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Direct measurements of carbon and carbonate export from a coral reef ecosystem (Moorea Island , French Polynesia)

Abstract The export of carbon and carbonate from coral reefs was investigated through a multidisciplinary investigation of the hydrological, geochemical, sedimentological and biological features of Tiahura reef on the northwestern coast of Moorea Island (French Polynesia). The hydrology of the fore-reef is characterised by prevailing longshore western currents and a strong thermocline. As revealed by turbidity structures (benthic and intermediate nepheloid layers) and by the amount of particles collected by near-bottom sediment traps, horizontal and downslope advections of particles dominate over offshore vertical transport. The exported material is rich in carbonate (ca. 80%) and poor in organic matter (ca. 4%). Sedimentation rates at 430 m depth, i.e. definitive export, reached 209.6 mg m^{-2} d^{-1} (dry weight). Estimates of carbon and carbonates export for Tiahura reef also reported here represent respectively 47% and 21% of the organic and inorganic carbon produced within the reef.

Keywords Export processes · Coral reefs · Organic carbon · Carbonates · French Polynesia

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Introduction

Coral reefs are one of the most productive ecosystems in the world which often develop in an oligotrophic oceanic environment. This paradox is not a recent idea, and it is now accepted as an oversimplification (Hatcher 1997). Nonetheless, it orientated most of the research conducted since the pionneer work of Sargent and Austin (1949) and Odum and Odum (1955) sought to characterise the trophic structure of reef systems. Numerous studies have investigated the carbon metabolism of reefs communities (see reviews by Kinsey 1985; Crossland et al. 1991) and the transport, often denominated by export, of either dissolved or particulate carbon (e.g. Johannes and Gerber 1974; Marshall et al. 1975; Westrum and Meyers 1978) or nutrients (e.g. Crossland and Barnes 1983) from reef flats towards backreefs areas and/or lagoons. In contrast, the export of organic and inorganic carbon, in the sense of a definitive loss from the whole reef ecosystem, has received far less attention.

These outputs can be divided in three categories. The first one is a geological component, calcium carbonate which is "fossilised" either in the reef frame or with organic matter trapped in sediments and not processed again by living organisms (Hubbard et al. 1990). The second type of output is a loss of carbon to the atmosphere: coral-dominated reefs are mostly a source of atmospheric CO_2 as suggested by Ware et al. (1992) and demonstrated by Gattuso et al. (1993, 1996). Carbon export to the ocean is the third type of carbon loss from the coral reef ecosystem. It has been assessed by direct measurement of either the organic carbon concentration in fore-reef waters (Qasim and Sankaranarayanan 1970; Reiswig 1981) or the organic and/or inorganic carbon fluxes from reefs (e.g. Gordon 1971; Hubbard et al. 1990; Sabine and McKenzie 1995). Carbon export has also been indirectly estimated in the building of carbon budgets (e.g. Smith et al. 1978). This approach has mainly deduced the organic carbon

export from comparison between the net excess organic production and deposition in the sediment (Smith and Jokiel 1978), or from a modelling approach to food-webs (Atkinson and Grigg 1984; Arias-Gonzáles et al. 1997). In contrast, few studies have compared carbonate precipitated within a reef versus that exported towards the ocean (Smith and Jokiel 1978).

In the present study, organic carbon and carbonate export processes to the ocean are quantified using hydrological, geochemical, sedimentological and biological approaches that have been successfully developed on temperate continental margins (Monaco et al. 1990). The aim of the present work is to evaluate export processes on Moorea Island, French Polynesia, where previous studies of carbon metabolism are available (e.g. Gattuso et al. 1993, 1996).

Material and methods

Geographical setting

The study area is the Tiahura reef at the northwestern end of the high volcanic island of Moorea (17°30′S, 149°54′W), French Polynesia. The northern coast is 16 km long and deeply indented by two bays, Opunohu and Cook Bays (Fig. 1), which collect most of the freshwater input from the island. The back-reef lagoon is narrow (about 840 m width) and is connected to the ocean by the Taotoi Pass which acts mainly as an outflow of water driven over the reef crest by waves.

