

Primary production, calcification and air-sea CO₂ fluxes in coral reefs: organism, ecosystem and global scales

by

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ABSTRACT

We summarize here data on primary productivity, calcification and air-sea CO₂ fluxes collected from a reef coral, a reef flat and a reef mesocosm and present a discussion on the global effect of marine calcification on atmospheric CO₂.

The respective effects of CO₂ uptake by photosynthesis and CO₂ release by respiration and calcification on the carbon budget of a zooxanthellate scleractinian coral were investigated in the laboratory. The air-sea CO₂ flux was inferred by modelling the CO₂ system. Its integration showed that the direction of the net daily flux is from sea to air (evasion).

Measurements of gross production and respiration of the "Tiahura barrier reef" (Moorea, French Polynesia) showed that the reef displayed a very small excess production. Net calcification was positive both during the day and at night. The measured air-sea CO₂ fluxes were close to zero in the open ocean but displayed a strong daily pattern at the reef front and the back reef. Integration of the fluxes over 24-h showed that the reef ecosystem was a source of CO₂ to the atmosphere.

Other investigations included a comparison of the main metabolic features of a 40 m² reef mesocosm set up in Monaco to those of a Red Sea coral

patch enclosed *in situ* in a 6 m³ chamber. The budget of organic production/consumption of the mesocosm reef was slightly negative while that of the coral patch was slightly positive. The captive reef and the coral patch exhibited high rates of precipitation and dissolution of CaCO₃ but the 24 h budgets of both systems were positive (net CaCO₃ deposition).

The role of marine calcification as a source of dissolved CO₂ is due to chemical equilibria and is therefore a function of the partial pressure of CO₂ in seawater (*p*CO₂). The present ratio of released CO₂/precipitated carbonate is 0.6 and calculations show that it will rise up to 0.76 for a doubling of the pre-industrial *p*CO₂. This would result in a net CO₂ source of approximately 2% of the present day fossil fuel flux.

INTRODUCTION

Coral reefs are a major feature of coastal and shallow-water tropical seas, and cover approximately 15 % of the oceanic sea floor between 0 and 30 m (SMITH, 1978). Measurements of organic production and calcification were carried out in a number of coral reef ecosystems (reviewed by KINSEY, 1985). Community gross primary production (*P*) is usually high, with an average value of 7 g C m⁻² d⁻¹ (KINSEY, 1985). Community respiration (*R*) is, however, of the same order of magnitude as *P*. Consequently, the community net productivity (also called excess production) is close to zero (0 ± 0.7 g C m⁻² d⁻¹; CROSSLAND *et al.* 1991). Organic carbon metabolism plays therefore a minor role in net carbon fluxes in coral reefs and the reef excess production is approximately 0.05% of the net CO₂ fixation rate of the global ocean (CROSSLAND *et al.*, 1991).

The average net calcification of coral reef flats is 4.0 ± 0.7 kg CaCO₃ m⁻² y⁻¹ (KINSEY, 1985). KINSEY and HOPLEY (1991) estimated that the global carbon fixation by coral reefs via calcification is 0.1 Gt y⁻¹ but the fact that calcification is also a source of CO₂ to the water column and atmosphere was not taken into account in their estimate. The direction and magnitude of the CO₂ flux at the air-sea interface depend on the difference in CO₂ partial pressure (*p*CO₂) between both phases and not on the difference in total inorganic CO₂ (TCO₂). Deposition of calcium carbonate increases *p*CO₂ and drives CO₂ from sea water to the atmosphere (evasion). The increase in *p*CO₂ resulting from calcification is well documented (e.g. GARRELS and MACKENZIE, 1980; BERGER, 1982) but was ignored for coral reefs until recently (CROSSLAND *et al.*, 1991; KINSEY and HOPLEY, 1991; WARE *et al.*, 1992; FRANKIGNOULLE and GATTUSO, 1993; GATTUSO *et al.*, 1993; FRANKIGNOULLE *et al.*, 1994) and no experimental data were available.

The aim of this paper is to summarize data collected by our group at the organism (FRANKIGNOULLE and GATTUSO, 1993), ecosystem (GATTUSO *et al.*, 1993; JAUBERT *et al.*, 1993) and global scales (FRANKIGNOULLE *et al.*, 1994). We refer the interested reader to the above-mentioned papers for more details.

