen, >0.3 µM phosphorus) have negative effects on coral growth rates (Hallock & Schlager 1986, Stambler et al. 1991, Ferrier-Pagès et al. 2000). A significant decrease in calcification was observed in *Montastraea annularis* at nitrate concentrations of <5 µM (Tomascik & Sander 1985, Bell & Tomascik 1993, Marubini & Davies 1996). However, Dollar (1994) noted no effect, and Atkinson et al. (1995) observed increased growth in corals exposed to increased nitrate concentrations.

Significant decreases in coral growth in response to phosphorus enrichment have been observed (Kinsey & Davies 1979, Walker & Ormond 1982, Tomascik & Sander 1985). A 60% decrease in the growth rate of *Stylophora pistillata* was observed at a phosphorus concentration of 2 µM (Ferrier-Pagès et al. 2000). However, increased growth of *Pocillopora damicornis* at elevated phosphorus levels has also been reported (Stambler et al. 1991, Steven & Broadbent 1997). The greatest reduction in coral growth rate is observed in the combined presence of nitrogen and phosphorus. At nutrient concentrations of 20 µM ammonium and 2 µM phosphorus, a 50% reduction in calcification rate

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was observed for a patch reef over a period of 6 mo, and a 75% decrease in the growth rate of *S. pistillata* was observed after 10 wk (Kinsey & Davies 1979, Ferrier-Pagès et al. 2000).

Increasing atmospheric CO_2 partial pressure (pCO_2) is likely to change ocean surface water carbonate saturation, and is predicted to result in reduced coral calcification and reef growth (Kleypas et al. 1999, Leclercq et al. 2000, Guinotte et al. 2003). Reduction of calcification from lowered pH and CO_3^{2-} has been observed to be greater than the reduction from nutrient enrichment and is expected to produce weaker skeletons, reduced extension rates, and increased erosion (Kleypas et al. 1999, Marubini & Atkinson 1999). The Intergovernmental Panel on Climate Change carbon cycle models forecast that atmospheric pCO_2 concentrations will reach 540 to 970 µatm (90 to 250% above the concentration in 1750) by the year 2100 (Houghton et al. 2002).

Thus, the trend of increasing coastal nutrification (increased nutrient supply) and rising atmospheric (and eventually ocean) pCO_2 requires investigation to predict the combined effects on coral condition and reef growth. The possible effects of these factors have been experimentally tested on some ecologically important Indo-Pacific corals, such as *Stylophora pistillata* and *Pocillopora damicornis* (Stambler et al. 1991, Ferrier-Pagès et al. 2000), but equivalent experiments investigating similar responses in Caribbean corals are sparse.

The scleractinian coral *Acropora cervicornis* is among the most important reef-builders in the Caribbean, with growth rates estimated at up to 71 mm yr^{-1} or higher (Gladfelter et al. 1978). In addition to its modern importance as a reef-builder, this species is also very often a major component of Pleistocene and Holocene reef deposits, indicating that the current decline of this species may be a unique event due to anthropogenic effects (Jackson 1992, Aronson et al. 1998, Greenstein et al. 1998, but see Miller et al. 2002). In 1999, *A. cervicornis* was added as a candidate to the List of Endangered and Threatened Species under the Endangered Species Act (Diaz-Soltero 1999). Learning more about the effects of a changing global climate and increasing coastal nutrient enrichment on a formerly dominant reef-builder is likely to provide more insight into the reasons for this decline and could aid in the management of the species.

In this study, the growth rate of *Acropora cervicornis* fragments was measured during and after exposure to elevated nitrogen, phosphate, and pCO_2 in order to examine (1) whether the growth rate is affected in the presence of increased nutrients and/or pCO_2 and (2) the recovery potential of this species after nutrient and CO_2 stress.

MATERIALS AND METHODS

Coral specimens. Coral 'nubbins' (192) (branch tips, approximately 5 cm long) were harvested from 2 populations of *Acropora cervicornis* found off Broward County, Florida, USA, designated Site A (located at 26° 10′ 01″ N, 80° 05′ 23″ W; referred to as Oakland I in Vargas-Ángel et al. 2003) and Site B (located at 26° 09′ 12″ N, 80° 05′ 32″ W; referred to as Coral Ridge in Vargas-Ángel et al. 2003). Nubbins were collected from haphazardly selected colonies, attached in an upright position to epoxy disks using cyanoacrylate gel glue and placed in a holding aquarium. The nubbins were then transferred to the treatment tanks after recovery from transport and handling.

