

Community metabolism and air-sea CO₂ fluxes in a coral reef ecosystem (Moorea, French Polynesia)

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ABSTRACT: Community metabolism (primary production, respiration and calcification) and air-sea CO₂ fluxes of the 'Tiahura barrier reef' (Moorea, French Polynesia) were investigated in November and December 1991. Gross production and respiration 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 g C m⁻² d⁻¹) and the reef displayed a slightly negative excess (= net) production. The contribution of planktonic primary production to reef metabolism was negligible (0.15 % of total gross production). Net calcification was positive both during the day and at night, its daily value was 243 mmol CaCO₃ m⁻² d⁻¹ (24.3 g CaCO₃ m⁻² d⁻¹). Reef metabolism decreased seawater total CO₂ by 433.3 mmol m⁻² d⁻¹. The air-sea CO₂ fluxes were close to zero in the ocean but displayed a strong daily pattern at the reef front and the back reef. Fluxes were positive (CO₂ evasion) at night, decreased as irradiance increased and were negative during the day (CO₂ invasion). Integration of the fluxes measured during a 24 h experiment at the back reef showed that the reef was a source of CO₂ to the atmosphere (1.5 mmol m⁻² d⁻¹).

INTRODUCTION

The coral reef carbon cycle is mainly driven by 2 biological processes: organic carbon metabolism (photosynthetic fixation and respiration) and inorganic carbon metabolism (precipitation and dissolution of calcium carbonate). The production of one mole of organic matter or calcium carbonate decreases the total inorganic carbon (TCO₂) by one mole for each. Conversely, respiration and calcium carbonate dissolution increase TCO₂ by one mole. Measurements of organic production, respiration and calcification have been 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 reef excess production is about 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 yr⁻¹ (Kinsey 1985). Kinsey & Hopley (1991) estimated that the global carbon fixation of coral reefs via calcification is 0.1 Gt yr⁻¹ but calcification is also a source of CO₂ to the water column and the atmosphere. The direction and magnitude of the CO₂ flux at the air-sea interface depend on the difference in CO₂ partial pressure (*p*CO₂) between the 2 phases rather than on the difference in TCO₂. The precipitation and dissolution of CaCO₃ can be described as follows (Smith & Key 1975):



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Deposition of calcium carbonate increases $p\text{CO}_2$ and should drive CO_2 from seawater to the atmosphere (evasion). The increase in $p\text{CO}_2$ resulting from calcification is well documented (e.g. Garrels & MacKenzie 1981, Berger 1982) but was ignored in considerations of coral reefs until recently (Crossland et al. 1991, Kinsey & Hopley 1991, Ware et al. 1992, Frankignoulle & Gattuso 1993).

It has been demonstrated experimentally that 0.6 mol CO_2 are liberated for each mole of CaCO_3 precipitated (Wollast et al. 1980). This was confirmed by theoretical considerations on the effect of calcification upon the seawater CO_2 system (Ware et al. 1992) and an analytical expression of ψ , the ratio of released CO_2 /precipitated CaCO_3 , has recently been derived (Frankignoulle et al. unpubl.). Frankignoulle & Gattuso (1993) incubated coral colonies in the laboratory and demonstrated that corals are a source of CO_2 for the atmosphere but found that ψ was less than 0.1 under their experimental conditions. Air-sea CO_2 fluxes have never been measured at the ecosystem level in coral reef areas and the indirect estimates available vary greatly depending on the study site (Smith 1973, 1974, Smith & Pesret 1974, Smith & Jokiel 1976, Pigott & Laughlin 1988).

This paper reports on the first direct measurements of air-sea CO_2 fluxes in a coral reef ecosystem. Productivity, calcification and air-sea CO_2 fluxes were measured simultaneously in order to derive a CO_2 budget for a barrier reef in Moorea, French Polynesia.

MATERIALS AND METHODS

All data were collected in November and December 1991. Field operations came to a halt for 4 d (9 to 12 December) due to the passage of a cyclone 500 km from the study site and associated wind speeds of up to 14 m s^{-1} .

Study area. The reef lies on the northern coast of Moorea Island ($17^\circ 29' \text{ S}$, $149^\circ 54' \text{ W}$), French Polynesia (Fig. 1). It is known locally as the Tiahura barrier reef. Two stations were considered on the barrier reef system. The upstream station was located ca 30 m from the reef front, behind the algal ridge. The downstream station was located near the back reef margin, next to a drainage channel. In addition, an oceanic station was selected, ca 1 mile from the reef front.

