Interacting effects of an increase of pCO_2 and temperature on photosynthesis and calcification in a scleractinian coral

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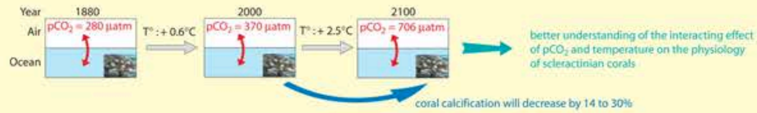
This poster is dedicated to Samantha Romaine-Lioud.

INTRODUCTION

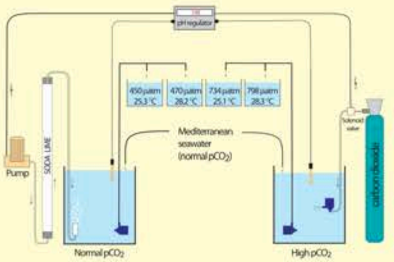


MATERIALS and METHODS

Biological material

Stylophora pistillata (40 nubbins suspended on nylon strings)
pCO_2 = 430 µatm
temperature = 25°C
irradiance = 380 µmol m^{-2} s^{-1}
12:12 photoperiod

} 2 weeks (until tissues have entirely recovered the skeleton)



Experimental set up

Four culture conditions:
* 450 µatm-25.3°C ("normal pCO_2, normal temperature")
* 470 µatm-28.2°C ("normal pCO_2, high temperature")
* 734 µatm-25.1°C ("high pCO_2, normal temperature")
* 798 µatm-28.3°C ("high pCO_2, high temperature").

All colonies were initially kept for 2 weeks under "normal pCO_2, normal temperature". Then, 10 colonies were randomly dispatched in each of the four tanks and the experiment ran for 5 more weeks.

Control of seawater pCO_2

Seawater pCO_2 was adjusted prior to the transfer into aquaria using a pH controller (R305, Consort Inc.) connected to pH electrodes (Orion, model 8102SC) as described by Leclercq et al. (2000). pH modifications were achieved by bubbling seawater with either pure CO_2 (to increase pCO_2) or with CO_2-free air (to decrease pCO_2).
Since pCO_2 was controlled by injecting gases, total alkalinity was not affected with the result that the changes of the carbonate chemistry were properly mimicking the changes predicted to occur during the next decades.

CONCLUSION

These results are of major interest from a predictive point of view. Several studies investigated the physiological relationship between calcification and pCO_2 or the aragonite saturation state. The consensus opinion is that calcification of tropical marine organisms and coral communities will decrease by an average 18-37% (Gattuso et al., 1999) between preindustrial time and the year 2100. However, none of these studies considered the effect of the forecast increase in temperature and its interaction with pCO_2 on photosynthesis and calcification.

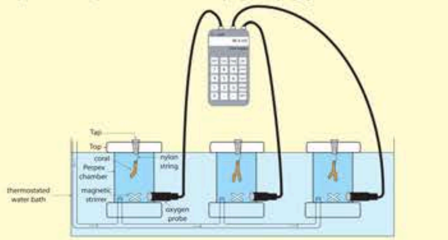
Our results demonstrate that the rate of calcification could decrease by 50% between the years 2000 and 2100. This temperature effect must be taken into consideration in subsequent investigations of future changes of coral physiology and reef metabolism. The present predictions must be re-evaluated as our results suggest that the decrease in the rate of calcification at the end of the century could be much higher than that forecast due to the synergistic effects of temperature and pCO_2.
There is a pressing need to manipulate environmental parameters in concert in order to determine the response of coral calcification to global environmental changes.