The outer reef slope is approximately 350 m wide and, according to the terminology defined by Battistini et al. (1975), displays, from shallow to deep, a spur and groove zone, a zone of buttresses and valleys, down to about 28 m depth, then a deeper sandy platform which slopes down gently to about 70 m depth. The living coral cover is 15 to 35% over these upper zones, whereas coral colonies are sparsely distributed on the sand. Finally, a subvertical (slope $> 70°$) dropoff extends down to 200 m depth, i.e. below the depth of coral growth, marking the limit of the reef area.

Sampling design

Sampling stations were located in the lagoon and on six cross-slope transects in the nearby ocean (Fig. 1). As the water flowing through the pass is usually pushed westward (i.e. along slope), due to north-eastern tradewinds, these transects were considered to be either upstream or downstream of the lagoon source point represented by the pass (Fig. 1). Instantaneous and time-integrated samplings were carried out during the period 3–16 September, 1993. The weather conditions prevailing during the study were exceptionally calm with no significant precipitation and little wind. Wind velocity and direction, recorded at the meteorological station of Faaa airport (northwest on the neighbouring island of Tahiti) were $< 10\ m\ s^{-1}$ from the southeast.

Conductivity and temperature were measured using a CTD HPT-D profiler fitted with a 25 cm nephelometer (Züllig AG Switzerland). Turbidity is expressed as the ratio of scattered versus transmitted light. This optical parameter is commonly replaced by FTU (Formazine Turbidity Unit), a universal conventional unit of turbidity. On the basis of instrument calibration, suspended matter concentration is given by the relation $y = 0.59x + 0.13$ where x is the turbidity in FTU and y is the concentration in mg l^{-1} (Hofmann and Dominik 1995).

Current meters with temperature and pressure sensors (SUBER, Brest, France) were deployed at two sites at 40 m and 430 m depth. Current speed and direction were recorded every 5 min for 11 days. A dense hydrologic grid was sampled by instantaneous measurements in the Tiahura lagoon and on the outer reef slope in order to map hydrological and nepheloid structures. Fifty five CTD profiles were made on the six cross-slope transects (Fig. 1). Suspended particulate matter (SPM) was sampled at the same stations between 15 and 150 m depth, using a 10 l Niskin bottle. Water samples were

