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## Primary production, respiration, and calcification of a coral reef mesocosm under increased CO<sub>2</sub> partial pressure

**Abstract**—The effect of increased CO<sub>2</sub> partial pressure (pCO<sub>2</sub>) on the community metabolism (primary production, respiration, and calcification) of a coral community was investigated over periods ranging from 9 to 30 d. The community was set up in an open-top mesocosm within which pCO<sub>2</sub> was manipulated (411, 647, and 918 μatm). The effect of increased pCO<sub>2</sub> on the rate of calcification of the sand area of the mesocosm was also investigated. The net community primary production (NCP) did not change significantly with respect to pCO<sub>2</sub> and was 5.1 ± 0.9 mmol O<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>. Dark respiration (*R*) increased slightly during the experiment at high pCO<sub>2</sub>, but this did not affect significantly the NCP:*R* ratio (1.0 ± 0.2). The rate of calcification exhibited the trend previously reported; it decreased as a function of increasing pCO<sub>2</sub> and decreasing aragonite saturation state. This re-emphasizes the predictions that reef calcification is likely to decrease during the next century. The dissolution process of calcareous sand does not seem to be affected by open seawater carbonate chemistry; rather, it seems to be controlled by the biogeochemistry of sediment pore water.

The metabolism of organic (photosynthesis and respiration) and inorganic (precipitation and dissolution of CaCO<sub>3</sub>) carbon are the two major biological processes affecting the biogeochemical carbon cycle of marine ecosystems. Coral reefs are of particular interest because calcification and photosynthesis are physiologically linked: scleractinian corals, calcifying algae, and coral reef communities exhibit an increased rate of calcium carbonate deposition during the daylight period (i.e., when photosynthesis occurs). Both processes consume dissolved inorganic carbon (DIC) and respond simultaneously to changes in environmental parameters such as light and temperature. It has been suggested (Smith and Buddemeier 1992), and recently demonstrated (Gattuso et al. 1999; Kleypas et al. 1999; Langdon et al. 2000; Leclercq et al. 2000), that an increase in the CO<sub>2</sub> partial pressure (pCO<sub>2</sub>) has a negative effect on coral and reef community calcification as a result of a decrease of the ara-

gonite saturation state ( $\Omega_{\text{arag}}$ ). The increase in atmospheric pCO<sub>2</sub> forecast for the next century led these authors to predict a significant decrease of marine calcification. This response is now well documented, but previous investigations of the response of reef community calcification to increased pCO<sub>2</sub> did not provide any data on the response of primary production and respiration of corals and coral reef communities (Langdon et al. 2000; Leclercq et al. 2000). Also, in some instances, the seawater DIC system was not manipulated by controlling pCO<sub>2</sub> but by modifying the concentrations of bicarbonate (HCO<sub>3</sub><sup>-</sup>) and carbonate (CO<sub>3</sub><sup>2-</sup>) ions (Langdon et al. 2000). It is important to have a good understanding of the response of primary production and respiration to increased pCO<sub>2</sub> because both processes are tightly coupled to calcification at the organism and community levels (Gattuso et al. 1999). An increase in photosynthetic CO<sub>2</sub> fixation under high pCO<sub>2</sub> could indeed counteract the decrease in calcification (Gattuso et al. 1999). Furthermore, this increase could have two consequences, depending on whether the response times of photosynthesis and calcification are similar or not. If they are similar, the increase in photosynthesis might partly balance the direct effect of increased pCO<sub>2</sub> on net calcification that would be more dramatic than the observed decrease; that is, what we see is an underestimate of the actual decrease of the calcification rate. Alternatively, if the response time of photosynthesis is longer than that of calcification, a delayed acclimation process could occur, and the decrease in calcification reported recently could be an acute response that could significantly diminish as photosynthesis increases; that is, what we see is a short-term decrease of the calcification rate that cannot be extrapolated over years. This issue could be investigated only by doing long-term experiments under varying pCO<sub>2</sub>.

Physiological studies have provided valuable information on the metabolic response of marine autotrophs to changes in the DIC system. Several authors have suggested that a carbon-concentrating mechanism (CCM) operates in some