No conspicuous zonation of the reef benthos was observed behind the algal ridge and, although changes in the relative abundance of the major epibiotic components were recorded, these changes were gradual when moving landwards towards the drainage channel. In the vicinity of the upstream station, live corals can cover up to 31 % of the substratum. They are

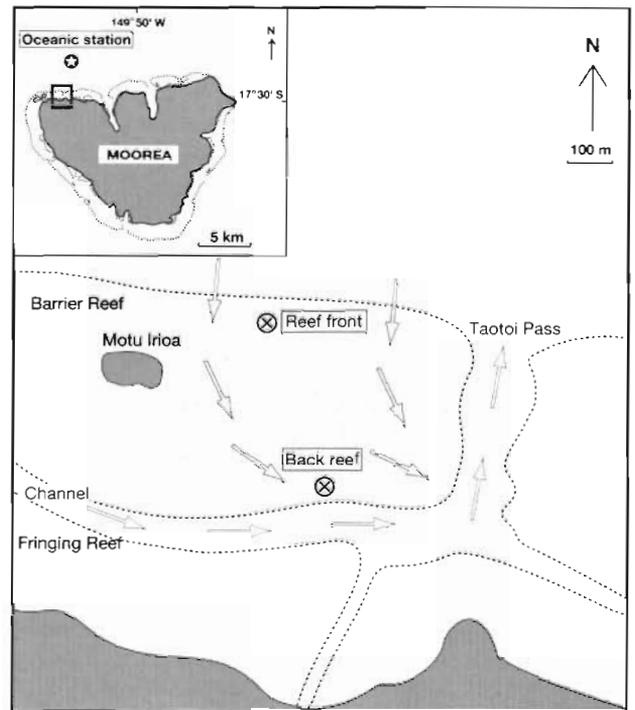


Fig. 1. Station locations and prevailing currents along the Tiahura barrier reef

represented by large colonies of massive *Porites* (*P. lutea* and *P. lobata*) and of the genus *Synaraea* often reaching close to the sea surface. Other species (*Pocillopora verrucosa*, *Napopora irregularis*, *Acropora* sp.) have much smaller colonies and are uncommon. Dead coral colonies can cover up to 20 % of the substratum. Because of the intensity of hydrodynamic activity, sedimentary deposits are mostly represented by rubble (up to 20 % substratum cover) with very little, mostly coarse, sand or gravel (less than 5 % substratum cover). Algae are only represented by coralline algae partially encrusting rubble or portions of dead coral colonies and by turf algae, also found on parts of dead coral colonies.

When moving landwards, the percentage of substratum covered by live corals decreases to below 2 %. One can still observe large, mostly massive, colonies but a significant part of their surface is dead, and their upper horizontal surface is covered by tall phaeophytes (mostly *Turbinaria ornata*) emerging at low tide. The large coral colonies are more scattered over the bottom than closer to the algal ridge. The sediment is predominantly sand, which may build up into submerged cays or hydrodynamically formed dunes near the drainage channel. In the eastern part of the study area the sedimentary deposits which developed along the channel margin are replaced by an accumulation of broken coral colonies (boulders, blocks and coarse gravel) that

are almost exposed at low tide. A reef rock pavement strewn with broken coral colonies and partly covered with a thin layer of sand extends northward from this detrital bank. In this zone, the tall phaeophytes *Tornata* and *Sargassum* spp. can cover up to 40 % of the substratum, whereas coral cover is less than 1 %.

Transects. Twelve transects were run on the reef flat from the upstream station to the downstream station. The location of the downstream site varied according to the direction of the current. A floating data-logger was used to monitor changes in dissolved oxygen, pH, irradiance (photosynthetic photon flux density) and seawater temperature while drifting across the reef flat. Its design is based on the original 'buoy' described by Barnes (1983). The following sensors were used: a galvanic oxygen electrode (Kent Eil), a combined pH electrode (Radiometer, GK 2401C), an underwater quantum sensor (Li-Cor, LI-192SA) and a stainless steel thermistor (Analog Devices, AC 2626 K4). Data from the 4 sensors were averaged every 10 s and stored in RAM. Replicate seawater samples were collected upstream and downstream for later determination of total alkalinity. The track of the data-logger was followed from the reef front site using a station pointer. The average length of the transects was 490 m and the average depth 1.4 m. The current velocity across the reef flat varied between 0.16 and 0.49 m s⁻¹. Incident irradiance was measured ashore during all field experiments using a LI-192SA quantum sensor, averaged and logged every minute on a LI-1000 data-logger. Wind speed was measured approximately every 30 to 60 min using a hand-held anemometer.