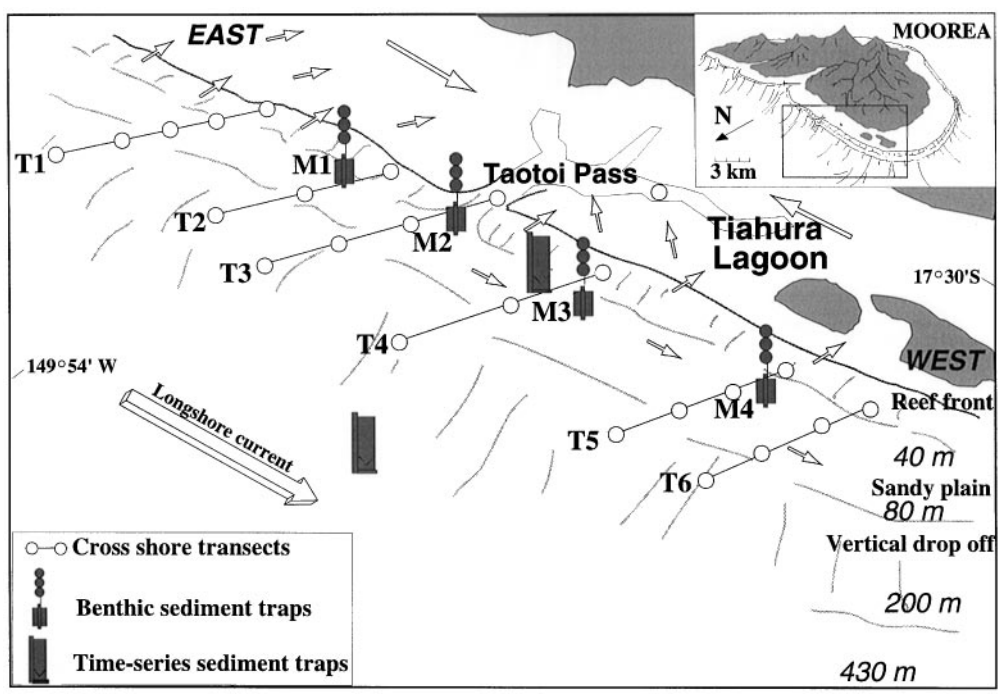

Fig. 1 Map of study area and schematic three-dimensional plot of the location of the cross-shore transects and of the two types of sediment traps. The direction of prevailing currents in the lagoon and on the outer slope is shown

kept in dim light and at ambient temperature until brought back to the laboratory.

Time-integrated samples of SPM were obtained using two types of sediment traps. The first were four small benthic traps deployed by divers on the sandy plain at 40 m depth. The traps were made of 8 PVC tubes 10 cm wide, 40 cm high and contained a 12.5% formalin-dense brine. They were placed 1.5 m above the bottom and left during the whole study period (12 days). The first mooring (M1) was located east of the Taotoi Pass. The second site (M2) was located in front of the pass. M3 and M4 sites were located downstream to the west (Fig. 1). In addition, two time-series sediment traps (Heussner et al. 1990) were moored at 40 m depth on the sandy plain near M3, and 430 m deep on the outer slope between 5–6 and 16 September. They were placed 10 m above the seabed. Each polyethylene receiving cup of the traps collected SPM for 3 days, except for the first cup at 430 m depth which collected SPM only during one day in order to compensate for the 1-day delay in the mooring of the two traps. Before deployment, they were filled with a buffered 5% (v/v) formaldehyde solution in 0.45 μm filtered sea water. The formaldehyde solution was used to limit degradation of settled particles and prevent mechanical disruption by "swimmers", i.e. planktonic organisms which had entered the trap alive during sample collection and were subsequently killed by the preservative.

Finally, sediments near the sandy plain sediment traps were collected to compare them with the settling particles. Sediment cores of undisturbed sediment and corresponding supernatant water were collected by a diver at the outer reef mooring sites (M) and in the lagoon using transparent perspex tubes, 7 cm wide and 20 cm high, vertically inserted into the sediment. Sediment (0–10 cm depth) was also sampled to investigate the meiofauna and bacteria using three 2 cm (internal diameter) 30 cm-long tubes. Both overlying water and sediment were preserved in buffered formaldehyde (4% final concentration) pending enumeration of meiofauna and bacteria.

Analytical procedures

Suspended particles

Seawater samples were filtered in the laboratory within 2 h of collection. Pre-weighed 4.7 cm Nuclepore filters (0.4 μm pore diameter) were used to determine the total suspended particulate matter (SPM); 4.7 cm Whatman GF/F precombusted glass fibre filters and an all-glass filter holder were used for particulate organic (POC) and inorganic (PIC) carbon determination. Duplicate 250 ml seawater samples were filtered on 2.5 cm GF/F filters and kept frozen pending chlorophyll-a determination. Phytoplankton cells were preserved in 4% neutral formalin.