marine photosynthetic organisms (e.g., Raven 1997). Indeed, these organisms can be divided into two physiological categories:  $\text{CO}_2$  users and  $\text{HCO}_3^-$  users.  $\text{CO}_2$  users rely on dissolved molecular  $\text{CO}_2$  for photosynthesis and might be carbon-limited under present  $\text{CO}_2$  concentration ( $\sim 10 \mu\text{mol kg}^{-1}$ ). Conversely,  $\text{HCO}_3^-$  users that can use the large reservoir of bicarbonate ( $\sim 2 \text{mmol kg}^{-1}$ ) and are less likely to be carbon limited. The increase in  $\text{pCO}_2$  from 367 to 706  $\mu\text{atm}$  by the year 2100, as forecast by the Intergovernmental Panel on Climate Change (IPCC, average scenario, IS95a; Houghton et al. 1996) would result in an increase in the dissolved  $\text{CO}_2$  and bicarbonate concentrations by a factor of 1.9 and 1.1, respectively. Such changes might have a larger effect on  $\text{CO}_2$  users than on  $\text{HCO}_3^-$  users (Zimmerman et al. 1997; Gattuso et al. 1999). Scleractinian corals that are  $\text{HCO}_3^-$  users (Goiran et al. 1996; Gattuso et al. 1999) might not be significantly affected by an increased  $\text{pCO}_2$ . However, the presence of potential  $\text{CO}_2$  users such as algae and seagrasses in some reef communities could lead to an increased rate of primary production under elevated  $\text{pCO}_2$ .

Another aspect of the community response to increased  $\text{pCO}_2$  relates to sedimentary processes. Interstitial water conditions and processes have been investigated by several authors (e.g., Sansone et al. 1988; Sarazin et al. 1988; Charpy-Roubaud et al. 1996), but the response of  $\text{CaCO}_3$  dissolution to increased  $\text{pCO}_2$  in the water column remains unknown in reef sediments. Because this process consumes  $\text{CO}_2$  and releases carbonate ions in seawater, it might partly counteract the predicted increase in  $\text{pCO}_2$  and decrease  $\Omega_{\text{arag}}$ .

This paper provides the first results on the response of primary production and respiration of a coral community after several weeks of exposure to increased  $\text{pCO}_2$  and on the response of net community calcification to changes in  $\Omega_{\text{arag}}$ . It also provides data on the response of a calcareous sand community to elevated  $\text{pCO}_2$ .

**Materials and methods**—The experimental coral community comprised coral sand and calcareous live rock on which were growing various reef organisms, mostly scleractinian corals, sea anemones, and calcareous red algae. Further details on the community composition can be found in Leclercq et al. (2000). The community was installed in a 155-L glass aquarium ( $0.58 \times 0.58 \times 0.58 \text{ m}$ ). Mediterranean seawater (salinity = 38.0) was continuously pumped from a depth of 50 m into a 80-L sump (Fig. 1). It was heated to  $26^\circ\text{C}$  (Réna, Biotherm 2000), and its pH was adjusted as described below. Seawater was delivered from the sump to the mesocosm at a rate of  $70 \text{ L h}^{-1}$ . Light was provided by a 400-W metal halide lamp (Osram Powerstar HQI-T/D) that ran on a 12:12 light:dark photoperiod. Irradiance was measured using a quantum  $4 \pi$  sensor (LI-193SA, LI-COR) and was set to  $220 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ . Water motion was ensured by a  $1,000 \text{ L h}^{-1}$  centrifugal pump (MJ1000, Aquarium Systems). The glass windows were cleaned daily to avoid algal growth.

The sump was maintained at mid- $\text{pCO}_2$  ( $647 \mu\text{atm}$ ) for more than 12 weeks during phase 1 of the experiment. It was bubbled with standard air (Fig. 1; setup 1);  $\text{pCO}_2$  was significantly higher than the present-day atmospheric value ( $370 \mu\text{atm}$ ) because the seawater pumped in the Mediterra-

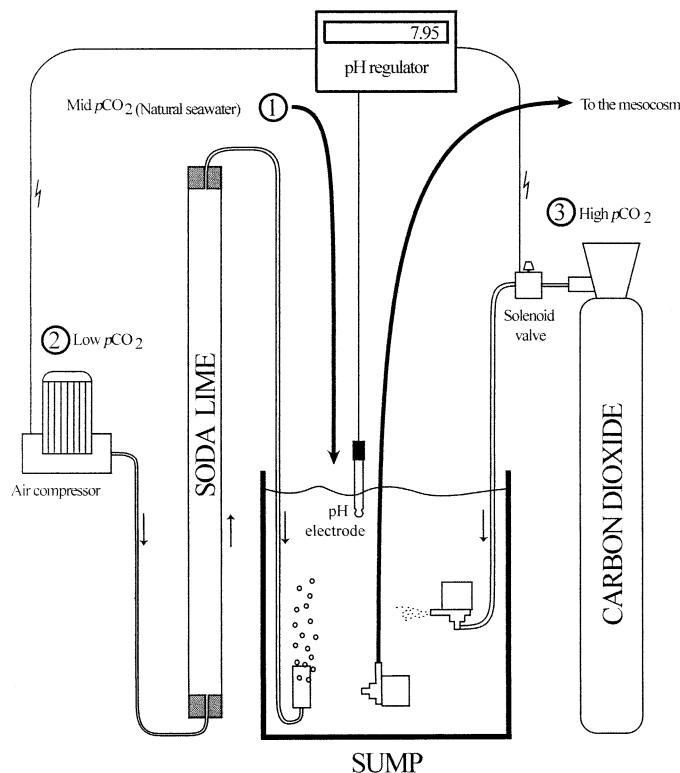


Fig. 1. Experimental setup used to control  $\text{pCO}_2$  (see text).