Experimental set-up. Experiments were carried out using 16 separate (8 l) closed system aquaria. All tanks were maintained under the same temperature, salinity, aeration, circulation and light conditions. Aquarium water consisted of reverse osmosis/deionized water, mixed with a commercial synthetic sea salt (Tropic Marin®) of known composition in an approximate 1:1 combination with filtered natural seawater. Water circulation and filtration were provided by Aquaclear Mini™ power filters, and weekly 25% water changes were performed to ensure consistent water quality. Gas exchange was facilitated by airstones. Light was provided by metal halide lamps (2 × 175 W, photoperiod 12:12 h). Irradiance was not measured. Nitrate, phosphate, CO_2, pH, total alkalinity (TA), temperature, and salinity levels were tested 3 times per week (Table 1). Salinity as determined by the refractive index method averaged 35.6 (±0.5) ppt. Temperature as measured with an Orion Research Model SA230 pH/mV/°C meter averaged 25.3 (±0.4)°C. Ammonia and nitrite measurements were made using Lamotte Scientific test kits, and remained below detection limits for the duration of the experiment.

Eight treatment conditions were maintained: control (C); nitrate enrichment only (N); phosphate enrichment only (P); nitrate and phosphate enrichment (N-P); CO_2 enrichment only (CO_2); CO_2 and nitrate enrichment (N-CO_2); CO_2 and phosphate enrichment (P-CO_2); and CO_2, nitrate, and phosphate enrichment (N-P-CO_2). The length of the incubation time was 16 wk, divided into 4 equal periods.

Period 1: The growth rate of each nubbin was measured weekly to establish a pre-treatment baseline. Repeated measures ANOVA of the growth rates of the nubbins in the 16 tanks during this control period determined that there was no significant difference between subsamples from the same colony in different tanks ($p > 0.01$). Therefore, observed trends were considered to be the effect of the treatments and not tank effects.

Table 1. Mean water quality parameters (±SD) for each treatment; SWS: sea water scale

