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Carbon Fluxes at the Water-sediment Interface in Reunion Island Fringing Reef

D. Taddei[1], G. Bucas[1], J. Clavier[2], P. Cuet[1], P. Frouin[1]
[1]*ECOMAR, Université de La Réunion, Saint-Denis de La Réunion, France;* [2]*UMR CNRS 6539, IUEM, Place Copernic, 29280 Plouzané, France*

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Abstract— To assess the contribution of soft-bottoms to the carbon cycle in coral reefs, the net community production (*p*) was measured in winter at 3 stations on La Saline inner reef flat (Reunion Island). Changes in pH and total alkalinity at different irradiances (*I*) were assessed using benthic chambers (0.2 m^2) during a 1-h incubation. Mean grain size, the silt and clay load and chlorophyll *a* content of the sediments were analysed in each chamber. Daily community production (*P*), gross community production (P_g) and community respiration (*R*) were estimated from *p-I* curves and daily irradiance variations (PAR, 400-700 nm). Sediment characteristics and chlorophyll *a* contents did not differ between the three sites, except for the silt and clay fraction at one station. *R* being higher than P_g (84.88 ± 7.36 and -62.29 ± 3.34 mmolC m^{-2} d^{-1} respectively), *P* value reached 22.59 ± 5.66 mmolC m^{-2} d^{-1}. The sediments were therefore heterotrophic with a mean P_g/R lower than 1 (0.74 ± 0.05) and appear to be a carbon source. Our data suggested the importance of the degradation process in the functioning of near-reef sediments.

INTRODUCTION

In tropical zones, coral reefs often develop in oligotrophic oceanic waters. They are nevertheless one of the most productive ecosystems in the world (Sorokin, 1993; Gattuso *et al.*, 1998) and they are important in global carbon cycling since they support both organic and inorganic carbon metabolism (Kinsey, 1985). Theoretically, the production of one mole of organic matter by photosynthesis or one mole of calcium carbonate by precipitation requires the consumption of one mole of dissolved inorganic carbon (DIC). On the other hand, the oxidation of one mole of organic matter or dissolution of one mole of calcium carbonate leads, respectively, to the production of one mole of DIC. Compared to the study of the trophic structure of communities (densities, biomasses), the measure of carbon fluxes appears to be a more appropriate and general approach to evaluate the contribution of coral reefs to the carbon cycle.

In such ecosystems, coral/algal communities are very productive (Sorokin, 1990), and have received much more attention than sedimentary areas (Gattuso *et al.*, 1998). However, sediment communities between the coast and the fringing reef coral/algal communities may support important biogeochemical processes as they receive organic matter (Frouin, 2000; Clavier *et al.*, 2005) and nutrients (Cuet *et al.*, 1988; Naim *et al.*, 2000) through freshwater run-off and/or groundwater discharge. Sediments represent a site of organic matter storage, derived from exogenous or autochtonous sources, and a site of organic matter degradation by heterotrophs (Rasheed *et al.*, 2004; Wild *et al.*, 2005). In coral reef ecosystems, soft-bottom substrata generally cover larger areas than hard-bottom (Gattuso *et al.*, 1998) and they may represent a significant part of the total

Corresponding Author: DT
E-mail: Dorothee.Taddei@univ-reunion.fr

productivity of the system (Clavier & Garrigue, 1999). Therefore, the soft-bottom contribution has to be considered for carbon budget calculations in coral reef ecosystem.

The aim of this study was to assess the trophic status of reef flat soft-bottoms in Reunion Island and to determine whether these sediments are a sink or a source within the carbon cycle. Eventually, this study evaluated the contribution of the sediment compartment to the reef flat carbon budget and therefore to that of the wider fringing reef ecosystem.