nean was enriched in  $\text{CO}_2$  by bacterial respiration during its residence time (10 h) in various storage tanks. The mesocosm was maintained under low ( $411 \mu\text{atm}$ ) and high ( $918 \mu\text{atm}$ )  $\text{pCO}_2$  during phases 2 and 3 of the experiment. Each phase lasted 4 weeks, during which time seawater  $\text{pCO}_2$  was adjusted in the sump (Fig. 1) prior to flowing into the mesocosm using a pH controller (R301, Consort) connected to a pH electrode (Orion, model 8102SC) calibrated on the Sea Water Scale (see below). This technique of controlling seawater  $\text{pCO}_2$  by manipulating pH relies on the following principle: seawater pH is a function of total alkalinity (TA) and  $\text{CO}_2$  concentration. The seawater used for this experiment had an average TA of  $2.6 \text{ mEq kg}^{-1}$ ; it did not change by more than  $0.05 \text{ mEq kg}^{-1}$  during the experiment. Such variation led to an uncertainty of  $\sim 10 \mu\text{atm}$  on the estimation of the seawater  $\text{pCO}_2$ , which is much lower than the changes of  $\text{pCO}_2$  throughout the experiment. A pH-stat system was used: seawater was bubbled with pure  $\text{CO}_2$  (to decrease pH and increase  $\text{pCO}_2$ ) or with  $\text{CO}_2$ -free air (to increase pH and decrease  $\text{pCO}_2$ ). During the incubations performed under low  $\text{pCO}_2$  (phase 2), the pH controller was set to pH 8.11, and it switched an air compressor on (airflow up to  $3,000 \text{ L h}^{-1}$ ) when pH decreased to 8.09.  $\text{CO}_2$ -free air was then injected in the sump until the desired pH was reached.  $\text{CO}_2$ -free air was obtained by passing it through a 2-m-long “ $\text{CO}_2$  scrubber”—a Perspex cylinder containing soda lime (R.P. Normapur AR, Prolabo; Fig. 1, setup 2). During high  $\text{pCO}_2$  incubations (phase 3), the pH controller was set to pH 7.87, and it controlled a solenoid valve that opened when pH rose to 7.89, thus injecting pure  $\text{CO}_2$  from a 35-kg compressed

Table 1. Seawater DIC system during the experiments performed on the coral and sand communities. Mean  $\pm$  SD.

	Temperature (°C)	pH (sws)	CO <sub>2</sub> <sup>*</sup> (mmol kg <sup>-1</sup> )	HCO <sub>3</sub> <sup>-</sup> (mmol kg <sup>-1</sup> )	CO <sub>3</sub> <sup>2-</sup> (mmol kg <sup>-1</sup> )	DIC (mmol kg <sup>-1</sup> )	pCO <sub>2</sub> ( $\mu$ atm)	$\Omega_{\text{arag}}$
Coral community								
Low pCO <sub>2</sub> ( <i>n</i> = 9,699)	25.4 $\pm$ 0.4	8.092 $\pm$ 0.120	0.011 $\pm$ 0.006	1.882 $\pm$ 0.138	0.303 $\pm$ 0.058	2.196 $\pm$ 0.085	411 $\pm$ 229	4.5 $\pm$ 0.9
Mid-pCO <sub>2</sub> ( <i>n</i> = 5,948)	24.9 $\pm$ 0.4	7.921 $\pm$ 0.085	0.018 $\pm$ 0.004	2.078 $\pm$ 0.084	0.220 $\pm$ 0.035	2.316 $\pm$ 0.053	647 $\pm$ 158	3.2 $\pm$ 0.5
High pCO <sub>2</sub> ( <i>n</i> = 11,433)	25.6 $\pm$ 0.6	7.806 $\pm$ 0.142	0.025 $\pm$ 0.010	2.162 $\pm$ 0.116	0.185 $\pm$ 0.049	2.373 $\pm$ 0.077	918 $\pm$ 362	2.7 $\pm$ 0.7
Sand community								
Low pCO <sub>2</sub> ( <i>n</i> = 4,881)	26.0 $\pm$ 0.2	8.090 $\pm$ 0.115	0.011 $\pm$ 0.002	1.881 $\pm$ 0.077	0.302 $\pm$ 0.093	2.194 $\pm$ 0.123	393 $\pm$ 57	4.5 $\pm$ 1.4
Mid-pCO <sub>2</sub> ( <i>n</i> = 5,588)	25.6 $\pm$ 0.8	7.995 $\pm$ 0.095	0.014 $\pm$ 0.002	1.995 $\pm$ 0.082	0.255 $\pm$ 0.034	2.265 $\pm$ 0.050	520 $\pm$ 82	3.8 $\pm$ 0.5
High pCO <sub>2</sub> ( <i>n</i> = 3,805)	25.9 $\pm$ 0.7	7.919 $\pm$ 0.068	0.018 $\pm$ 0.003	2.067 $\pm$ 0.066	0.225 $\pm$ 0.028	2.309 $\pm$ 0.041	641 $\pm$ 118	3.3 $\pm$ 0.4

cylinder to the sump until the desired pH was reached (Fig. 1, setup 3).