Calcification and partitioning of organic and inorganic carbon metabolisms were computed using the alkalinity anomaly technique (Smith & Key 1975). Some data had to be discarded because of the unusual drift of the pH electrode or missing seawater samples for alkalinity. Differences in oxygen and carbon dioxide between the upstream and the downstream stations were corrected for O₂ and CO₂ exchange with the atmosphere using the procedure outlined in Wanninkhof (1992) and the relationships for the variation of the gas exchange coefficient with wind speed given by Liss & Merlivat (1986). Metabolic rates per unit area were obtained using the difference in concentration, the volume transport of water and the area covered by the data-logger (see Barnes & Devereux 1984). Rates of productivity (expressed both in terms of O₂ and CO₂) and calcification, as well as changes in TCO₂ were plotted as a function of the average atmospheric irradiance measured during transect experiments. An exponential function was fitted to the data using the freeware package CurveFit:

$$y = a(1 - \exp(-I/b)) + c$$

where: a = horizontal asymptote; I = irradiance; b = irradiance at which the initial slope intercepts the horizontal asymptote; and c = y -intercept. When rates of productivity are considered: $y = p$ (rate of net photosynthesis); $a = P_{\text{max}}$ (rate of maximal gross photosynthesis), $b = I_k$ and $c = r$ (respiration rate).

Nighttime, daytime and daily (24 h) rates of gross production, respiration and calcification were estimated by numerically integrating (1 min intervals) the data for the fitted lines against irradiance in air measured on 13 to 14 December (daily incident irradiation = 51.2 mol m⁻² d⁻¹, duration of night and day were, respectively, 604 and 836 min).

By convention, small letters refer to instantaneous and hourly fluxes (f_{CO_2} , g , p , r) while capital letters (F_{CO_2} , G , P , R) refer to fluxes integrated over the day, night or 24 h.

Fixed stations. Dissolved oxygen, light, seawater temperature, total alkalinity and air-sea CO₂ exchange were measured at fixed stations (ocean, reef front, back reef; see Fig. 1). A full 24 h cycle was carried out at the back reef station on 13 to 14 December and several series of short-term (1 to 2 h) measurements were made at the 2 other sites. Dissolved oxygen, light and seawater temperature were measured using the data-logger described above. Replicate seawater samples were collected (every 60 to 90 min at the back reef) for later determination of total alkalinity. Air-sea CO₂ fluxes were obtained by directly measuring changes in atmospheric $p\text{CO}_2$ over 10 min inside a bell floating on the sea surface (Frankignoulle & Distèche 1984, Frankignoulle 1988). The bell had a surface exchange of 0.506 m² and a total volume of 0.202 m³. The CO₂ partial pressure in the bell was monitored using a LiCor 6252 infrared gas analyser (IRGA) calibrated against commercial CO₂ standard (350 ± 9 ppmV) and pure nitrogen. An air pump created a continuous air flow through the analyser.

Analytical procedures. The oxygen sensor and pH electrode were calibrated daily. The oxygen sensor was calibrated against air-saturated seawater and a saturated solution of sodium dithionite (zero oxygen). The pH electrode was calibrated against U.S. National Bureau of Standards (NBS) buffers: pH 6.865 and 7.413 at 37 °C (Radiometer). Seawater for total alkalinity (TA) determinations was filtered immediately after sampling on Whatman GF/C membranes and stored in BOD bottles in darkness at 4 to 10 °C pending analysis. TA was measured potentiometrically, within 2 d, on 20 ml subsamples using a Mettler DL 70 titrator. The pH electrode of the titrator (Orion, 81-02) was calibrated daily against NBS buffers: pH 4.008 (Ingold) and pH 7.000 (Radiometer) at 25 °C. A fixed volume (4.3 ml) of saline (NaCl: 35.85 g l⁻¹; Merck, 6404) 0.01 N HCl (Merck Titrisol, 9974) was added to the

sample; HCl was subsequently added in 0.1 ml increments. Increments were not added until pH had stabilised (± 0.003 unit in 5 s). The samples, the hydrochloric acid and the titration vessel were kept at constant temperature (25°C). Measurements were carried out on 4 replicates. Upon completion of the titration, data on HCl volumes and pH values were saved on a laptop computer.

Total alkalinity was computed using the Gran equation corrected for sulphate and fluorides (Hansson & Jagner 1973) with pH values ranging from 4.2 to 3.0. The average precision ($2 \times \text{SD}/\text{mean}$) was 0.16%.

CO₂ speciation calculation. Dissolved inorganic carbon was calculated from measurements of pH and total alkalinity. The distribution of ionic species was computed using the CO₂ acidity constants (Mehrbach et al. 1973), the CO₂ solubility coefficient (Weiss 1974), the borate acidity constant (Hansson 1973) and the water dissociation constant (Lyman 1957). The total borate molality was calculated using the Culkin (1965) ratio to salinity.