Total and particulate organic carbon (TC and POC) were measured by dry combustion of the GF/F filters in a LECO CS 125 analyser. The procedure followed the recommendations of Cauwet (1975). Filters were acidified with 2 N HCl in order to remove carbonates prior to the analyses of POC. Acidification was performed in ceramic boats in order to avoid losses of acid-soluble organic compounds. Hydrochloric acid was chosen to completely remove inorganic carbon from samples. The quantity of HCl added depended upon the carbonate content and complete removal was assessed by the absence of effervescence in the boat. The sample was placed on a pre-heated plate after acidification to prevent any loss of volatile organic compounds (Cauwet 1975). Carbon was determined with a standard deviation of 2%. Results were expressed in terms of $\mu g\ l^{-1}$ and of % dry weight of POC and PIC (PIC is the difference between TC and POC).

Chlorophyll-a, active chlorophyll percentage (i.e. the ratio between chlorophyll-a and the sum of chlorophyll-a and pheophytin-a) and microphytoplankton composition were determined according to the methods described in Delesalle et al. (1993).

Sediment traps and surface sediments

The cups of the sediment trap were stored at 2–4 °C in the dark. The samples were brought back to France in iceboxes where laboratory processing was conducted within two months after collection. Large "swimmers" were removed by wet sieving the samples through a 1 mm nylon mesh. Subsamples were prepared for subsequent analyses, using a high precision wet sample splitting system (Heussner et al. 1990). The pH of the cup supernatant was checked for each sample. Values were always higher than the critical value of 7.0.

In each sediment core, sub-samples were taken from the first 0.5 cm and every cm to 20 cm depth. Sediment samples were frozen immediately after sampling. Chemical compounds were analysed on milled, freeze-dried, weighed subsamples.

Sediments and sediment trap samples were subjected to the following analytical procedures: grain size was measured using AFNOR standard sieves. Nitrogen was determined by the Kjeldahl method (Büchi automatic analyser) after mineralisation (H_2SO_4 + catalyst at 400 °C). Total and organic carbon concentrations (TC and OC, respectively) were measured on homogenised, precisely weighed samples in LECO pre-cleaned ceramic boats using the same procedure and precautions as for the suspended particulate matter. Results in % dry weight of POC and PIC were then related to the total flux in terms of total organic matter and calcium carbonate ($mg\ m^{-2}\ d^{-1}$ and % of the total flux). Total organic matter (TOM) was assumed to be 1.8 the organic carbon concentration. Calcium carbonate content was calculated from mineral carbon using the molecular mass ratio ($CaCO_3$:C = 100:12). Residual (i.e. non-carbon) material was determined as the difference between the total flux and the sum of the organic matter and the calcium carbonate fluxes. The nature of this residual material was not determined.

Additional analyses were performed on the sediments. Hydrolysable organic carbon (HOC) was obtained by the fraction of OC hydrolysed by 6N HCl for 16 h at 110 °C. Total amino acids (AA) were assayed by a colorimetric method (Stevenson and Cheng 1970). Absorption of the products resulting from the amino acid-ninhydrin reaction was measured at 570 nm using a Technicon automatic analyser. The analyses were

performed on a standard scale of D-Leucine from 0 to 10 $\mu g\,ml^{-1}$. Total sugars (SUG) were measured as glucose equivalents by the method of Dubois et al. (1956) adapted for sediments by Liu et al. (1973). The optical density was measured at 485 nm using a Beckman spectrophotometer.

Meiofauna samples were gently washed with filtered (20 µm) top water through a 40 µm sieve. The metazoans retained on the sieve were extracted from the sediment by centrifugation in Ludox, washed and resuspended in water. Organisms were identified in to major taxa and counted under a stereoscopic microscope.

Total bacteria were determined by direct counts with an epifluorescence microscope (Olympus BH) using the method described by Hobbie et al. (1977). Results are expressed per ml of wet sediment.