Net community primary production (NCP), dark respiration (*R*), and net calcification (*G*) were measured throughout each of the three experimental phases. Incubations (*n* = 14, 11, and 24, respectively, for low, mid-, and high pCO<sub>2</sub>) of 1–3 h in duration were performed at various times of the light and dark periods. Seawater input in the mesocosm was then switched off, water motion was maintained, but no aeration was provided so that air–seawater gas exchange was minimized. NCP and *R* were derived from changes in the concentration of dissolved oxygen using the multiple regression method described by Leclercq et al. (1999). The concentration of dissolved oxygen was measured using an amperopolarographic electrode (Ponselle, oxythermometric model OXY TS), which was calibrated daily. Air-saturated sea water (500 ml) stirred (magnetic stirrer), aerated (air pump, Réna Alizé, running with one air stone), and heated to 30°C in a beaker was allowed to cool slowly (50–70 min) to 20°C. The decrease of seawater temperature resulted in a change of the oxygen content. The electrode was calibrated against the theoretical values of the oxygen content of air-saturated seawater (Wanninkhof 1992). pH was measured using glass combination electrodes (Orion, model 8102SC and Radiometer, model GK2401C) calibrated daily against the Sea Water Scale (SWS) buffers: TRIS and AMP (Department of Energy 1994) pH and dissolved oxygen data were averaged and logged every minute using two data loggers (LI-1000, LI-COR). Water temperature was measured ( $\pm$ 0.05°C) and logged every minute (Seamon, Hugerun). Net community calcification was estimated using the alkalinity anomaly technique (Smith and Key 1975). Seawater was sampled (200 ml) at the beginning and at the end of each incubation, filtered on 0.45- $\mu$ m membranes (cellulose nitrate membrane filters, Whatman), and stored at 4°C pending TA determinations. The water body located underneath the sediment layer was sampled twice during the experiment for determination of pH and TA. TA was determined by potentiometric titration using automatic titrators (Mettler, DL25 or DL70). Measurements of pH and TA were used, together with the computation of the carbonate equilibrium constants, to derive the concentration of the carbonate species (Department of Energy 1994). The aragonite saturation state ( $\Omega_{\text{arag}}$ ) was calculated as described by Mucci (1983). The  $\Omega_{\text{arag}}$  values of the preindustrial period and years 2065 and

2100 used in this work are from Gattuso et al. (1999; Table 4).

On completion of the initial three phases of the experiment, all rocks, corals, algae, and other macrofauna were removed from the mesocosm to estimate the net calcification of the sediment community. The water level was lowered (total volume of 70 L), and water motion was ensured by a 250 L h<sup>-1</sup> pump (MJ250, Aquarium Systems). The three phases of the experiment were then repeated. The sand community was subject to mid-pCO<sub>2</sub> (520  $\mu$ atm) for 4 weeks (phase 4) and to low and high pCO<sub>2</sub> (393 and 641  $\mu$ atm, respectively) for 9 and 18 d (phases 5 and 6).

Statistical testing was performed using JMP 3.1 (SAS Institute) for Macintosh computers.

**Results**—Coral reef community: CO<sub>2</sub> exchanges slowly between air and water because of its low transfer velocity (Wanninkhof 1992). This, together with changes in pCO<sub>2</sub> due to the community metabolism, resulted in a relatively poor control of pH and pCO<sub>2</sub> during the experiment. The average pCO<sub>2</sub> values in the mesocosm were 647  $\pm$  158  $\mu$ atm (mean  $\pm$  SD) for the mid-pCO<sub>2</sub> incubation, 411  $\pm$  229  $\mu$ atm for the low-pCO<sub>2</sub> incubation and 918  $\pm$  362  $\mu$ atm for the high-pCO<sub>2</sub> incubation (Table 1).