MATERIAL AND METHODS

Study site

Reunion Island is situated in the Indian Ocean (21°07'S, 55°32'E), 700 km east of Madagascar. The study was carried out at three sites, Trou d'Eau (TE), Planch'Alizés (PA) and Club Med (CM), on La Saline fringing reef, along the western coast of Reunion Island (Fig. 1). They are located in the inner reef flat (1.0 to 1.5 m depth) which is covered

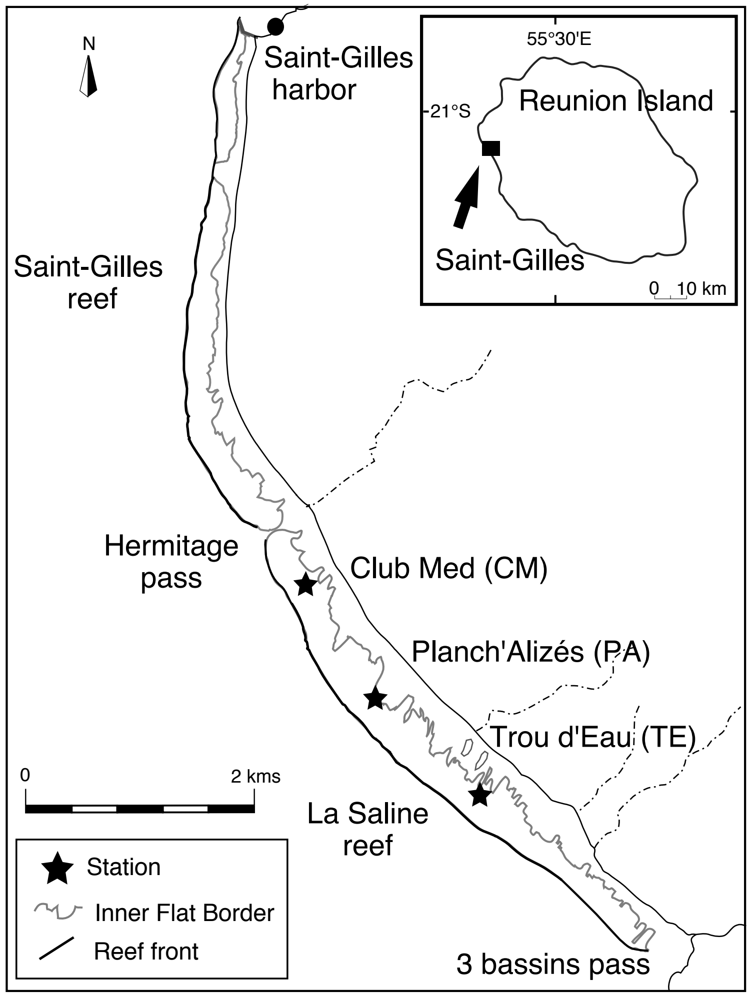

Fig. 1. Location of the sampling stations in Reunion Island (700 km east of Madagascar)

by transverse bands of branched corals separated by narrow sediment channels composed of coarse sand scattered with coral fragments. Sampling measurements were undertaken in winter (2003 and 2004), extending from July to October, with oceanic water temperatures between 23.4°C and 24.6°C (Conand *et al*., 2007). During this period, the reef was under influence of the southeast swell (1 to 2 m amplitude) and could be affected by 5 to 6 m-high swell generated by polar depression around Marion Island (associated with the 'Roaring Forties').

Environmental factors

At each station, 9 replicated sediment cores (2.9 cm diameter; 5 cm deep) were collected to determine the silt and clay fraction, and chlorophyll *a* content. The silt and clay fraction was expressed as the percentage of dry weight after wet sieving through a 63 μm mesh. Chlorophyll *a* was extracted in 90 % acetone for 12 h at 5°C, in dark conditions. After centrifugation, pigment concentrations were measured according to Lorenzen (1967) and expressed as mg per m^{-2}. Mean grain size was determined according to Folk and Ward (1957), using three replicated sediment cores (4.3 cm diameter, 5 cm deep).

In situ measurements

Net community production (*p*) was calculated from total dissolved inorganic carbon (DIC) fluxes at the water-sediment interface using the *in situ* incubation procedure described by Boucher *et al.* (1994). Fluxes were measured in benthic chambers composed of a PVC ring pushed into the sediment to a depth of ca. 7 cm, covered with a transparent acrylic hemisphere. The volume of the enclosed water, continuously homogenised with adjustable submersible pumps (2 L min^{-1}), varied from 66 to 69 L. At each station, eight runs of triplicated incubations, lasting about 60 min, were performed over two diel cycles, in order to cover the whole range of irradiance. Two runs of incubation (one per day of sampling) were performed at night, to assess respiration. Between incubations, enclosures were opened during 60 min to restore ambient conditions. A quantum sensor (LI-1400) was deployed inside one of the benthic enclosures to measure the irradiance (*I*), defined as the photosynthetically active radiation (PAR, 400 to 700 nm) available for microphytobenthic algae.