Treatment	Parameter	Period 1	Period 2	Period 3	Period 4
Control	Nitrate (µM)	0.44 (±0.08)	0.54 (±0.10)	0.70 (±0.07)	0.23 (±0.04)
	Phosphate (µM)	0.06 (±0.02)	0.08 (±0.03)	0.08 (±0.01)	0.08 (±0.03)
	pCO_2 (µatm)	361 (±13)	357 (±17)	360 (±22)	361 (±14)
	$pH_{(sws)}$	8.06 (±0.02)	8.10 (±0.03)	8.04 (±0.05)	8.06 (±0.02)
	TA (meq l^{-1})	2.14 (±0.08)	2.09 (±0.05)	2.11 (±0.08)	2.14 (±0.06)
N	Nitrate (µM)	0.41 (±0.06)	5.13 (±0.12)	9.93 (±0.14)	0.20 (±0.02)
	Phosphate (µM)	0.03 (±0.02)	0.07 (±0.02)	0.07 (±0.02)	0.10 (±0.01)
	pCO_2 (µatm)	366 (±17)	363 (±17)	367 (±19)	366 (±18)
	$pH_{(sws)}$	8.05 (±0.03)	8.04 (±0.02)	8.05 (±0.01)	8.06 (±0.04)
	TA (meq l^{-1})	2.10 (±0.05)	2.12 (±0.06)	2.17 (±0.09)	2.16 (±0.03)
P	Nitrate (µM)	0.41 (±0.08)	0.45 (±0.10)	0.73 (±0.13)	0.18 (±0.02)
	Phosphate (µM)	0.05 (±0.02)	2.15 (±0.07)	4.14 (±0.16)	0.08 (±0.03)
	pCO_2 (µatm)	357 (±23)	362 (±11)	362 (±14)	362 (±18)
	$pH_{(sws)}$	8.06 (±0.02)	8.09 (±0.01)	8.05 (±0.01)	8.07 (±0.01)
	TA (meq l^{-1})	2.11 (±0.05)	2.14 (±0.06)	2.16 (±0.05)	2.13 (±0.05)
N-P	Nitrate (µM)	0.40 (±0.05)	4.98 (±0.11)	10.01 (±0.14)	0.19 (±0.04)
	Phosphate (µM)	0.02 (±0.01)	2.09 (±0.10)	4.06 (±0.10)	0.09 (±0.01)
	pCO_2 (µatm)	358 (±16)	373 (±13)	363 (±15)	373 (±12)
	$pH_{(sws)}$	8.06 (±0.03)	8.04 (±0.02)	8.04 (±0.01)	8.05 (±0.02)
	TA (meq l^{-1})	2.09 (±0.07)	2.11 (±0.07)	2.10 (±0.08)	2.11 (±0.03)
CO_2	Nitrate (µM)	0.53 (±0.09)	0.52 (±0.10)	0.56 (±0.11)	0.22 (±0.05)
	Phosphate (µM)	0.04 (±0.01)	0.07 (±0.02)	0.10 (±0.03)	0.11 (±0.05)
	pCO_2 (µatm)	367 (±13)	714 (±85)	771 (±78)	365 (±11)
	$pH_{(sws)}$	8.03 (±0.01)	7.72 (±0.07)	7.66 (±0.07)	8.05 (±0.03)
	TA (meq l^{-1})	2.15 (±0.05)	1.72 (±0.09)	1.70 (±0.03)	2.13 (±0.05)
N-CO_2	Nitrate (µM)	0.45 (±0.02)	5.11 (±0.15)	10.08 (±0.10)	0.19 (±0.04)
	Phosphate (µM)	0.04 (±0.02)	0.05 (±0.02)	0.08 (±0.03)	0.09 (±0.01)
	pCO_2 (µatm)	363 (±18)	714 (±85)	768 (±45)	366 (±13)
	$pH_{(sws)}$	8.02 (±0.02)	7.70 (±0.06)	7.67 (±0.07)	8.06 (±0.04)
	TA (meq l^{-1})	2.11 (±0.05)	1.73 (±0.07)	1.70 (±0.04)	2.15 (±0.06)
P-CO_2	Nitrate (µM)	0.46 (±0.08)	0.51 (±0.09)	0.57 (±0.12)	0.20 (±0.03)
	Phosphate (µM)	0.01 (±0.01)	2.13 (±0.10)	4.17 (±0.05)	0.08 (±0.03)
	pCO_2 (µatm)	363 (±16)	728 (±80)	764 (±51)	359 (±11)
	$pH_{(sws)}$	8.05 (±0.03)	7.73 (±0.07)	7.70 (±0.08)	8.01 (±0.02)
	TA (meq l^{-1})	2.12 (±0.07)	1.75 (±0.11)	1.72 (±0.05)	2.11 (±0.03)
N-P-CO_2	Nitrate (µM)	0.47 (±0.13)	5.08 (±0.06)	9.88 (±0.16)	0.21 (±0.03)
	Phosphate (µM)	0.02 (±0.01)	2.19 (±0.07)	4.35 (±0.04)	0.20 (±0.09)
	pCO_2 (µatm)	357 (±31)	722 (±87)	766 (±66)	352 (±10)
	$pH_{(sws)}$	8.00 (±0.04)	7.70 (±0.07)	7.69 (±0.05)	8.07 (±0.03)
	TA (meq l^{-1})	2.12 (±0.06)	1.74 (±0.08)	1.71 (±0.02)	2.12 (±0.04)

Period 2: Nutrient concentrations were raised to 5 µM NO_3^- and 2 µM P-PO_4^{3-}, and the pCO_2 level was increased to ~700 to 800 µatm in the appropriate tanks.

Period 3: Nutrient concentrations were raised to 10 µM NO_3^- and 4 µM P-PO_4^{3-}. The pCO_2 level was maintained at the same level as the previous period.

Period 4: The conditions in the 16 treatment aquaria were returned to the conditions of Period 1 in order to assess the recovery potential of the coral nubbins after exposure to nutrient and pCO_2 stress.