Changes in dissolved oxygen concentration during the light and dark incubations were linear. No diel change in *R* was observed, and NCP exhibited no significant variation during the daylight period (data not shown). The multiple regression method (Leclercq et al. 1999) indicated that the oxygen transfer velocity (KO<sub>2</sub> = 0.4  $\pm$  4.6 cm h<sup>-1</sup>; *n* = 12) was not significantly different from zero (*t*-test, *P* = 0.75). Moreover, NCP and *R* were not significantly different when computed with KO<sub>2</sub> set to zero (*n* = 7, *P* = 0.51 for NCP; *n* = 5, *P* = 0.63 for *R*). Therefore, air–seawater O<sub>2</sub> exchanges were neglected and oxygen metabolism was estimated using a linear fit, as in the standard respirometric approach. NCP was 5.3  $\pm$  1.2 mmol O<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> (*n* = 8) for the low-pCO<sub>2</sub> incubations, 4.7  $\pm$  0.5 mmol O<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> (*n* = 6) for the mid-pCO<sub>2</sub> incubations, and 5.2  $\pm$  0.8 mmol O<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> (*n* = 11) for the high-pCO<sub>2</sub> incubations (Fig. 2A). NCP was not significantly affected by seawater pCO<sub>2</sub> (ANOVA, *P* = 0.42), and the average NCP was 5.1  $\pm$  0.9 mmol O<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> (*n* = 25). *R* was 4.9  $\pm$  0.7 mmol O<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> (*n* = 6) for the low-pCO<sub>2</sub> incubations, 5.0  $\pm$  0.7 mmol O<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> (*n* = 5) for the mid-pCO<sub>2</sub> incubations, and 6.0  $\pm$  0.5 mmol

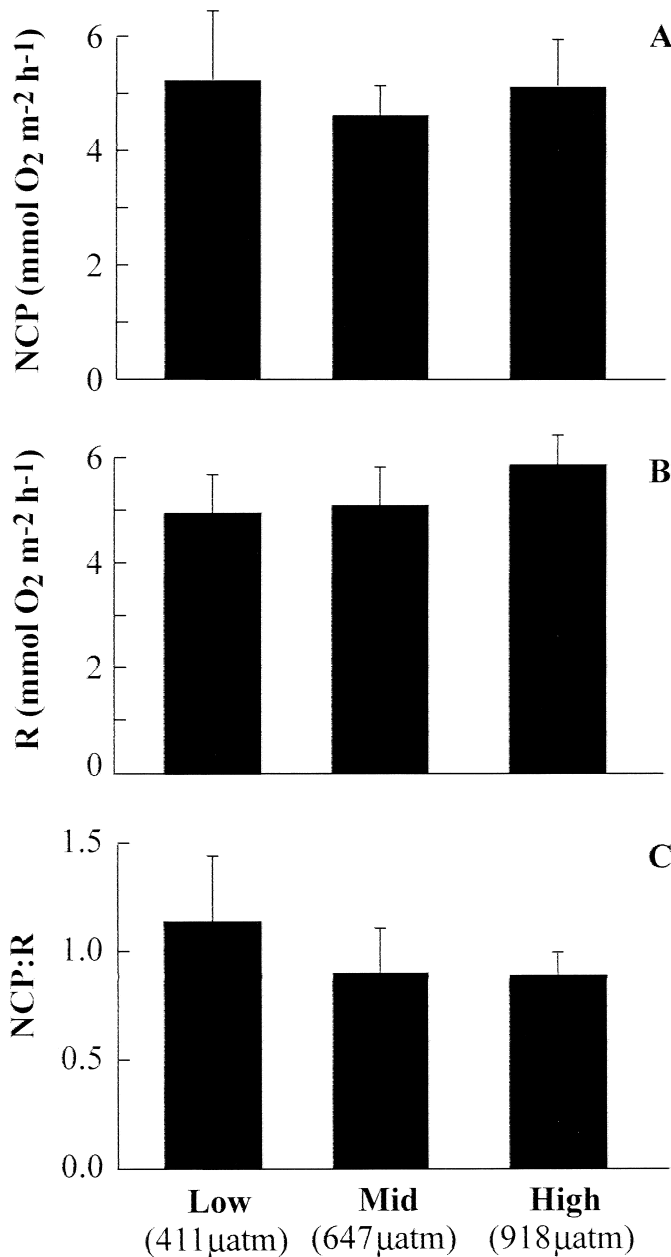


Fig. 2. Net community production (NCP), community respiration ( $R$ ), and NCP: $R$  ratio at low, mid-, and high  $p\text{CO}_2$ . Mean  $\pm$  SD.

$\text{O}_2 \text{ m}^{-2} \text{ h}^{-1}$  ( $n = 13$ ) for the high- $p\text{CO}_2$  incubations (Fig. 2B).  $R$  was significantly affected by the seawater  $p\text{CO}_2$  ( $P = 0.002$ ) and was significantly higher under high  $p\text{CO}_2$  (post hoc test) (Fig. 2B). NCP: $R$  ratios (Fig. 2C) were  $1.1 \pm 0.3$  ( $n = 6$ ),  $0.9 \pm 0.2$  ( $n = 5$ ), and  $0.9 \pm 0.1$  ( $n = 7$ ), respectively, for the low-, mid-, and high- $p\text{CO}_2$  incubations. The NCP: $R$  ratio, however, was not significantly affected by seawater  $p\text{CO}_2$  (nonparametric Wilcoxon test,  $P = 0.47$ ), and the average NCP: $R$  was  $1.0 \pm 0.2$  ( $n = 18$ ).