Temperature and salinity were recorded with multiparameter probes (YSI 6920). Sea water samples were collected inside the chamber at the beginning and at the end of each incubation. Sea water samples were poisoned with HgCl (20 μL of the saturated solution for 100 mL of sample) and stored in darkness at 5°C pending subsequent potentiometric determination of pH and total alkalinity (TA) (DOE, 1994). Samples intended to TA measurement were filtered onto Whatman GF/C membranes.

Analytical methods

DIC concentrations (mmol L^{-1}) were determined using pH, TA, temperature and salinity (Lewis & Wallace, 1998). Within 2 days of collection, pH (± 0.002) was measured by referring to the total hydrogen ion concentration (mol Kg-SW^{-1}) pH scale, using a Ross combination electrode (Orion 81-83) calibrated against Tris/HCl and 2-aminopyridine/HCl buffer solutions (DOE, 1994). To measure TA, inflection point titrations (Radiometer TIM 865) were carried out using 20 mL subsamples (4 replicates) maintained at 25°C (± 0.1°C) and slowly neutralized with saline (0.7 M NaCl) HCl 0.1 M solution. TA was obtained from the second inflection point of the curve. Reproducibility was higher than 0.003 mEq L^{-1}.

ΔDIC (biological CO_2 flux) expressed as mmol m^{-2} h^{-1}, was calculated as the difference in concentrations of DIC between the end and the start of the incubation, corrected from half the TA variation, to take into account the effects of carbonate dissolution and precipitation (Gattuso *et al*., 1999).

Statistical analyses

One way ANOVA were performed on mean grain size, the silt and clay fraction and chlorophyll a content. Newman-Keuls test was performed as post-hoc comparison of means. Homogeneity of variance was assessed using Levene's test, which, according to Underwood (1981), is strong enough to allow analysis on non normal data. Normalisation of data was therefore excluded. Respiration measurements *in situ* were compared using the non parametric U-test (Mann-Whitney).

To build up irradiance response curves (*p-I*), ΔDIC were first plotted against *in situ* irradiance, then the data were fitted with the exponential model (Boucher *et al.*, 1998; Martin *et al.*, 2005):

$$p = p_{max}\,(1 - \exp(-I/I_k)) + r$$

where p = net community production in mmolC m^{-2} h^{-1}; p_{max} = maximum gross community production in mmolC m^{-2} h^{-1}; I = irradiance and I_k = optimal irradiance (irradiance at which the initial slope of the curve intercepts with the horizontal asymptote) in μmol m^{-2} s^{-1} and r = community respiration (net production during the night) in mmolC m^{-2} h^{-1}. *p-I* curves were compared using the bootstrap method described by Martin *et al.* (2005). By convention, small letters referred to hourly fluxes (p, r), while capital letters (P: community production, P_g: gross community production, R: community respiration) referred to fluxes integrated over 24 h, in mmolC m^{-2} d^{-1}. Model parameters and irradiance values were used to calculate fluxes every minute over a 24-h period. P is the sum of the 1440 values per minutes. R was calculated from r assuming the respiration was constant over a 24 h period (Forja *et al.*, 2004).

Finally, P_g was calculated as the difference between P and R.

RESULTS

Environmental factors

During our study, daylight lasted for 12 hours from 6h30 am to 6h30 pm. The underwater maximum mean irradiance at the soft-bottom level was 909 μmol m^{-2} s^{-1} around midday (Fig. 2). Water temperature fluctuated daily from 22 to 28°C and the average was 25.15 ± 1.17°C. The mean sediment characteristics and cholorophyll *a* contents are shown in Table 1. Mean grain sizes were not significantly different between the three stations (ANOVA F = 0.76; p = 0.51) and corresponded to coarse sand on the Wentworth (1922) scale. The silt and clay fraction content was significantly higher in CM reef flat than in other stations (ANOVA: F = 12.88; p < 0.001). The mean chlorophyll *a* content was 12.01 ± 6.42 mg m^{-2} and did not differ significantly between the three stations (ANOVA F = 1.10; p = 0.35).