RESULTS

Changes in dissolved oxygen, CO₂ resulting from organic carbon metabolism (CO₂^o), total CO₂ (TCO₂), and calcification (*g*) during the transect experiments are shown as a function of average incident irradiance in Fig. 2. The parameters of the lines fitted to the data sets are given in Table 1. All coefficients of correlation were significantly different from 0 except for *g* for which data scattering was important. These parameters were used to construct daytime, nighttime and 24 h budgets (Table 2). The O₂ consumed at night is nearly balanced by the O₂ released during the day and the net 24 h budget is close to zero ($-1.8 \text{ mmol m}^{-2} \text{ d}^{-1}$). The release of CO₂ at night is close to the O₂ uptake (243.1 vs $-264.2 \text{ mmol m}^{-2} \text{ d}^{-1}$) but the 24 h CO₂ budget is not balanced due to the relatively high value for CO₂^o during the day. Calcification is nearly 3 times higher during the day than it is at night. The increase in TCO₂ at night is much lower than the uptake during the day and the 24 h budget is $-433.3 \text{ mmol m}^{-2} \text{ d}^{-1}$. Metabolic performances of the reef flat are shown in Table 3.

Fig. 3 shows the whole set of air-sea CO₂ flux data versus time obtained during the entire field trip in the ocean, the reef front and the back reef. Air-sea CO₂ fluxes (f_{CO_2}), measured on 2 occasions (during the

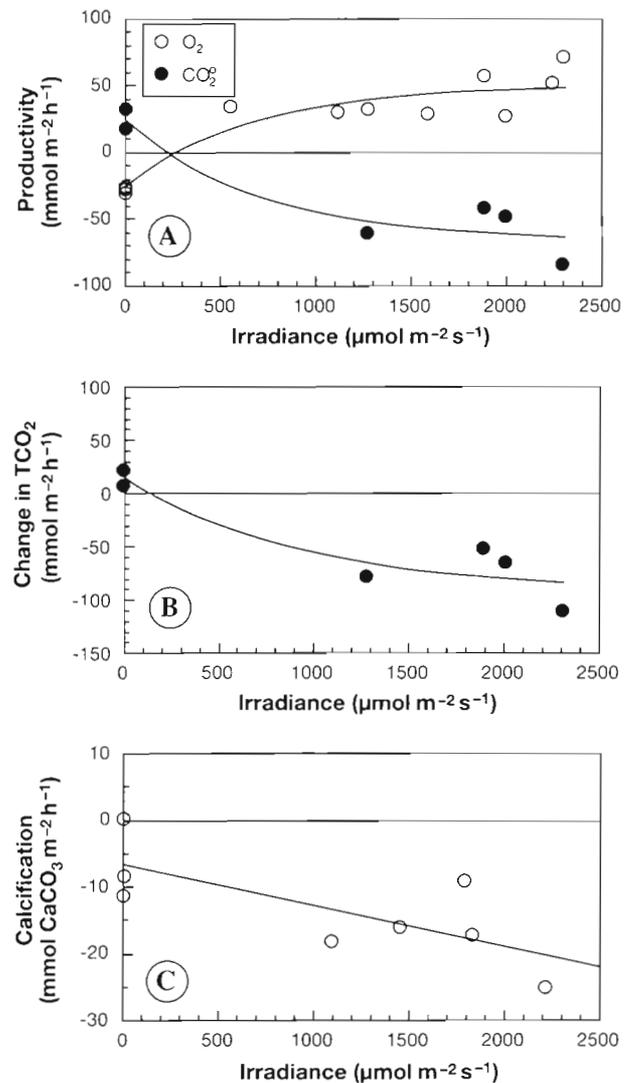


Fig. 2. (A) Productivity, (B) changes in total inorganic carbon and (C) calcification, as a function of the average incident irradiance during the transects. An exponential function is fitted to the data (see Table 1)

Table 1. Curve-fitting parameters for fluxes of total CO₂ (TCO₂), O₂, CO₂ resulting from organic carbon metabolism (CO₂^o) and calcification (*g*) vs irradiance using an exponential function for the first 3: $[y = a(1 - \exp(-I/b)) + c]$, ± 1 asymptotic standard error; and a linear function for the calcification data: $g = AI + B$, where *I* = irradiance ($\mu\text{mol m}^{-2} \text{ s}^{-1}$); ± 1 SE. n: no. of measurements; *r*²: coefficient of determination