RESULTS AND DISCUSSION

Organism scale

Productivity and calcification of the zooxanthellate scleractinian coral *Stylophora pistillata* (ESPER, 1797) were measured in the laboratory on

colonies collected at depths of 3-5 m at Davies Reef (Great Barrier Reef). Net CO₂ fixation via photosynthesis during the day was higher than CO₂ production through respiration at night with a day:night ratio higher than 3 (figure 1). Calcification consumed CO₂ species over the whole 24-h cycle and was 1.6 times higher during the day than at night. ΔTCO₂, which integrates the effects of production/respiration and calcification, was negative throughout the cycle with a day:night ratio of 44.4. The instantaneous flux of CO₂ across the air-sea interface (*f*_{CO₂}) was modelled. It was negative (CO₂ invasion) during the day and positive (CO₂ evasion) at night. Integration of *f*_{CO₂} over 24-h (F) showed that the coral was a slight source of CO₂ for the atmosphere.

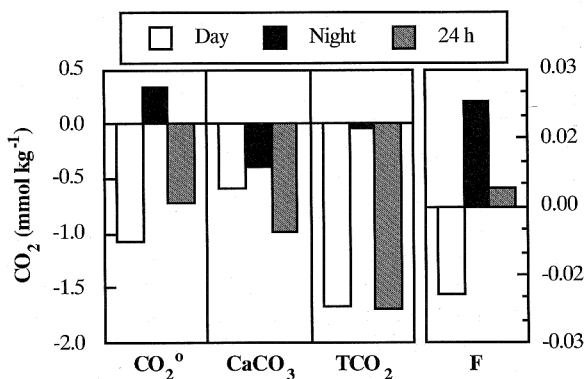


Figure 1 – Budget of the effect of a scleractinian coral on the CO₂ system. CO₂ fluxes resulting from photosynthesis and respiration (CO₂^o), calcification (CaCO₃), all metabolic processes (TCO₂) and air-sea exchange (F). From FRANKIGNOULLE and GATTUSO (1993).

Ecosystem scale

Gross production and respiration of the “Tiahura barrier reef” (Moorea, French Polynesia) were respectively 640.2 to 753 and 590.4 to 641.5 mmol (O₂ or CO₂) m⁻² d⁻¹ (7.7 to 9.0 and 7.1 to 7.7 gC m⁻² d⁻¹) and the reef displayed a very small excess production at the time of measurement (November-December 1991). Planktonic primary productivity represented less than 0.15 % of the total productivity. Net calcification was positive both during the day and at night (figure 2); its daily value was 243 mmol CaCO₃ m⁻² d⁻¹ (24.3 g CaCO₃ m⁻² d⁻¹). Reef metabolism decreased TCO₂ by 433.3 mmol m⁻² d⁻¹.

Figure 3 shows the air-sea CO₂ flux data *versus* time in the ocean, and at the reef front and the back reef. Instantaneous air-sea CO₂ fluxes (*f*_{CO₂}), measured on two occasions (during the day only) in oceanic water one mile off the reef, were close to zero (0.7 ± 0.3 and 0.2 ± 0.9 mmol m⁻² s⁻¹) and did not display any light-dependence from 305 to 1200 μmol m⁻² s⁻¹. Fluxes measured at the reef front (figure 3A) and back reef (figure 3B) stations displayed a strong daily pattern. There was a CO₂ evasion at night (up to 88 mmol m⁻² s⁻¹) and a CO₂ invasion during the day (up to -71 mmol m⁻² s⁻¹). The net fluxes during the day and at night were respectively -0.2 and 1.7 mmol m⁻² (figure 2). The direction and magnitude of *f*_{CO₂} were light-dependent at

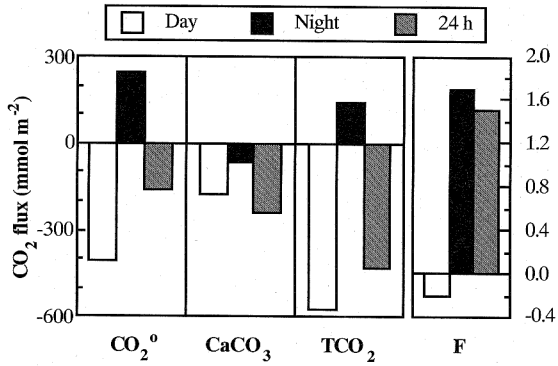


Figure 2 – Budget of the CO₂ system in November-December 1991. CO₂ fluxes resulting from photosynthesis and respiration (CO₂[°]), calcification (CaCO₃), all metabolic processes (TCO₂) and air-sea exchange (F). From GATTUSO *et al.* (1993).