Nutrient enrichment. Elevated nutrient concentrations were achieved by the addition of concentrated solutions of KNO_3 and KH_2PO_4 to the appropriate tanks. Nitrate concentration was determined with a Technicon Autoanalyzer II utilizing the method described in Armstrong et al. (1967). Phosphate concentration was determined with an Ocean Optics CHEM2000 Miniature Fiber Optic Spectrophotometer utilizing the method described in Parsons et al. (1984).

pCO_2 enrichment. Elevated pCO_2 concentrations were achieved by controlled low-pressure injection of pure CO_2 into the airstreams used to aerate the appropriate tanks (modeled on the method of Leclercq et al. 2000). Although the pCO_2 of the air was not measured, multiple daily pH and TA measurements were made to monitor seawater pCO_2 until the tanks equilibrated (a period of several days), with appropriate adjustments made to the CO_2 injection level, until the pCO_2 level stabilized between 700 to 800 µatm. pCO_2 and $pH_{(SWS)}$

(SWS: sea water scale) were determined from $pH_{(NBS)}$ and TA measurements using the program developed for CO_2 System Calculations by Lewis & Wallace (1998). TA and $pH_{(NBS)}$ were determined by potentiometric titration (electrode calibrated with NBS standard buffers of pH 2, 7 and 9) using the USGS Alkalinity Calculator, version 2.10Tk (Almgren & Fonselius 1976, S. Rounds 2003[1]). TA decreased over time in the pCO_2 treatment tanks, unlike in other experiments utilizing CO_2 to manipulate pH where TA remained constant. This may be an artifact of the closed system design, as a decrease in TA of ~0.5 over 24 h was observed by Leclercq et al. (2000) in a coral community exposed to increased pCO_2 without continuous seawater input. Leclercq et al. (2000) reported that this had no effect on the rate of community calcification.

Growth rate determination. The buoyant weight of each nubbin was measured approximately once weekly according to the method outlined in Davies (1989) to examine growth rate in response to the treatments. This method is simple, places minimal stress on the coral, and has been used experimentally by several authors (Davies 1984, Dodge et al. 1984, Edmunds & Davies 1986).

Data analysis. In order to satisfy parametric statistics requirements of homoscedasticity and normality, the growth rates were first normalized to the weight of each nubbin at the beginning of each growth period (Ferrier-Pagès et al. 2000). The normalized growth rate values were then transformed with the logarithmic transformation [$G' = \log (G \times 100\,000)$] following the recommendation of Sokal & Rohlf (1995). ANOVA was then used to compare the normalized and transformed growth rates between each treatment and treatment period. As the growth of each nubbin was measured under different experimental conditions, repeated-measures ANOVA was carried out using the GLM (General Linear Models) module of STATISTICA 6.0. The null hypothesis was that growth rates remained constant as a function of time.

RESULTS

The effects of nutrient and pCO_2 enrichment are presented in Fig. 1 and Table 2, as mean normalized growth rates (mg d^{-1}) for each treatment over the 4 treatment periods, and (in Table 2) as the percentage change compared to both the previous period and to Period 1. Newman-Keuls post-hoc analysis was used to determine statistical similarity between periods for each treatment and between treatments for each period (indicated by the letter assigned to each treatment mean, Fig. 1). During Period 1, the mean normalized growth rate in all of the treatment tanks remained nearly constant or increased slightly (overall mean growth rate of 1.492 mg d^{-1}), with no significant difference in growth rates between treatments. The growth rate in the C (control) treatment tanks remained statistically similar between all periods. Percent mortality for each treatment compared to Period 1 is shown in Table 2. An indeterminate percentage of this mortality was likely a consequence of residual collection and confinement stress. However, as there was no significant difference in mortality between treatments during Period 1, or between periods in the C (control) treatment tanks ($p > 0.05$), mortality in Periods 2 to 4 was considered to be a result of the treatments.