Type of flux	<i>a</i> (mmol m ⁻² h ⁻¹)	<i>b</i> ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	<i>c</i> (mmol m ⁻² h ⁻¹)	n	<i>r</i> ²
TCO ₂	-109 ± 64	995 ± 1684	14 ± 18	6	0.86
O ₂	76 ± 13	655 ± 367	-27 ± 8	11	0.87
CO ₂ ^o	-91 ± 31	686 ± 1027	25 ± 14	6	0.89
	<i>A</i>	<i>B</i>		<i>n</i>	<i>r</i> ²
<i>g</i> (CaCO ₃)	-0.006 ± 0.002	-6.7 ± 3.2		8	0.55

Table 2. Metabolic budgets for fluxes of O₂, CO₂ resulting from organic carbon metabolism (CO₂^o), calcium carbonate (CaCO₃) and air-sea CO₂ exchange (F_{CO₂}). All data in mmol m⁻²

Net flux	O ₂	CO ₂ ^o	TCO ₂	CaCO ₃	F _{CO₂}
During the day	262.4	-405.3	-575.0	-177	-0.2
At night	-264.2	243.1	141.7	-66.2	1.7
24 h	-1.8	-162.2	-433.3	-243.2	1.5

day only) in oceanic water 1 mile off the reef, were close to zero (0.7 ± 0.3 and 0.2 ± 0.9 nmol 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 (Fig. 3A) and back reef (Fig. 3B) stations displayed a strong daily pattern. There was a CO₂ evasion at night (up to 88 nmol m⁻² s⁻¹) and a CO₂ invasion during the day (up to -71 nmol m⁻² s⁻¹). CO₂ flux data at the back reef station were numerically integrated using Simpson's rule. The net fluxes during the day and at night were respectively -0.2 and 1.7 mmol m⁻². The direction and magnitude of f_{CO₂} were light-dependent at both the reef front and back reef stations (Fig. 4). f_{CO₂} 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_{CO₂} decreased with increasing irradiance; a linear equation could be fitted through the data points collected at the reef front ($y = 18.8 - 0.033x$; r² = 0.66, p < 0.0001) but relatively high scattering of the data prevented us from satisfactorily fitting any function to the back reef data set.

DISCUSSION

The gross production and respiration of the Tiahura reef flat were, respectively, 753 and 590.4 mmol CO₂ m⁻² d⁻¹ (9.0 and 7.1 g C m⁻² d⁻¹). Using the oxygen data and setting the photosynthetic and respiratory quotients to 1, gross production and respiration were both 7.7 g C m⁻² d⁻¹. The lower number of data points and the higher scattering of the data for CO₂ resulted

Table 3. Daily metabolic parameters measured using the O₂ and CO₂ techniques. CO₂^o: CO₂ resulting from organic C metabolism; P: gross primary production; R: 24 h respiration; E: excess production. Absolute values of P/R are reported. All data in mmol m⁻² d⁻¹, except P/R which is dimensionless

Parameter	O ₂	CO ₂ ^o
P	640.2	-753
R	-641.5	590.4
E	-1.3	-162.6
P/R	1	1.3

in larger confidence intervals of the photosynthesis-irradiance (PI) curve parameters than for the O₂ data. This relatively higher uncertainty of CO₂-based PI curves could explain part of the difference between community metabolism estimated by the 2 techniques. It is reasonable to assume that the metabolic performances computed using the oxygen data set are more reliable in the present paper than those computed

using the CO₂ data. The gross production measured in this study is within (or slightly higher than) the 'standard' range for reef flats (7 ± 1 g C m⁻² d⁻¹; Kinsey 1985) and compares well with data obtained using the same transect technique at Davies Reef, Great Barrier Reef (8.8 g C m⁻² d⁻¹; Barnes & Devereux 1984).

Community metabolism of the Tiahura barrier reef has been studied by several investigators since 1981 (Table 4). They used the standing water method which assumes that there was no significant water flow during the experiments. Although such a situation seems to occur occasionally (see Pichon 1985), the validity of this assumption is questionable. Should