The rate of net community calcification decreased linearly as a function of decreasing  $\Omega_{\text{arag}}$  and increasing  $p\text{CO}_2$  (Fig. 3). The relationship was significant both during the light period and at night (Table 2).

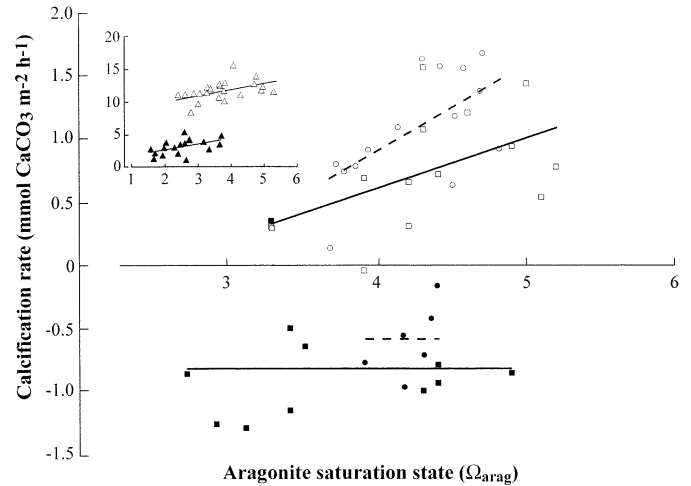


Fig. 3. Net calcification as a function of  $\Omega_{\text{arag}}$  for the whole community (triangles, insert), the sand community (squares), and the soft-bottom community investigated in situ by Boucher et al. (1998) (circles). Data shown were obtained in the light (open symbols) and at night (filled symbols). Linear fittings are also plotted for the whole community and the sand community (continuous lines), as well as for the soft-bottom community investigated by Boucher et al. (1998; dotted line). Negative values indicate net calcium carbonate dissolution.

**Sand community:** The average  $p\text{CO}_2$  during the three phases of the experiment was:  $393 \pm 57 \mu\text{atm}$  for the low- $p\text{CO}_2$  incubation,  $520 \pm 82 \mu\text{atm}$  for the mid- $p\text{CO}_2$  incubation, and  $641 \pm 118 \mu\text{atm}$  for the high- $p\text{CO}_2$  incubation (Table 1). The total ranges of  $p\text{CO}_2$  and  $\Omega_{\text{arag}}$  were, respectively,  $283\text{--}856 \mu\text{atm}$  and  $2.7\text{--}5.2$ . The water body located underneath the sediment layer exhibited a pH of 7.65 and a TA of  $2.56 \text{ mmol kg}^{-1}$ ;  $\Omega_{\text{arag}}$  was 1.9. The rate of net calcification (Fig. 3) decreased linearly as a function of decreasing  $\Omega_{\text{arag}}$  during the light period but was not correlated with  $\Omega_{\text{arag}}$  at night (Table 2). The dark dissolution was  $-0.81 \pm 0.48 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$ .

**Relationship between calcification and  $\Omega_{\text{arag}}$ :** Equations of the calcification rate as a function of  $\Omega_{\text{arag}}$  for the coral reef and the sand communities were integrated over 24 h and expressed as a percentage of the preindustrial calcification rate ( $\Omega_{\text{arag}} = 4.9$ ; Table 3). Yearly calcification was then estimated for  $p\text{CO}_2$ s corresponding to periods ranging from the last glaciation to the year 2100 (Table 4). Those equations are compared, in Table 3, with those reported for several tropical marine systems.

**Discussion**—Changes in the dissolved oxygen concentration during the incubations exhibited the same trend as in the standard respirometric approach (i.e., linear changes, McCloskey et al. 1978). Thus, setting the oxygen transfer velocity ( $\text{KO}_2$ ) to zero, by providing no aeration during the incubations, enabled us to mimic the respirometric method: changes in the oxygen concentration were only due to consumption/production by the community with negligible interference from air-seawater exchange. It is therefore possible to use an open-top aquatic mesocosm like a sealed

Table 2. Rates of calcification ( $\text{mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$ ) in the light and dark for the coral and sand communities and for the natural community described by Boucher et al. (1998).