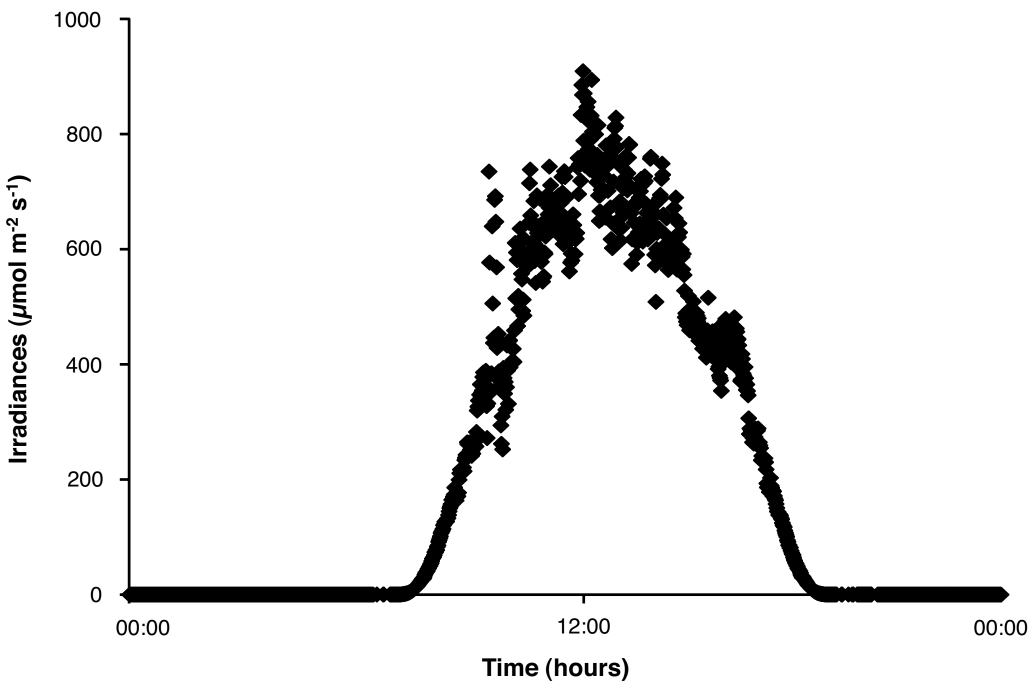

Fig. 2. Daily evolution of irradiance on the bottom during the winter season

Table 1. Mean values of sediment characteristics (SD are given in brackets). MS: phi value of the mean grain size; % silt and clay: percentage of particles <63μm in the sediments; Chl *a*: chlorophyll *a* (mg m^{-2}); one way ANOVA between stations *: p < 0.001

	Club Med 21°05'13.2"S - 55°13'32.3"E	Planch'Alizés 21°05'45.8"S - 55°13'56.8"E	Trou d'Eau 21°06'05.6"S - 55°14'21.2"E
MS	0.53 (0.10)	0.31 (0.27)	0.49 (0.28)
% Silt and clay	2.30 (0.32)*	1.57 (0.21)	1.62 (0.46)
Chl *a* (mg m^{-2})	9.43 (4.67)	13.24 (8.26)	13.37 (5.73)

Fluxes

ΔDIC at the water-sediment interface ranged from -7.56 to 5.75 mmolC m^{-2} h^{-1} (Fig. 3). The exponential curve-fitting parameters are given in Table 2. Coefficients of determination were higher than 0.82. Values of respiration calculated from the model (Table 2) matched those measured in situ (CM: 3.89 ± 0.96 mmolC m^{-2} h^{-1}; PA: 3.28 ± 0.79 mmolC m^{-2} h^{-1} and TE: 3.44 ± 1.48 mmolC m^{-2} h^{-1}) and were not significantly different between the three stations (U-test, p > 0.05). *p-I* curve at PA was significantly different from TE and CM (with 500 bootstrap replicates: PA-CM F_{obs} = 5.15 p = 0.007; TE-PA F_{obs} = 2.78 p = 0.013), while *p-I* curves at TE and CM were not significantly different (with 500 bootstrap replicates: TE-CM F_{obs} = 0.47 p = 0.570). *p-I* curve-fitting parameters I_k and p_{max}, showed the highest absolute values at PA station (Table 2).