Effect of nutrient enrichment

The N or P treatments did not result in a significant decrease in growth rate at low concentrations during Period 2 ($p = 0.54$, $p = 0.08$). However, the growth rate at high nutrient concentrations during Period 3 was significantly less than in Periods 1 and 2 ($p < 0.05$). These observations are similar to reports by others for increased nitrate and phosphate levels (Kinsey & Davies 1979, Walker & Ormond 1982, Tomascik & Sander 1985, Bell & Tomascik 1993, Marubini & Davies 1996, Ferrier-Pagès et al. 2000). There was no significant difference in growth rate between the N or P treatments during either enrichment period. The effect of nitrate and phosphate combined on the growth rate of *Acropora cervicornis* appeared additive at low concentrations. During Period 2, the N-P treatment resulted in a significant 55% decrease in growth rate ($p \ll 0.05$), while the added percent decrease in growth rate for the separate N and P treatments was 53%. The growth rate during Period 3 for this treatment was significantly less than in Periods 1 and 2 ($p < 0.05$), and the high nutrient concentrations appeared to produce an antagonistic combined effect; the N-P treatment resulted in a 61% decrease in growth rate, and the added percent decrease in growth rate for the separate N and P treatments was 116% (Table 1). Similar findings were obtained by Kinsey & Davies (1979) and Ferrier-Pagès et al. (2000) for *Stylophora pistillata*.

Effect of pCO_2 enrichment

The effect of pCO_2 enrichment on the growth rate of *Acropora cervicornis* was greater than that of nutrient enrichment. During Period 2, growth rates of all the

[1]Alkalinity calculator, Version 2.10Tk. http://oregon.usgs.gov/alk/

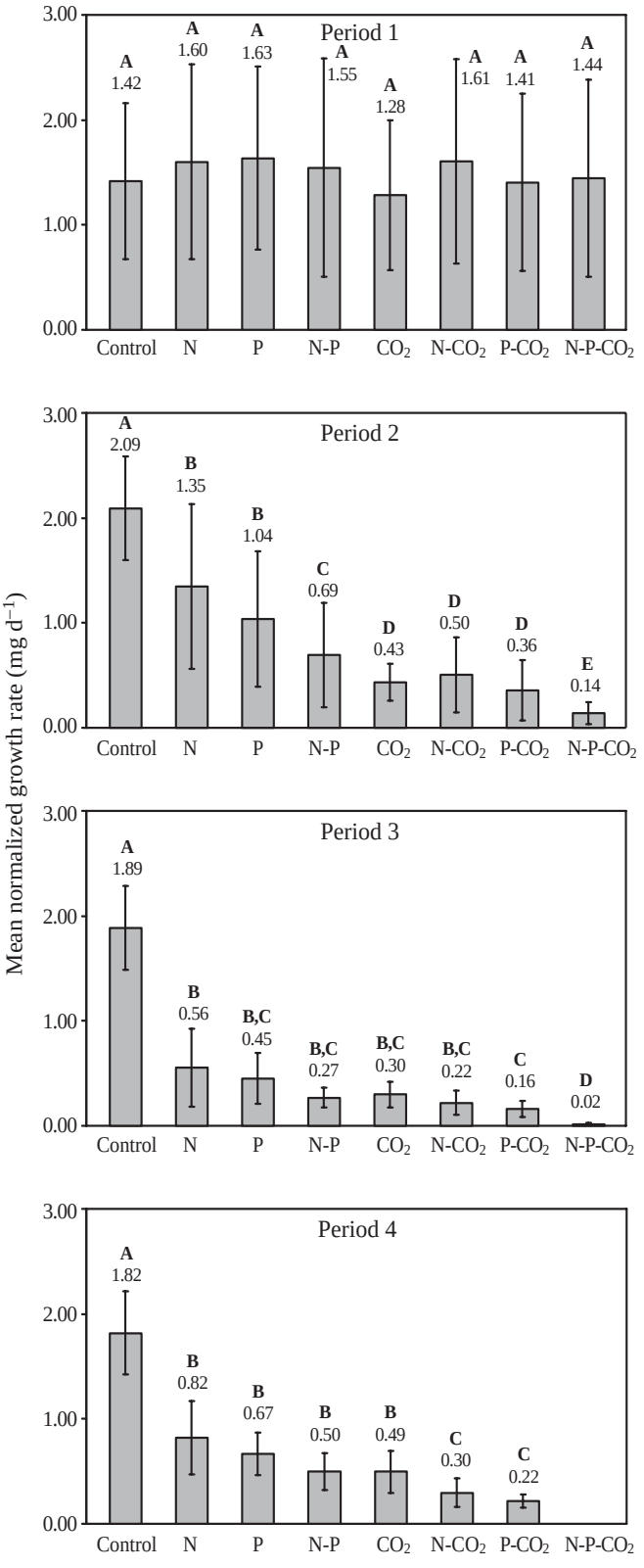

Fig. 1. *Acropora cervicornis*. Mean normalized treatment growth rates (±SD) for each period. Letters assigned to each treatment indicate statistically similar growth rates based on Newman-Keuls post-hoc probabilities ($p < 0.05$)