System	Light	Dark
Coral community		
$\Omega_{\text{arag}}$	$8.65 + 0.81\Omega_{\text{arag}}$ $r = 0.45, n = 22, P = 0.04$	$0.77 + 0.90\Omega_{\text{arag}}$ $r = 0.50, n = 18, P = 0.04$
pCO <sub>2</sub>	$13.510 - 0.004 \text{ pCO}_2$ $r = 0.45, n = 22, P = 0.04$	$4.765 - 0.002 \text{ pCO}_2$ $r = 0.51, n = 18, P = 0.03$
Sand community		
$\Omega_{\text{arag}}$	$-1.06 + 0.40\Omega_{\text{arag}}$ $r = 0.61, n = 13, P = 0.03$	No relation with $\Omega_{\text{arag}}$ or pCO <sub>2</sub> The average calcification rate is:
pCO <sub>2</sub>	$1.711 - 0.002 \text{ pCO}_2$ $r = 0.45, n = 22, P = 0.04$	$-0.81 \pm 0.48$ $n = 11, P = 0.98$
Sand community		
Boucher et al. (1998)	$-2.0 + 0.71\Omega_{\text{arag}}$ $r = 0.41, n = 14, P = 0.01$	$-0.60 \pm 0.24$ $n = 6, P = 0.18$

container for metabolic studies by providing no aeration and moderate water motion. The polynomial method (Leclercq et al. 1999) should be used when air–seawater exchanges are not negligible.

The stimulation of the growth rate or net photosynthesis by the increased availability of dissolved CO<sub>2</sub> has been demonstrated for some diatoms (Riebesell et al. 1993), the green calcareous alga *Halimeda* sp. (Borowitzka and Larkum 1976), the red calcareous alga *Corallina pilulifera* (Gao et al. 1993), and seagrasses (Zimmerman et al. 1997). Such stimulation was not observed in the scleractinian corals *Galaxea fascicularis* (Goiran et al. 1996) and *Stylophora pistillata* (Burriss et al. 1983). However, only two studies are ecologically relevant (Riebesell et al. 1993; Zimmerman et al. 1997) because they altered the seawater carbonate chemistry by directly manipulating pCO<sub>2</sub>. The other studies used various chemicals, rather than gaseous CO<sub>2</sub>, to modify the DIC

system. Net community primary production of our mesocosm is not significantly affected by variations in pCO<sub>2</sub>, suggesting that most photosynthetic organisms (corals and algae) of the community were HCO<sub>3</sub><sup>-</sup> users. The dark community respiration was slightly affected by variations of pCO<sub>2</sub> and was higher under high-pCO<sub>2</sub> conditions, but as a result of a greater uncertainty, the NCP:R ratio exhibited no significant change in the course of the experiment. No change in the dark rate of respiration was found for the scleractinian coral *Stylophora pistillata* when incubated under elevated pCO<sub>2</sub> (Leclercq et al. unpubl. data), and a reduced mitochondrial respiration was found under a higher pCO<sub>2</sub> in green plants (Drake et al. 1998; Luo et al. 1999). It is difficult to make conclusions on the response of gross primary production because there is currently no technique available to measure rates of respiration of a community in the light. Preliminary data suggest that the dark respiration rate of our

Table 3. Relative rate of calcification of some tropical marine systems. Calcification is expressed as a percentage of the rate found at  $\Omega_{\text{arag}} = 4.9$  (preindustrial period).

System	Relative calcification rate	Reference
Scleractinian corals		
<i>Stylophora pistillata</i>	$228 \left( 1 - \exp \left[ -\frac{\Omega_{\text{arag}}}{0.69} \right] \right) - 128$	Gattuso et al. 1998
<i>Porites porites</i>	$51 + 10\Omega_{\text{arag}}$	Marubini and Thake 1999
Red calcareous algae		
<i>Amphiroa foliacea</i>	$-1 + 21\Omega_{\text{arag}}$	Borowitzka 1981 in Gattuso et al. 1999
<i>Porolithon gardneri</i>	$29 + 15\Omega_{\text{arag}}$	Agegian 1985 in Gattuso et al. 1999
Reef communities		
Okinawa reef flat	$4(\Omega_{\text{arag}} - 1)^{2.36}$	Odhe and van Woessik 1999
Biosphere 2 ocean	$-67 + 34\Omega_{\text{arag}}$	Langdon et al. 2000
Coral community	$31 + 14\Omega_{\text{arag}}$	Leclercq et al. 2000
Coral community	$52 + 10\Omega_{\text{arag}}$	Present study
Sand community	$-1,533 + 333\Omega_{\text{arag}}$	Present study
Sand community	$-287 + 79\Omega_{\text{arag}}$	Boucher et al. 1998

Table 4. Rates of calcification ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ) of the coral reef and sand communities in the glacial and interglacial periods (Gattuso et al. [1999] updated for  $\text{pCO}_2$  by CDIAC [2001]). Negative values indicate net calcium carbonate dissolution.

	Last glacial maxi- mum	1880	2000	2065	2100
$\text{pCO}_2$ ( $\mu\text{atm}$ )	200	280	368	560	706
$\Omega_{\text{arag}}$	5.9	4.9	4.3	3.4	3.0
Coral reef community	8.6	7.8	7.4	6.7	6.4
Sand community	0.2	0.0	-0.1	0.2	-0.3

mesocosm measured immediately after the light period is higher than that measured during the remainder of the dark period. This may indicate that light has a significant effect on the rate of community respiration. Nevertheless, no increase in the net community primary production that could counteract the decrease in calcification occurred (Gattuso et al. 1999).