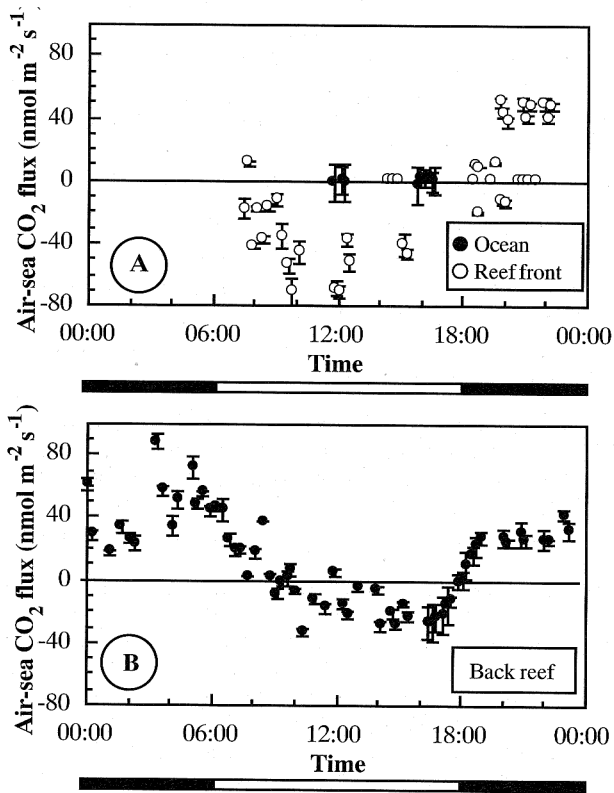


Figure 3 – Air-sea CO₂ flux: A, in the ocean and the reef front; B, at the back reef. Confidence intervals are ± 1 SD. All data collected during the field trip are shown. From GATTUSO *et al.* (1993).

both the reef front and back reef stations. f_{CO_2} was positive when irradiance was zero and fluxes at the back reef were significantly higher than at the reef front (36 ± 4 vs 19 ± 6 $nmol\ m^{-2}\ s^{-1}$, $p = 0.02$). f_{CO_2} decreased with increasing irradiance (data not shown); a linear equation could be fitted through the data points collected at the reef front ($Y = 18.8 - 0.033 X$; $r^2 = 0.66$, $p < 0.0001$) but relatively important scattering of the data prevented to satisfactorily fit any function to the back reef data set.

The coral mesocosm and its natural homologue (the *in situ* enclosed coral patch) were respectively investigated in Monaco (JAUBERT *et al.*, 1993) and in the Gulf of Aqaba (COPIN-MONTÉGUT *et al.*, 1992). Both systems exhibit similar metabolic performances (table I). During the day pO_2 and pH increase while pCO_2 decreases. Opposite trends are recorded at night. Both daily photosynthesis/respiration ratios are close to 1 in the mesocosm and the coral patch (0.9 and 1.1, respectively) and the community net primary production of the coral patch is slightly positive while that of the mesocosm reef is slightly negative. The latter condition probably results from the presence of carnivorous fish that feed on allochthonous organic matter.

TABLE I

Carbon and calcium balances of the captive reef coral (mesocosm) and of the natural coral patch. Data are expressed in $g\ m^{-2}\ d^{-1}$. C_{org} and C_{calc} correspond to the organic carbon and the inorganic carbon fixed respectively by photosynthesis and calcification.

$N = 10$ in the mesocosm and $N = 3$ for the coral patch. Mean \pm s.d.

	Gross		Net	
	Mesocosm	Coral patch	Mesocosm	Coral patch
C_{org}				
Productivity	6.9 ± 0.03	2.1 ± 0.003	-0.7 ± 0.03	0.2 ± 0.003
Respiration	7.6 ± 0.03	1.9 ± 0.003		
C_{calc}				
Calcification	3.6 ± 0.09	1.5 ± 0.019	0.4 ± 0.18	0.1 ± 0.04
Dissolution	3.2 ± 0.09	1.4 ± 0.019		
$CaCO_3$				
Calcification	29.6 ± 0.73	12.2 ± 0.16	3.4 ± 1.46	0.8 ± 0.03
Dissolution	26.3 ± 0.73	11.4 ± 0.16		

Both systems exhibit high rates of calcium carbonate deposition and dissolution. There is a net deposition of $CaCO_3$ during the day and a net dissolution at night but over a period of 24 hours the budget of production/consumption of inorganic C is positive. The calcification rate of the mesocosm reef was 3.4 ± 3.1 $g\ CaCO_3\ m^{-2}\ d^{-1}$ while that of the coral patch was 0.7 ± 0.6 $g\ CaCO_3\ m^{-2}\ d^{-1}$.