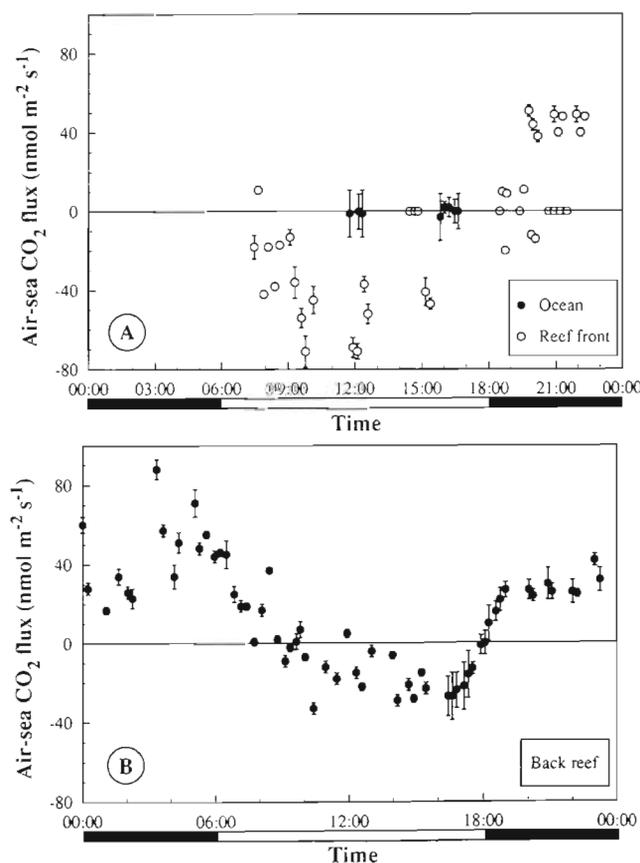


Fig. 3. Air-sea CO₂ flux: (A) in the ocean and the reef front; (B) at the back reef. Confidence intervals are ± 1 SD. All data collected during the field trip are shown

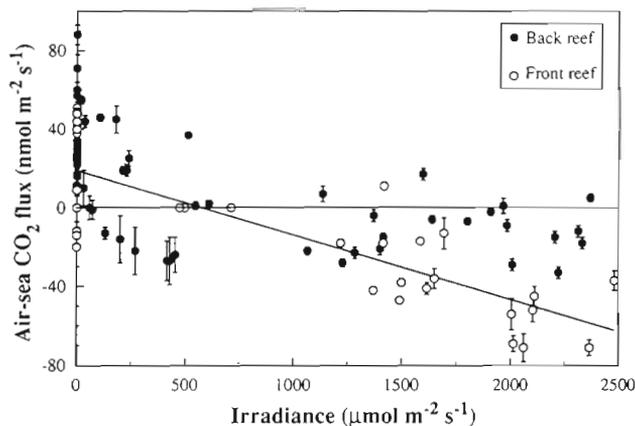


Fig. 4. Air-sea CO_2 flux at the reef front and the back reef as a function of average incident irradiance. Confidence intervals are ± 1 SD. Data at the back reef were collected during a 24 h experiment; all data collected at the reef front during the field trip are shown. The regression line was obtained using the reef front data only

the water be still for 24 h, it seems difficult to extend results obtained on a very small portion of the reef to the whole reef flat. Results from previous authors indicate that there is a very wide range of variation for P and R , 3.1 to 31.4 and 3.4 to 33.6 $\text{g C m}^{-2} \text{d}^{-1}$ respectively. The data collected in November and December 1991 are within these ranges. We suggest that the large variation of P and R partly results from uncertainties related to the standing water technique.

There is also some evidence of large seasonal changes in community metabolism. Payri (1987) showed that P was higher in summer (October to December: 10.4 $\text{g C m}^{-2} \text{d}^{-1}$) than in winter (June to August: 6.6 $\text{g C m}^{-2} \text{d}^{-1}$). Such seasonal pattern seems widespread in coral reefs (reviewed by Kinsey 1985). Planktonic primary production in the Tiahura reef system was measured in a companion study (B. Delesalle, M. Pichon, M. Frankignoulle & J. P. Gattuso unpubl.). It represents only 0.15% of the total productivity (13.9 $\text{mg C m}^{-2} \text{d}^{-1}$) which confirms previous results in the same site (Sournia et al. 1981) and the suggestion that

phytoplankton contribution to reef metabolism can generally be considered as negligible (Kinsey 1985).

In November and December 1991, calcification occurred both during the day and at night except on a single occasion where a slight dissolution was measured at night, although within experimental error. Calcification data were noisy and the significance of the curve fitting was rather poor. This might be a general rule; Barnes & Devereux (1984) suggested that noisy calcification data measured over reef flats may result from changes of the track of the instrument package from one transect experiment to the next. The calcification rate varies according to changes in the proportion of hard and sandy substrates encountered by the drifter due to slight changes of its track. The daily calcification rate was 24.3 $\text{g CaCO}_3 \text{m}^{-2} \text{d}^{-1}$, a high value compared to other studies of the Tiahura barrier reef (Table 4). Payri (1987) reported a strong seasonal pattern of G at this site, the highest value (33 $\text{g CaCO}_3 \text{m}^{-2} \text{d}^{-1}$) being measured in December. This prevents any attempt to extrapolate our data to yearly calcification.