The rates of light and dark community calcification exhibited the same response to changes in  $\Omega_{\text{arag}}$  than previously reported for short-term (24 h) experiments (test on the slopes:  $P > 0.3$ ; Leclercq et al. 2000), suggesting that no acclimation induced by a longer exposure to elevated  $\text{pCO}_2$  and lower  $\Omega_{\text{arag}}$  occurs. This is in agreement with two recent studies that used slightly different approaches. Marubini and Atkinson (1999) reported that the decrease of the rate of calcification in response to changes in the carbonate system was immediate and reversible in the scleractinian coral *Porites compressa*. Also, Langdon et al. (2000) found that the response of the community calcification rate of the Biosphere 2 ocean is not significantly different during short-term (days) and long-term (months) changes in  $\Omega_{\text{arag}}$ . This result confirms that reef community calcification is controlled by  $\Omega_{\text{arag}}$ , that no acclimatization appears to occur, and that the global increase in  $\text{pCO}_2$  might be a serious threat for coral reefs (Gattuso et al. 1999; Kleypas et al. 1999; Leclercq et al. 2000).

Experiments performed on the sand community provide the first results on the effect of  $\Omega_{\text{arag}}$  on the dissolution of calcareous sand in a reef mesocosm. Net calcification decreased as a function of  $\Omega_{\text{arag}}$  during the day, with a slope steeper than that found for the whole community (Fig. 3). The small net  $\text{CaCO}_3$  deposition in the light is presumably due to the red calcareous algae that grew on top of the sand layer.  $\text{CaCO}_3$  dissolution in the dark is not correlated with  $\Omega_{\text{arag}}$  of the seawater, suggesting that it is a function of the interstitial seawater  $\Omega_{\text{arag}}$ . The pH of the water located underneath the sediment layer was low (7.65) and consistent with values reported in interstitial water of reef sediments (Sansone et al. 1988; Sarazin et al. 1988; Charpy-Roubaud et al. 1996; Thomsen and Kristensen 1997) because of elevated  $\text{CO}_2$  concentrations resulting from bacterial respiration (Hales et al. 1994). This suggests that changes of open seawater pH from 8.1 to 7.9 (Table 1) have little effect on the interstitial pH and  $\Omega_{\text{arag}}$  (1.9). Reanalysis of data collected on reef sediments in situ by Boucher et al. (pers. comm.)

exhibits a similar behavior to the one observed in the mesocosm. The rate of net calcification as a function of  $\Omega_{\text{arag}}$  found for this reef sediment is of the same order of magnitude as that obtained in the present study (Table 2; Fig. 3). This suggests that the sand community investigated here is a good model of some soft-bottom communities encountered in coral reefs.

Predictions of the calcification rate of calcifying organisms during the next century can be derived from the equations presented in Table 3, together with estimates of  $\Omega_{\text{arag}}$  provided by Gattuso et al. (1999). The data describing the relationship between net calcification and  $\Omega_{\text{arag}}$  published so far show that corals and calcareous algae exhibit a similar response to increasing  $\text{pCO}_2$  (Table 3). A decrease of  $\Omega_{\text{arag}}$  from its preindustrial value (4.9) to its predicted value for 2100 (3.0) reduces the calcification rate of scleractinian corals and red calcareous algae by 11 and 32%, respectively. Other systems, mainly communities, show a greater variability. Odhe and van Woelk (1999) investigated the response of a reef flat in Japan without isolating the signal of  $\Omega_{\text{arag}}$  from that of the light intensity. Langdon et al. (2000) worked on the ocean of Biosphere 2 that featured large sandy areas and that was dominated by a red calcareous alga, *Ampiroa fragilissima* (Atkinson et al. 1999).

The present-day calcification ( $\Omega_{\text{arag}} = 4.3$ ) of the community dominated by scleractinian corals is 94% of the preindustrial rate and will be 82% of the preindustrial rate by the year 2100 when  $\text{pCO}_2$  will reach 706  $\mu\text{atm}$  ( $\Omega_{\text{arag}} = 3.0$ ), which is a 14% decrease from year 2000 to 2100. These predictions are in agreement with, but lower than, previous results (Gattuso et al. 1999; Kleypas et al. 1999; Leclercq et al. 2000). Net primary production might not be modified by an increase in  $\text{pCO}_2$  in communities dominated by scleractinian corals. However, this result cannot be extended to communities dominated by macrophytes, which are likely to be  $\text{CO}_2$  users.

The present experiment has been carried out using a coral mesocosm, which is inherently different from a natural reef for several reasons, notably including the water-motion regime. In that context, the present results should be interpreted with caution until the relationship between the response of such a mesocosm and that of a real reef is better understood.

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