Table 2. Curve-fitting parameters for dissolved organic carbon fluxes versus irradiance at the three soft-bottom reef flat stations. p_{max}: maximal gross community production in mmolC m^{-2} h^{-1}; I_k: optimal irradiance in μmol m^{-2} s^{-1}; r: community respiration in mmolC m^{-2} h^{-1} and r^2: coefficient of determination

	Club Med	Planch'Alizés	Trou d'Eau
p_{max}	-7.97	-11.89	-8.16
I_k	204.18	623.03	256.26
r	3.88	3.44	3.30
r^2	0.82	0.90	0.84

Community production (P), gross community production (P_g) and community respiration (R) are shown in Table 3. Average values were respectively 22.59 ± 5.66 mmolC m^{-2} d^{-1} for P, -62.29 ± 3.34 mmolC m^{-2} d^{-1} for P_g and 84.88 ± 7.36 mmolC m^{-2} d^{-1} for R, resulting in a P_g/R ratio of 0.74 ± 0.05. Fluxes calculated for one year resulted in a community production of 98.94 ± 24.81 gC m^{-2} y^{-1}.

Table 3. Mean values of the metabolic parameters at the three soft-bottom reef flat stations. P: community production, P_g: gross community production and R: community respiration in mmolC m^{-2} d^{-1}

	Club Med	Planch'Alizés	Trou d'Eau
P	27.60	23.72	16.44
P_g	-65.52	-58.84	-62.52
R	93.12	82.56	78.96
P_g/R	0.70	0.71	0.79

DISCUSSION

In marine ecosystems, gross production is enhanced by irradiance and temperature (Littler & Arnold, 1980). These two factors are high and relatively constant throughout the year in most coral reef ecosystems, which are among the most productive ecosystem in the world. Soft-bottoms, with their primary producers, may constitute an important contributor to overall coral reef primary production (Gattuso *et al.*, 1998; Clavier & Garrigue, 1999; Heil *et al.*, 2004). In Reunion Island, macroalgae and seagrasses are scattered and grow mainly in summer (Semple, 1997). Therefore large areas appear to be only covered by sediments, with microphytobentos representing the main primary producer, particularly during the winter season. It is usually dominated by diatoms accompanied by cyanobacteria, dinoflagellates and chlorophytes (Uthicke & Klumpp, 1998). Chlorophyll *a* content for the first ten cm of sediment was used to evaluate the amount of autotrophic biomass as it is a good proxy for the microphytobenthic biomass (Mitbavkar & Anil, 2002). Compared to other coral reef ecosystems, the microphytobenthic biomass in sediments of Reunion Island (12.01 ± 6.42 mg m^{-2}) is at the lower limit on a scale ranging from 8 to 907 mg m^{-2} (Bunt *et al.*, 1972; Sournia, 1976; Boucher & Clavier, 1990; Charpy