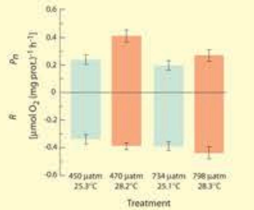
BIBLIOGRAPHY

Coles SL, Jokiel PL (1978) Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. Mar Biol 49, 187-195
Davies PS (1989) Short-term growth measurements of corals using an accurate buoyant weighing technique. Mar Biol 101, 389-395
Gattuso J-P, Allemand D, Frankignoulle M (1999) Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: A review on interactions and control by carbonate chemistry. Am zool 39, 160-183
Gattuso JP, Frankignoulle M, Bourge I, Romaine S, Buddemeier RW (1998) Effect of calcium carbonate saturation of seawater on coral calcification. Glob Planet Change 18, 37-46
Goiran C, Al-Moghrabi S, Allemand D, Jaubert J (1996) Inorganic carbon uptake for photosynthesis by the symbiotic coral/dinoflagellate association. J Exp Mar Biol Ecol199, 207-225
Jokiel PL, Maragos JE, Franzisket L (1978) Coral growth: buoyant weight technique. Stoddart DR, Johannes RE. Coral reef: research methods. 379-396. Paris, Unesco
Kajiwara K, Nagai A, Ueno S, Yokochi H (1995) Examination of the effect of temperature, light intensity and zooxanthellae concentration on calcification and photosynthesis of scleractinian coral *Acropora pulchra*. J
Langdon C, Takahashi T, Marubini F, Atkinson MJ, Sweeney C, Aceves H, Barnett H, Chipman D, Goddard J (2000) Effect of calcium carbonate saturation state on the rate of calcification of an experimental coral reef. Glob Biogeochem cycles 14, 639-654
Langdon C, Broecker WS, Hammond DE, Glenn E, Fitzsimmons K, Nelson SG, Peng T-H, Hajdas I, Bonani G (2003) Effect of elevated CO_2 on the community metabolism of an experimental coral reef. Glob Biogeochem Cycles 17, 11.1-11.14
Leclercq N, Gattuso J-P, Jaubert J (2000) CO_2 partial pressure controls the calcification rate of a coral community. Glob Change Biol 6, 1-6
Leclercq N, Gattuso J-P, Jaubert J (2002) Primary production, respiration, and calcification of a coral reef mesocosm under increased CO_2 partial pressure. Limnol Oceanogr 47, 558-564
Marubini F, Atkinson MJ (1999) Effects of lowered pH and elevated nitrate on coral calcification. Mar Ecol Progr Ser 188, 117-121
Marubini F, Ferrier-Pagès C, Cuif, JP (2003) Suppression of growth in scleractinian corals by decreasing ambient carbonate ion concentration: a cross-family comparison. Proc Royal Society B 270, 179-184
Marubini F, Thake B (1999) Bicarbonate addition promotes coral growth. Limnol Oceanogr 44, 716-720
Muscatine L, Cernichiari E(1969) Assimilation of photosynthetic products of zooxanthellae by a reef coral. Biol Bull 137, 506-523
Muscatine L, Ferrier-Pagès C, Blackburn A, Gates RD, Baghdasarian G, Allemand D (1998) Cell-specific density of symbiotic dinoflagellates in tropical anthozoans. Coral Reefs 17, 329-337

Photosynthesis and respiration

Net photosynthesis (P_n) and dark respiration (R) were measured on 3 colonies taken in each of the four tanks. 3 Perspex chambers (240 ml) filled with the seawater used in each treatment were used simultaneously in a thermostated water bath. The incubation medium was continuously agitated. Dissolved O_2 was measured using a Ponselle polarographic electrode and monitored every 1 min using a data-logger (LI-1000, Li-COR). Rates of net photosynthesis and respiration were estimated by regressing O_2 against time.





P_n of each colony measured during the 5 weeks subsequent to the perturbation did not vary with time (repeated measures ANOVA, P = 0.15).
P_n was affected by temperature (ANOVA, P = 0.0005) and pCO_2 (ANOVA, P = 0.009).
Respiration was not affected by temperature (ANOVA, P = 0.12), nor by pCO_2 (ANOVA, P = 0.11).

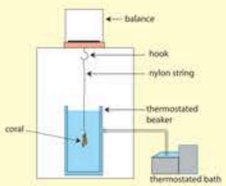
The increase of photosynthesis with increasing temperature under normal pCO_2 is in agreement with previous studies performed on corals (Coles & Jokiel, 1978; Kajiwara et al., 1995).

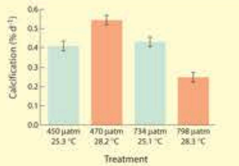
Elevated pCO_2 did not stimulate photosynthesis, which even slightly decreased. Langdon et al. (2003) also showed that net community production did not change in response to elevated pCO_2.