CO_2 treatments were significantly less than the nutrient-only treatments, and all of the pCO_2 treatments caused significant decreases in growth rate compared to Period 1 ($p << 0.05$). During Period 3, the N-CO_2 and P-CO_2 treatment growth rates were significantly less than in Periods 1 and 2 ($p < 0.05$), and the CO_2 and N-P-CO_2 treatment growth rates were significantly less than in Period 1 ($p << 0.05$) but were not significantly different from Period 2 ($p = 0.37$, $p = 0.08$). These findings are in agreement with previous studies, where the rate of calcification decreased immediately after an increase in pCO_2, with no acclimation (Marubini & Atkinson 1999, Langdon et al. 2000, Reynaud et al. 2003).

There was no significant difference between the growth rates of the CO_2, N-CO_2, and P-CO_2 treatments during either enrichment period (Fig. 1). Only when CO_2 was combined with nitrate and phosphate was there a significant difference in growth rate among the pCO_2 treatments; the growth rate of the N-P-CO_2 treated corals was significantly less than all other treatments ($p \ll 0.05$) during both enrichment periods. Unlike the nutrient-only treatments, the effect of combined nitrate, phosphate, and pCO_2 appeared to be antagonistic at low nutrient concentrations and additive at high concentrations (compared to those nutrients paired with CO_2 separately). The 100% mortality of the N-P-CO_2-treated corals indicates the severe stress this combination induces (Table 2).

Recovery

Growth rate recovery potential after transient increases in pCO_2, nitrate, and phosphate was assessed in Period 4 (Fig. 1). Only the N treatment growth rate recovered enough to be statistically similar to the growth rate observed during Period 1 ($p = 0.06$). The recovery of the N-P-CO_2 treatment corals could not be determined, as none of these corals survived to the end of Period 4.

DISCUSSION

This study clearly demonstrates that elevated levels of nitrate, phosphate, and pCO_2 affect the growth rate of *Acropora cervicornis*, and thus adds to the body of literature that provides evidence of detrimental effects on corals of increased pCO_2 alone or in combination with other factors (Gattuso et al. 1999, Ohde & van Woesik 1999, Leclercq et al. 2000, 2002, Langdon et al. 2003, Marubini et al. 2003, Reynaud et al. 2003).

The implications of increasing pCO_2 levels and continued coastal nutrification are many, and occur on multiple levels, in addition to observed decreases in

Table 2. *Acropora cervicornis.* Mean period normalized growth rates (±SD), percentage changes in growth rate and percent mortality

Treatment	Growth rate (mg d^{-1})			
	Period 1	Period 2	Period 3	Period 4
Control	1.418 (±0.744)	2.092 (±0.497)	1.887 (±0.398)	1.818 (±0.395)
N	1.602 (±0.931)	1.347 (±0.787)	0.557 (±0.371)	0.820 (±0.353)
P	1.635 (±0.874)	1.037 (±0.643)	0.451 (±0.243)	0.665 (±0.206)
N-P	1.545 (±1.038)	0.694 (±0.497)	0.267 (±0.094)	0.497 (±0.176)
CO_2	1.281 (±0.716)	0.432 (±0.175)	0.300 (±0.123)	0.494 (±0.198)
N-CO_2	1.606 (±0.973)	0.504 (±0.356)	0.218 (±0.115)	0.297 (±0.138)
P-CO_2	1.405 (±0.846)	0.359 (±0.287)	0.162 (±0.076)	0.220 (±0.062)
N-P-CO_2	1.445 (±0.938)	0.139 (±0.107)	0.015 (±0.011)	0.032 (±0.026)
			Percent of previous period	
Control		148	90	96
N		84	41	147
P		63	43	148
N-P		45	39	186
CO_2		34	69	165
N-CO_2		31	43	136
P-CO_2		26	45	135
N-P-CO_2		10	11	211
			Percent of Period 1	
Control		148	133	128
N		84	35	51
P		63	28	41
N-P		45	17	32
CO_2		34	23	39
N-CO_2		31	14	19
P-CO_2		26	12	16
N-P-CO_2		10	1	2
			Percent mortality (compared to Period 1)	
Control		9	13	13
N		26	43	47
P		25	58	66
N-P		39	95	95
CO_2		59	81	95
N-CO_2		43	60	60
P-CO_2		37	75	79
N-P-CO_2		69	95	100