Calcium carbonate dissolution always took place under conditions of calcium carbonate super-saturation. It seems therefore that dissolution is a biologically-mediated process that affects the calcareous reef frame as well as the surrounding sediment. However, the hypothesis of night-time losses of calcium carbonate by calcifying organisms should not be discarded *a priori* (CHISHOLM *et al.*, 1990). The C_{calc}/C_{org} ratio of the mesocosm reef (0.5) is significantly different from that of the coral patch (0.7). The low C_{calc}/C_{org} of the mesocosm reef probably results from the relatively high concentrations of nutrients which may enhance the production of organic C rather than the production of inorganic C. This phenomenon seems to indicate that the ratio C_{calc}/C_{org} could be used as an index of the degree of eutrophication of a "photo-calcifying" ecosystem.

It must be emphasized that these results are limited to short-term measurements. Yet, they show that the coral mesocosm is a promising tool for investigating the metabolism of coral reef communities (JAUBERT *et al.*, 1993).

Global scale

Deposition of calcium carbonate can be described by two equations which have the same significance in terms of chemical dynamics:

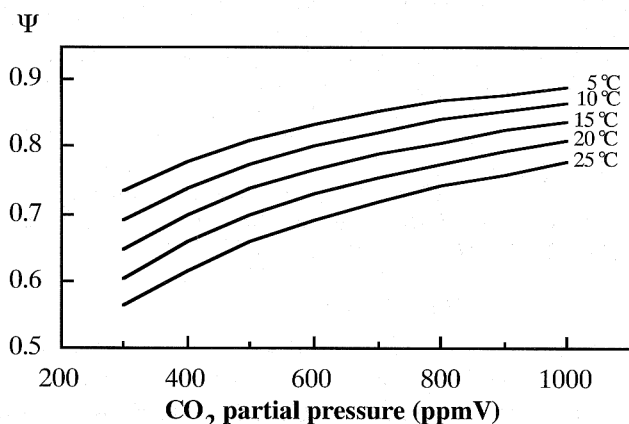
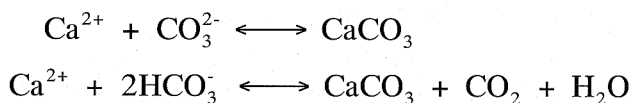


Figure 4 – Released CO₂/precipitated carbonate ratio (mol kg⁻¹/mol kg⁻¹) as a function of seawater pCO₂. S = 35, t = 25 °C and total alkalinity = 2400 μeq kg⁻¹, N.B.S. pH scale). After FRANKIGNOULLE *et al.* (1994).

There is a 1:1 relationship between the CO₂ released and the CaCO₃ precipitated in freshwater but not in seawater, due to the buffering effect of the latter. WOLLAST *et al.* (1980) showed experimentally that the ratio of released CO₂/precipitated CaCO₃ was 0.6 in seawater. A similar value was obtained empirically by WARE *et al.* (1992). We have derived an analytical expression enabling the computation of the ratio of released CO₂/precipitated CaCO₃ (Ψ) using a set of buffer factors newly described (FRANKIGNOULLE, 1994).

Ψ mainly depends on temperature and pCO₂ (figure 4). Its value is 0.6 for t = 25 °C and pCO₂ = 350 ppmV. There is a positive feedback of pCO₂ on Ψ: the amount of CO₂ released during calcification increases as a function of increasing seawater pCO₂. We could also show that the average Ψ value was 0.63 in 1880 (pCO₂ = 280 ppmV, t = 15 °C, S = 35 and TA = 2400 μEq kg⁻¹) and would reach 0.75 for pCO₂ = 560 ppmV (t = 15 °C, S = 35 and TA = 2400 μEq kg⁻¹). A doubling of the pre-industrial pCO₂ would result in a net CO₂ source of 130 Gt C y⁻¹, approximately 2% of the present day fossil fuel CO₂ flux.

CONCLUSION

These data provide new insight on the role of corals and coral reefs on the CO₂ cycle. Experimental data suggest that scleractinian corals and coral reef ecosystems are sources of CO₂ to the atmosphere due to their high rate of calcium carbonate deposition. We have also shown that marine calcification will release more CO₂ to the atmosphere as a result of the anthropogenic increase in atmospheric CO₂.

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