Corals are known to rely on bicarbonate for photosynthesis (Goiran et al., 1996). The increase in pCO_2 results in higher concentrations of dissolved CO_2 and bicarbonate, but the increase of the bicarbonate reservoir in which corals pump carbon for photosynthesis is likely too small (9 to 10%) to lead to a measurable increase of photosynthesis.

Calcification

The skeletal dry weight was measured every week by weighing each colony using the buoyant weight technique (Jokiel et al., 1978; Davies, 1989).





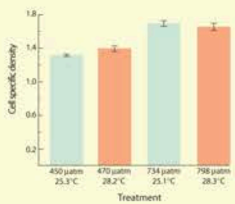
The rate of calcification of each colony did not vary significantly after the perturbation (repeated measures ANOVA, P = 0.3).
The calcification rate was significantly affected by the treatment (ANOVA, $P < 0.0001$ for pCO_2 and P = 0.3 for temperature). The significant interaction ($P < 0.001$) between pCO_2 and temperature demonstrates that there was a response to a change in temperature but that it differs depending on the level of pCO_2.

The rate of calcification declined immediately after the rise in pCO_2 and did not change afterwards, demonstrating that no acclimation process occurred. This is in agreement with previous studies:
* Marubini & Atkinson (1999) reported that the decrease of calcification in response to changes in the carbonate system is immediate in *Porites compressa*.
* Langdon et al. (2000) found that the response of the community calcification rate of the Biosphere 2 ocean is not different during short-term (days) and long-term (months) changes in Ω_{arag}.

Calcification of colonies maintained at elevated temperature declined by 50% in response to increased pCO_2. However, calcification was not affected by elevation of pCO_2 in colonies maintained at normal temperature. This is not in agreement with several papers that describe a negative relationship between calcification and CO_2, or a positive relationship with the aragonite saturation state (Gattuso et al., 1998; Marubini & Atkinson, 1999; Langdon et al., 2000; Leclercq et al., 2000; Leclercq et al., 2002; Langdon et al., 2003; Marubini et al., 2003). However, in some of these studies, Ω_{arag} has not been changed by manipulating pCO_2 but by changing the Ca^{2+} concentration (Gattuso et al., 1998), or by addition of acid (Marubini & Thake, 1999; Marubini et al., 2003) or sodium bicarbonate (Marubini & Atkinson, 1999). These results demonstrate that pCO_2 and temperature significantly interact to control calcification. The physiological basis of the different response at two temperatures does not result from an indirect effect of temperature on the seawater carbonate chemistry. Indeed, the change of pH and aragonite saturation state due to increased temperature was similar at both pCO_2s (ΔpH: -0.02 to -0.03; $\Delta\Omega_{arag}$: 0.18 to 0.25) and approximately 10 times lower than the changes resulting from increased pCO_2.

Cell Specific density (CSD)

3 nubbins from each treatment were used to determine the average number of zooxanthellae per animal cell (cell specific density). Corals were crushed with a hammer, placed in a 50 ml flask, and macerated by agitation (Muscatine & Cernichiari, 1969). Approximately 330 host cells from each colony were observed and ranked according to the number of zooxanthellae (from one to eight) that each contained.



The CSD increased under "high pCO_2" (ANOVA, $P < 0.001$) without being affected by the change in temperature (ANOVA, P = 0.4).
There was a dominance of singlets over doublets or triplets under "normal pCO_2" (70% of singlets and 30% of doublets). The frequency distribution changed at elevated pCO_2 with 47% of singlets, 41% of doublets and 11% of animal cells containing more than 2 zooxanthellae.

Under normal pCO_2, the CSD was identical at both temperature and equal to 1.4. The same value has been reported in the same species (Muscatine et al., 1998), and indicates that there is a dominance of singlets. This seems to be the standard condition of the symbiosis.
The CSD increased to 1.7 under elevated pCO_2 suggesting a higher rate of algal division compared to the division of animal cells. A change in CSD indicates a disruption of the balance between the growth rate of algal and animal cells.