Oceanic water was in equilibrium with the atmosphere with respect to CO_2 in December 1991 as shown by the very small air-sea CO_2 fluxes measured in the ocean. This is consistent with measurement of $p\text{CO}_2$ along a transect in the vicinity of Tahiti in November 1991 (Y. Dandonneau pers. comm.). The water mass, however, was not in equilibrium with atmospheric CO_2 when it reached the upstream station located ca 35 m landwards of the reef edge and f_{CO_2} displayed a clear diel pattern. This could result from a combination of 2 factors. Firstly, the seawater CO_2 system can be significantly modified by the metabolism of the communities located between the ocean and the reef front site (reef slope and reef flat margin). Secondly, the water mass impinging on the reef crest is a mixture of true oceanic water and water recycled from the reef system through the nearby pass (Fig. 1). This pass collects the water which crossed ca 8 km of reef and should therefore display a $p\text{CO}_2$ diel pattern. Recirculation depends on the direction and magnitude of the swell and the wind; E. Wolanski (pers. comm.) has esti-

Table 4. Published values for community metabolism of the Tiahura barrier reef. P : gross primary production; R : 24 h respiration; E : excess production; G : net calcification. P , R and E : $\text{g C m}^{-2} \text{d}^{-1}$; G : $\text{g CaCO}_3 \text{m}^{-2} \text{d}^{-1}$; P/R : dimensionless

Source	P	R	E	P/R	G
Sournia et al. (1981)	16.4 to 31.4	15.6 to 33.6	-2.2 to 0.8	0.9 to 1.0	0 to 1.6
Pichon (1985)	6.2	5.2	1	1.2	7.4
Payri (1987)	3.1 to 13	3.4 to 14.3	-1.8 to 1.2	0.7 to 1.1	-0.7 to 33.0
Present study					
O_2 technique	7.7	7.7	0.02	1	24.3
CO_2 technique	9.0	7.1	2	1.3	24.3

mated that 10% of the water flowing out of the pass recirculated onto the reef in September 1992.

Respiration and calcification release CO₂ at night thereby increasing seawater *p*CO₂ and favouring CO₂ evasion to the atmosphere. The 2-fold increase in nighttime CO₂ evasion between the upstream and the downstream stations (36 vs 19 nmol m⁻² s⁻¹) is the result of the effect of both biological processes. The relatively higher scattering of *f*_{CO₂} data at the back reef compared to the reef front (Fig. 4) could result from changes in the track of the water mass during the 24 h cycle but also to changes in the direction and velocity of the current. The magnitude of *f*_{CO₂} can be expected to increase when the distance travelled by the water mass increases or when the current velocity decreases.

Several processes occur during the day, either increasing (calcification) or decreasing (photosynthesis) the seawater *p*CO₂ level. If photosynthesis was the only biological process involved, *p*CO₂ should be lower and invasion should be higher at the back reef than at the reef front. CO₂ invasion is, however, lower at the back reef with some values close to zero (Fig. 4). CO₂ evasion was even measured on some occasions which suggests that the decrease in *p*CO₂ due to photosynthesis during the day is lower than the increase of *p*CO₂ due to calcification.

The daily budget of air-sea CO₂ exchange at the back reef is 1.5 mmol m⁻² d⁻¹ (CO₂ evasion). The direct method used in the present study to measure air-sea fluxes is useful to derive qualitative estimates but it suppresses the direct effect of wind and could prevent quantitative estimation of the true fluxes. Frankignoulle (1988) showed that the gas exchange coefficient using the direct method is of the same order of magnitude as the one given by wind tunnel experiments under conditions similar to those prevailing during the experiment (low wind speed, averaging 2.6 m s⁻¹, and calm sea state) and that it is underestimated by 30% in the worst case. The true daily integrated air-sea CO₂ flux should therefore range between 1.5 and 2 mmol m⁻² d⁻¹.

There are no other direct measurement of air-sea CO₂ exchange in the literature, but a few indirect estimates are available. Smith (1973) suggested that a negligible atmospheric CO₂ invasion takes place in seawater overlying the Eniwetok reef flat community. Smith (1974) reported a CO₂ evasion on the Eniwetok reef flat and the Fanning Island lagoon (0 to ± 0.06 mmol m⁻² d⁻¹). Smith & Pesret (1974) estimated that there is a net evasion (47 mmol m⁻² d⁻¹) in the Fanning Island lagoon. Smith & Jokiel (1976) found a CO₂ evasion in Canton Atoll (1 to 12 mmol m⁻² d⁻¹). Pigott & Laughlin (1988) also indirectly estimated that CO₂ evasion takes place in Discovery Bay (Jamaica) where it is 5 orders of magnitude higher than the CO₂

