Effect of light on skeletal ^{13}C and ^{18}O, and interaction with photosynthesis, respiration and calcification in two scleractinian corals

S. Reynaud-Vaganay[1], A. Juillet-Leclerc[2], J. Jaubert[1], and J.-P. Gattuso[1,3]

[1] Observatoire Océanologique Européen, Centre Scientifique de Monaco, Avenue Saint-Martin, MC-98000 Monaco, Principality of Monaco

[2] Laboratoire des Sciences du Climat et de l'Environnement, Laboratoire mixte CNRS-CEA, F-91180 Gif-sur-Yvette Cedex, France

[3] Observatoire Océanologique, Laboratoire d'Océanographie CNRS-UPMC, BP 28, 06234 Villefranche-sur-mer Cedex, France

INTRODUCTION

Causes of the variations in the ^{13}C of coral skeletons have been a matter of debate (Erez, 1978; Swart, 1983; McConnaughey, 1989). Aragonite deposited by scleractinian corals is usually depleted in ^{13}C relative to equilibrium with ambient seawater as a result of kinetic and metabolic fractionation.
The two external sources of carbon available to corals are dissolved inorganic carbon (DIC) in seawater (^{13}C close to 1‰) and zooplankton (^{13}C <<1‰). The physiological processes that alter the carbon pool available to corals are photosynthesis, respiration and feeding.

It has been suggested that calcification takes place from an internal inorganic carbon pool (Goreau, 1977; Erez, 1978) composed of carbon derived from seawater and from metabolic activity, and modified by fractionation during CO_2 uptake by photosynthesis. It was suggested that the light isotope (^{12}C) was preferentially used by zooxanthellae for photosynthesis, leading to an increased concentration of $^{13}CO_2$ in the carbon pool available for calcification. Therefore skeleton precipitated during periods of high photosynthesis should be isotopically heavier (Swart, 1983; McConnaughey *et al.*, 1997). Increased heterotrophy should have an opposite effect leading to a decrease in skeletal ^{13}C levels. As heterotrophy and photosynthesis are tightly linked in the field, coral culture in the laboratory is the only way to investigate the effect of light on skeletal isotopic composition. Futher details can be found in Reynaud-Vaganay *et al.* (sbm).

MATERIALS AND METHODS

The experiment was conducted in the laboratory using colonies of *Stylophora pistillata* and *Acropora* sp. The tips were glued on glass slides as described by Reynaud-Vaganay *et al.* (1999). All colonies were initially cultured for 6 weeks at a light intensity of 132 µmol m^{-2} s^{-1}. The skeleton deposited on the glass slide was then removed with a scalpel. Thereafter, the same colonies were cultured for 6 weeks at a light intensity of 258 µmol m^{-2} s^{-1} and the skeleton sampled again. The photoperiod was 12:12 in each case.
The carbon and oxygen isotope composition of seawater was measured on samples collected once a week. By subtracting the $^{13}C_{DIC}$ from the skeletal ^{13}C, the true change in ^{13}C can be calculated. The skeletal ^{18}O was also corrected for changes in seawater oxygen isotopic composition (Hut, 1987).

Photosynthesis and respiration were measured using the oxygen technique. Each coral was placed in a perspex chamber (240 ml) containing filtered seawater, for a 30 min pre-incubation in the light (132 or 258 µmol photons m^{-2} s^{-1}, depending on the culture condition). The colony was then incubated for 1h in order to measure the oxygen production. The chamber was then flushed, and the coral pre-incubated for 30 min in the dark, and after 1h in the dark to measure the respiration rate. The incubation medium was continuously agitated. Oxygen concentration was monitored using a data-logger. Dissolved O_2 was measured using a polarographic electrode calibrated each day. The rates of net photosynthesis and respiration were estimated using a linear regression of O_2 against time. Photosynthesis and respiration values were then normalized with the surface of the coral.
Corals were weighted using the buoyant weight technique (Jokiel *et al.*, 1978; Davies, 1989) at the beginning and at the end of the experiment to estimate the rate of calcification.

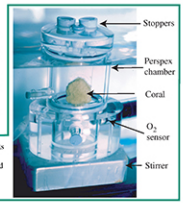


Fig 1. Measurements of O_2 production (photosynthesis) and consommation (respiration)

RESULTS

Calcification

The calcification rate of *Acropora* sp. under **HL** was 2.5 fold higher than under **LL**, the difference was 17 fold for *S. pistillata*.

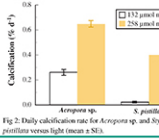


Fig 2: Daily calcification rate for *Acropora* sp. and *Stylophora pistillata* versus light (mean ± SE).

Photosynthesis and respiration

The average net photosynthesis of *Acropora* sp. was higher under **HL** than under **LL**. The difference was not significant for *S. pistillata*. We have measured an increase of P_g when the light was doubled.
We did not find a significant effect of irradiance on the respiration rate.

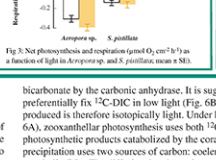


Fig 3: Net photosynthesis and respiration (µmol O_2 cm^{-2} h^{-1}) as a function of light in *Acropora* sp. and *S. pistillata*; mean ± SE).

Stable carbon isotope

The seawater $^{13}C_{DIC}$ remained constant both during a diel cycle and during several months. The average skeletal ^{13}C of *Acropora* sp. was lighter under **LL** than under **HL**. The skeletal ^{13}C value of *S. pistillata* deposited under **LL** appeared also more negative than under **HL**. The skeletal ^{13}C of *Acropora* sp. was significantly correlated with the rate of calcification, in both light treatment.
No correlation was found, in *Acropora* sp., between the skeletal ^{13}C and net and gross photosynthesis, respiration, and the P_g/R ratio.