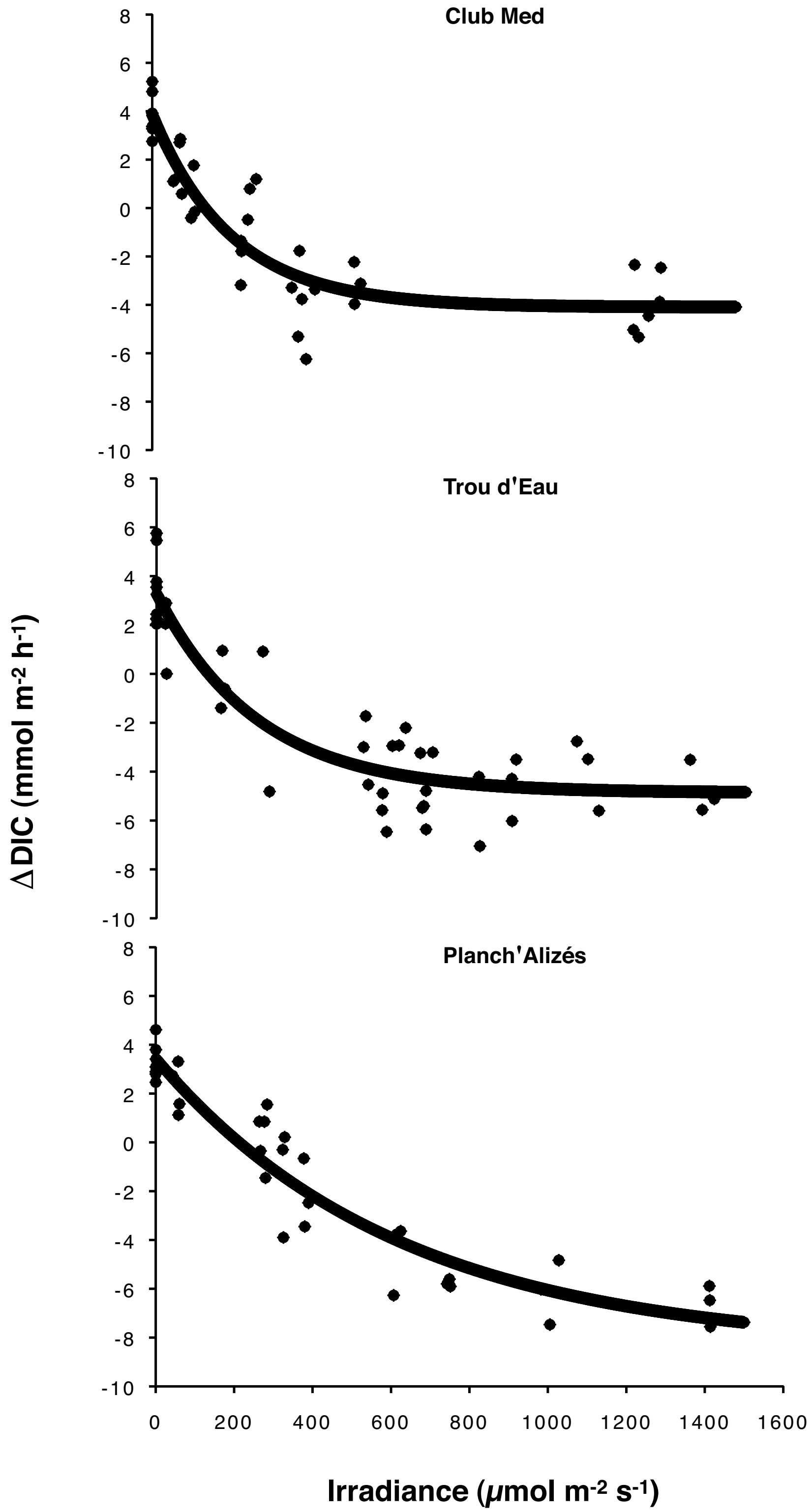

Fig. 3. Net community production at the three reef flat soft-bottom stations during the winter season. CM: Club Med; PA: Planch'Alizés and TE: Trou d'Eau

& Charpy-Roubaud, 1990; Sorokin, 1993; Boucher *et al.*, 1998; Heil *et al.*, 2004; Clavier *et al.*, 2005). Located in shallow waters near the reef front, soft-bottoms in Reunion Island reef flat are subject to important hydrodynamic processes (Naim, 1993), where current velocity reaches up to 77 cm s^{-1} (Cordier, com. pers.), resulting in the presence of coarse sand (phi value of the main grain size on the reef flat reached 0.44 ± 0.23). Large granulometric size composition of the soft-bottoms is involved in the limited microphytobentos development, since diatom biomass is positively correlated with fine sediment (Facca *et al.*, 2002). Moreover, strong movements of the overlying water masses induce a resuspension resulting in decrease of microphytobenthic biomass (Mitbavkar & Anil, 2002). This direct effect of hydrodynamic processes is more probably responsible for low microphytobenhtic biomass in Reunion Island soft-bottoms, as gross community production measured in this study (P_g = -62.29 ± 3.34 mmolC m^{-2} d^{-1}) is relatively high compared to other coral reef ecosystems. At Lizard Island (Australia), P_g reaches -6 mmolC m^{-2} d^{-1} (Moriarty *et al.*, 1985). For the whole lagoon of New Caledonia, Clavier and Garrigue (1999) measured a P_g equal to -33 mmolC m^{-2} d^{-1}. Hydrodynamic processes appear as a dominant factor of microphytobenthic biomass through resuspension while granulometry also plays a role, only to a lesser extent.