fluxes resulting from organic and inorganic carbon metabolism. Such a high value, which has never been reported elsewhere, is of the same order of magnitude as advective fluxes. The CO₂ control at Discovery Bay was suggested to be greatly dominated by physical transport processes, both biological and chemical processes playing a minor role (Pigott & Laughlin 1988). The discrepancy in the direction of exchange (evasion or invasion) and in their magnitude (0 to 60 mmol m⁻² d⁻¹) may seem puzzling but can be explained by several factors. The CO₂ partial pressure of water impinging the reef varies widely depending on the study site and, presumably, on the season: it can be lower (Smith 1973), similar (Smith & Jokiel 1976, present study) or higher (Smith & Pesret 1974) than atmospheric *p*CO₂.

The net effect of a coral reef on the air-sea CO₂ fluxes can be masked if oceanic water is already out of equilibrium with atmospheric CO₂ before it enters the reef system. For example, if the oceanic CO₂ partial pressure is lower in the ocean than in the atmosphere, an increase of *p*CO₂ due to reef metabolism may not be high enough to counterbalance the original difference in CO₂ partial pressures and thus no CO₂ evasion would be measured. It must be pointed out that even in this case, the reef remains a source of CO₂ since it reduces the invasion of carbon dioxide that would have occurred otherwise.

The residence time of the water in the reef system must also be taken into account to ascertain the net effect of reef systems on air-sea CO₂ exchange. Studies of community metabolism encompass a wide range of time scales: from a few minutes up to 50 d. The fluxes measured are instantaneous when the residence time is short (a few minutes), such as in the present study. Since CO₂ exchange across the air-sea interface is a slow process, it is unlikely that seawater *p*CO₂ is in equilibrium with atmospheric *p*CO₂ at the back reef station and so equilibration will continue after the water mass has crossed the reef. The situation is different when the residence time is longer since the water mass should have enough time to equilibrate with the atmosphere before it exits the reef system.

Lastly, differences in the community structure and in the percentage of substratum cover made up of living corals and coralline algae are also likely to have a significant effect on air-sea CO₂ exchange since *f*_{CO₂} partly depends on photosynthesis, respiration and calcification.

This paper presents the first direct evidence that coral reefs are a source of CO₂ to the atmosphere and confirms conclusions drawn from theoretical considerations on the effect of calcification on the seawater CO₂ system (Ware et al. 1992). Derivation of integrated estimates of CO₂ evasion was hampered by the lack of a precise mapping of *p*CO₂ on the reef flat. It is therefore not possible at this stage to use *f*_{CO₂}

data at the ecosystem level to address the discrepancy between the theoretical ratio of released CO_2 /precipitated calcium carbonate (0.6) and the actual ratio measured in corals (0.1). Such difference may be partly due to a tight coupling between the CO_2 released by calcification and the photosynthetic uptake of CO_2 (Smith & Veeh 1989, S. V. Smith pers. comm.). A new set of experiments is planned in order to (1) compare f_{CO_2} measured using the direct method with f_{CO_2} estimated using the difference of CO_2 partial pressure between air and seawater and (2) estimate quantitatively the total effect of the reef on the incoming water.

Acknowledgements. Thanks are due to the workshop staff of the Australian Institute of Marine Science for constructing the drifter, to J.-M. Bouqueneau and C. Canon for field work assistance and to F. Teaniniuraiteoana for help with positioning the stations. This work was supported by grants from Centre National de la Recherche Scientifique (Sciences de la Vie and INSU-équipements mi-lourds), Programme Récifs Coralliens (INSU-ORSTOM, PRCO), French-Australian Science and Technology Agreement, Fonds National Belge de la Recherche Scientifique (Crédit aux chercheurs #1.5.044.91F), Commission of the European Community (MAST Programme, contract #0019) and from the Department of Industry Technology and Commerce (DITAC). This is a contribution of PRCO.

NOTE ADDED IN PROOF

Le Campion-Alsumard et al. (1993) recently reported on calcification rates measured in October and November 1988 on the Tiahura barrier reef flat. They considered an upstream and a downstream station which were not similar to those described in the present paper. The daily net calcification was 10 times higher at the downstream than at the upstream site (5.22 vs $0.45 \text{ g CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$). The significance of these rates is difficult to estimate since they were computed using the standing water method (T. Le Campion-Alsumard pers. comm. May 1993) although the assumption of no water flow was not valid (range of current velocity: 0 to 0.19 m s^{-1}).

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This article was submitted to the editor

Manuscript first received: February 16, 1993

Revised version accepted: April 27, 1993