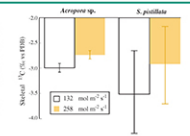
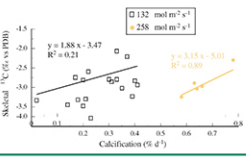


Fig 4: Skeletal ^{13}C versus light in both species (mean ± SE).



Stable oxygen isotope

$^{18}O_{sw}$ remained constant during the experiment. The average skeletal ^{18}O were more negative under **LL** than under **HL**. The results obtained here raise the question of using oxygen isotopic composition in paleoenvironmental reconstruction.

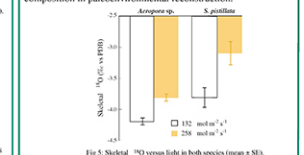
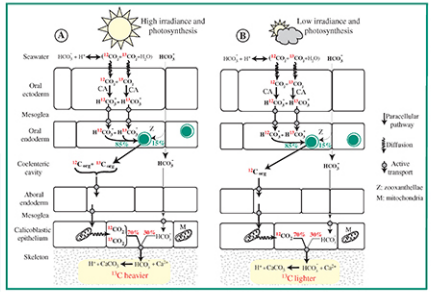


Fig 5: Skeletal ^{18}O versus light in both species (mean ± SE).

MODEL

The increase of skeletal ^{13}C with increasing light supports the model of Goreau (1977). However the model needs to be revised to accommodate the recent finding that calcification and photosynthesis draw carbon from two reservoirs (seawater and metabolic DIC), and that respiratory CO_2 is the major source of DIC for calcification (Furla *et al.*, in press).
Since photosynthesis is a rapid process, the diffusional pathway of does not provide enough carbon to sustain photosynthesis. Zooxanthellae must actively pump bicarbonate, leading an isotopic fractionation (Fig. 6). CO_2 diffuses from seawater across the oral ectoderm layer, and is converted into bicarbonate by the carbonic anhydrase. It is suggested that zooxanthallae preferentially fix ^{12}C-DIC in low light (Fig. 6B); the organic matter produced is therefore isotopically light. Under high light condition (Fig. 6A), zooxanthellar photosynthesis uses both ^{12}C- and ^{13}C-DIC, the photosynthetic products catabolized by the coral is therefore heavier. $CaCO_3$ precipitation uses two sources of carbon: coelenteric bicarbonates and metabolic CO_2. The diffusional pathway is unaffected by light variations, but this pathway represents only 30% of the total carbon into the skeleton (Furla *et al.*, in press). Assuming that 70% of the DIC used for calcification is metabolic CO_2, the skeleton deposited under high light is isotopically heavier. On the other hand, in low light (Fig. 6B), the organic matter respired, the CO_2 released, and the $CaCO_3$ deposited are isotopically lighter.



BIBLIOGRAPHY

Davies PS (1989) Short-term growth measurements of corals using an accurate buoyant weighing technique. *Mar Biol* 101: 389-395

Erez J (1978) Vital effect on stable-isotope composition seen in foraminifera and coral skeletons. *Nature* 273: 199-202

Furla P, Galgani I, Durand I, Allemand D (in press) Sources and mechanisms of inorganic carbon transport for coral calcification and photosynthesis. *Journal of Experimental Biology*

Hut G (1987) Stable isotope reference samples for geochemical and hydrological investigations. Consultant group meeting IAEA. Vienna 16-18 September 1985. Report to the Director General, IAEA, Vienna

Juillet-Leclerc A, Gattuso J-P, Montaggioni LF, Pichon M (1997) Seasonal variation of primary productivity and skeletal ^{13}C and ^{18}O in the zooxanthellate scleractinian coral Acropora formosa. *Mar Ecol Prog Ser* 157: 109-117

Jokiel PL, Maragos JE, Franzisket L (1978) Coral growth: buoyant weight technique. *In:* Stoddart, D. R., Johannes, R. E (Eds.) Coral reef: research methods. Unesco, 379-396

Goreau TJ (1977) Coral skeletal chemistry: physiological and environmental regulation of stable isotopes and trace metals in *Montastrea annularis*. *Proceedings of Royal Society of London*, series B, 291-315

McConnaughey T (1989) ^{13}C and ^{18}O isotopic disequilibrium in biological carbonates. I. Patterns. *Geochim Cosmochim Acta* 53: 151-162

McConnaughey TA, Burdett J, Whelan JF, Paull CK (1997) Carbon isotopes in biological carbonates: respiration and photosynthesis. *Geochim Cosmochim Acta* 61: 611-622

Reynaud-Vaganay S (1999) A novel culture technique for scleractinian corals: application to investigate changes in skeletal ^{18}O as a function of temperature. *Mar Ecol Prog Ser* 180: 121-130

Reynaud-Vaganay S (sbm) Effect of light on skeletal ^{13}C and ^{18}O, and interaction with photosynthesis, respiration and calcification in two zooxanthellate scleractinian corals. *Pal Pal Pal.*

Swart PK (1983) Carbon and oxygen isotope fractionation in Scleractinian corals: a review. *Earth-Science Reviews* 19: 51-80

ACKNOWLEGEMENTS: Thanks are due to M. Boiseau, P. Furla, D. Allemand, M. Stievenard and H. Spero.

This poster is dedicated to the memory of Samantha Romaine-Lioud; she is sorely missed.