growth rate. Although population declines of *Acropora cervicornis* (and *A. palmata*) have been blamed mainly on coral diseases, local eutrophication may have played a role by increasing coral stress, resulting in increased disease susceptibility and severity (Aronson & Precht 1997, Aronson et al. 1998, Porter et al. 2001, Patterson et al. 2002, Bruno et al. 2003). Nutrient enrichment is typically regarded as having relatively local or regional effects; however, nutrient enrichment in general, and nitrate enrichment in particular, has been observed to reduce coral fecundity, fertilization success, normal embryo development, and settlement success of coral larvae (Hunte & Wittenburg 1992). This aspect of the consequences of nutrification may cause dependency on asexual modes of reproduction, effectively reducing the genetic variability of the coral population within the affected area. While this may also seem to be a localized effect, it has the potential to reduce the genetic diversity of scleractinian corals as a whole. A decrease in the size of the genetic pool may lead to a significant reduction in the ability of the coral population to adapt to global environmental change, particularly increasing atmospheric pCO_2.

While it is not appropriate to discount the effects of increased nutrient concentrations on corals, this study indicates that elevated pCO_2 had the most negative effect on growth rate, an effect that was exacerbated in the presence of increased nutrient levels. This result is supported by the literature which generally concurs in attributing negative effects on coral growth rate in response to increased CO_2 levels, but which are far less clear on the effects of nutrients (Gattuso et al. 1999, Ohde & van Woesik 1999, Leclercq et al. 2000, 2002, Langdon et al. 2003, Marubini et al. 2003, Rey-

naud et al. 2003). The worst case climate change models of the IPCC estimate that the ocean surface waters will remain almost entirely supersaturated with calcium carbonate, but the decrease in aragonite saturation state could result in a competitive advantage for non-calcifying reef organisms (i.e. fleshy algae) or calcite secretors, further disadvantaging scleractinian coral populations (Kleypas et al. 1999). Our results indicate a significant interaction between nutrients and pCO_2. This may result in greater impacts in populated coastal areas where nutrification is of increased concern. As reefs off large population centers generally represent a significant tourist draw, their decline stands to have a marked impact on the local and/or regional economy. Another element to be considered is the interaction between pCO_2 and temperature. Under increased pCO_2, significant decreases in calcification have been observed at high temperatures (ca. 28.2°C) but not at normal temperatures (ca. 25.2°C), in cultured *Stylophora pistillata* (Reynaud et al. 2003). This result is not in agreement with our study; while temperature was not directly manipulated, it remained within the 'normal' range over the course of the experiment. The diversity of coral response to increased pCO_2 and the variety of methods used to manipulate pCO_2 found in the literature underlines the need for continued experimentation with multiple species.

As studies clearly demonstrating increased nutrient levels on coral reefs are lacking, this makes the real-life value of the nutrient-enrichment experiments in this study (and indeed of many experiments in the literature) somewhat uncertain. However, this study, at the very least, quantitatively supports what has been reported elsewhere in a more generalized way, namely that increasing atmospheric pCO_2 levels will almost certainly have deleterious effects on reef corals (Kleypas et al. 1999, Langdon et al. 2000, Guinotte et al. 2003). Thus, if these results accurately predict coral response in the natural environment, it is reasonable to speculate that the survival and reef-building potential of this species will be significantly negatively impacted by continued coastal nutrient enrichment and projected pCO_2 increases. In terms of recovery potential, our study indicates that *Acropora cervicornis* populations may never return to their previous state. Although this species may be well-adapted to surviving natural change, it is possible that anthropogenic environmental changes have occurred too quickly and may have overcome their homeostatic capacity, thus effectively reducing or eliminating the reef-building capability of this species.

We believe that this experiment is the first to examine the interaction between a local/regional scale factor (nutrients) and a global factor (CO_2). Future experimentation should continue to focus on the interacting effects of nutrients, CO_2, and temperature on coral condition and growth, employing histopathology and molecular techniques to expand our understanding of these influences to the tissue and cellular levels.

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