Available data on sediment-water interface fluxes result from studies based in French Polynesia, the Great Barrier Reef, New Caledonia, the Caribbean Sea, but only one from the Indian Ocean (see Table 4 for references). Production, gross production and respiration of the communities measured on the reef flat sediments of Reunion Island are consistent with these studies (Table 4). Even though some authors have reported an excess of community production of organic matter (Plante-Cuny, 1973; Charpy-Roubaud, 1988; Boucher *et al.*, 1998) Reunion Island sediments are heterotrophic with a P_g/R ratio lower than 1 as is frequently observed in other coral reefs (Kinsey, 1985; Hatcher, 1990; Johnstone *et al.*, 1990; Yap *et al.*, 1994; Clavier & Garrigue, 1999; Yates & Halley, 2003; Clavier *et al.*, 2005). In such communities, the respiration process prevails and the amount of autochthonous material generated by the local gross community production is insufficient to support the community respiration. Inputs of organic matter from other highly productive compartments are necessary. Wild *et al.* (2004a) have demonstrated that coral mucus is a valuable degradable substrate for soft-bottom fauna, and it contributes to the maintenance of the heterotrophic status with rate of exportation reaching 117 mgC m^{-2} h^{-1} (Wild *et al.* 2004b). In the water column at La Saline reef, the presence of mucus and cyanobacteria, which is confirmed by observations and found to be more prominent

Table 4. Review on fluxes at the water-sediment interface in coral reef ecosystems. P_g: gross community production, *R*: community respiration and *P*: community production, in mmolC m^{-2} d^{-1}. GBR : Great Barrier Reef

P_g	R	P	P_g/R	Location (reference)
			0.7	Puerto Rico (Goreau et al., 1960 In Kinsey, 1985)
		-34		Madagascar, Nosy-Bé (Plante-Cuny, 1973)*
-241.7	258.3	16.2	0.9	GBR, One Tree Island (Kinsey and Domm, 1974 In Kinsey, 1985)
-199.2	178.3	-20.9	1.1	Hawaii, French Frigate Shoals (Atkinson & Grigg, 1984)
-58.48	19.4	39.08	3.0	French Polynesia, Tikehau (Charpy-Roubaud, 1988)**
		-0.3 to 4.2		GBR, One Tree Island (Johnstone et al., 1990)
			0.6	Philippine, Santiago Island (Yap et al., 1994)
-91.0	84.7	-6.3	1.1	French Polynesia, Moorea (Boucher et al., 1998)
-33.0	37.5	4.5	0.9	New Caledonia (Clavier & Garrigue, 1999)
-0.3	2.6		0.1	Hawaii (Yates & Halley, 2003)
-1.8	2.0		0.9	Florida (Yates & Halley, 2003)
-32.2	42.1	9.9	0.8	New Caledonia, (Clavier et al., 2005)
-62.3 ± 3.3	84.9 ± 7.4	22.6 ± 5.7	0.7	Present study

* ^{14}C fixation measurements

** In first five cm with the community photosynthetic and community respiratory quotients equal to 1 during dusk, constitutes a potential source of organic matter for the benthos. On the other hand, residential settlements and urban development in the coastal areas have vastly expanded in Reunion Island during the last three decades (Conand, 2002). An increase of terrestrial organic matter inputs, resulting from anthropogenic activities, also constitutes a significant source of enrichment. At the reef scale, the carbon demand reaches 98.94 ± 24.81 gC m^{-2} y^{-1}. This study was conducted in winter during the dry season, therefore this pattern may be reinforced in summer, as benthic metabolism observed in other coral reef sediments showed a seasonal variation (Johnstone *et al*., 1990; Uthicke & Klumpp, 1998; Clavier & Garrigue, 1999). During heavy rain episodes, superficial waters and submarine groundwater are discharged to the La Saline reef, particularly in the back reef (Taddei, 2006). Furthermore, submarine groundwater occasionally reaches the reef flat at Planch'Alizés station (Cuet *et al*., 1988), leading to critical eutrophication (Naim, 1993). Higher production of sediments is therefore likely to take place in summer, especially at this station.

This novel study, one of the first dealing with the fluxes at the sediment-water interface in the South West Indian Ocean, supports the worldwide pattern suggesting that reef flat sediments are heterotrophic. The community respiration is enhanced by the transfer of matter from other highly productive areas of the reef and terrestrial inputs. Sediments therefore appear to be a source for carbon cycle. Further information on spatial and temporal distribution of benthic community production is under analysis to establish an accurate annual budget which may contribute to the explanation for the role of soft-bottoms in one of the most productive ecosystem of the world.

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