Results

Hydrology

Physical structures

Two distinct water masses could be distinguished in the first 150 m of the water column from salinity, temperature and turbidity data (Fig. 2). They were separated by a strong temperature gradient between 120 and 150 m, where the temperature decreased from 27 °C to 20 °C. The well-mixed surface layer consisted of a warm homogeneous water with relatively low salinity (35.8 psu). At about 120 m depth a well-defined thermocline separated this surface layer from an intermediate colder and saltier (> 36 psu) layer (south subtropical water, SSW) extending down to 200 m. This water mass originated from the central Pacific gyre, located east of the Tuamotu archipelago where evaporation is high and precipitation is low (Rancher and Rougerie 1995). Close to the pass, thermohaline structures reflected the outflow of lagoonal waters which were warmer (27.6 °C versus 27.4 °C) and less saline (35.75 psu versus 35.85 psu) but still less dense than the oceanic waters (density anomaly σ_t of 23.1 versus 23.2 kg m^{-3}).

Currents

Longshore currents prevailed during the study (Fig. 3). The resulting displacement of water masses showed a western drift. The average current speeds were low (50% of the instantaneous values were $< 10\,cm\,s^{-1}$). At 40 and 430 m depths, current directions changed according to the tide, as evidenced from the spectral analysis computed from the registered frequencies. Dominant modes were the semi-diurnal M2 component and its harmonic M4.

Current velocity at 40 m depth showed a NW longshore permanent component with inversions which peaked at about 40 cm s^{-1} (Fig. 3). Cross-shore currents had a predominantly southern component with maximum velocity of 20 cm s^{-1}. The currents recorded at 430 m depth presented a W-SW drift, a combination of major longshore westward movements with max-

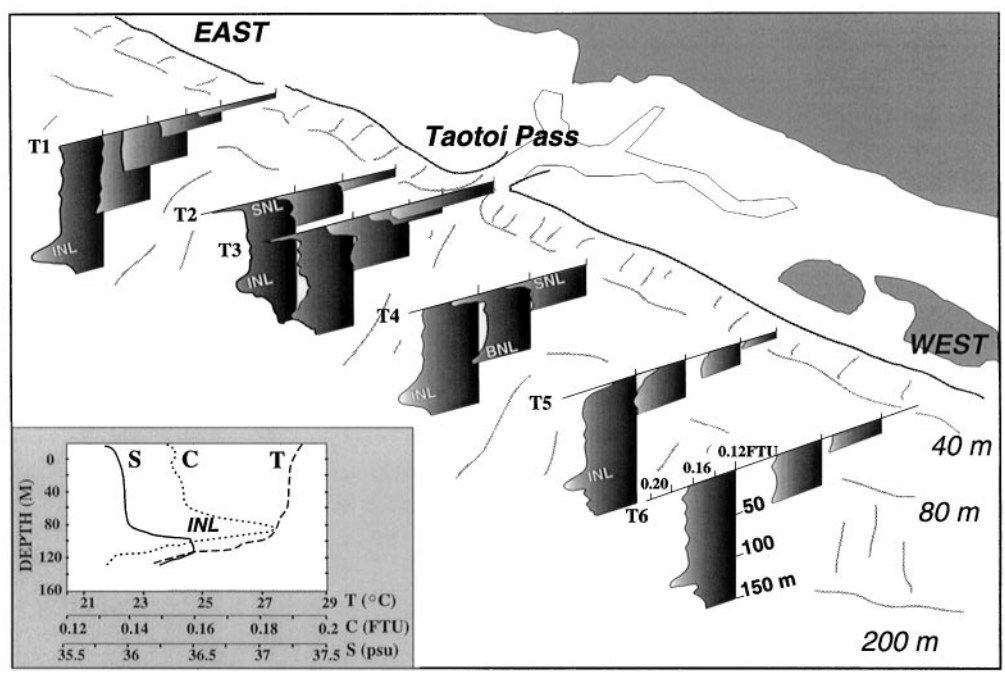

Fig. 2 Vertical distribution of turbidity (Formazin Turbidity Unit, FTU) along the 6 cross-shore transects. An example of CTD/nephelometer profile is shown in the inset. SNL, INL, BNL: surface, intermediate and benthic layers

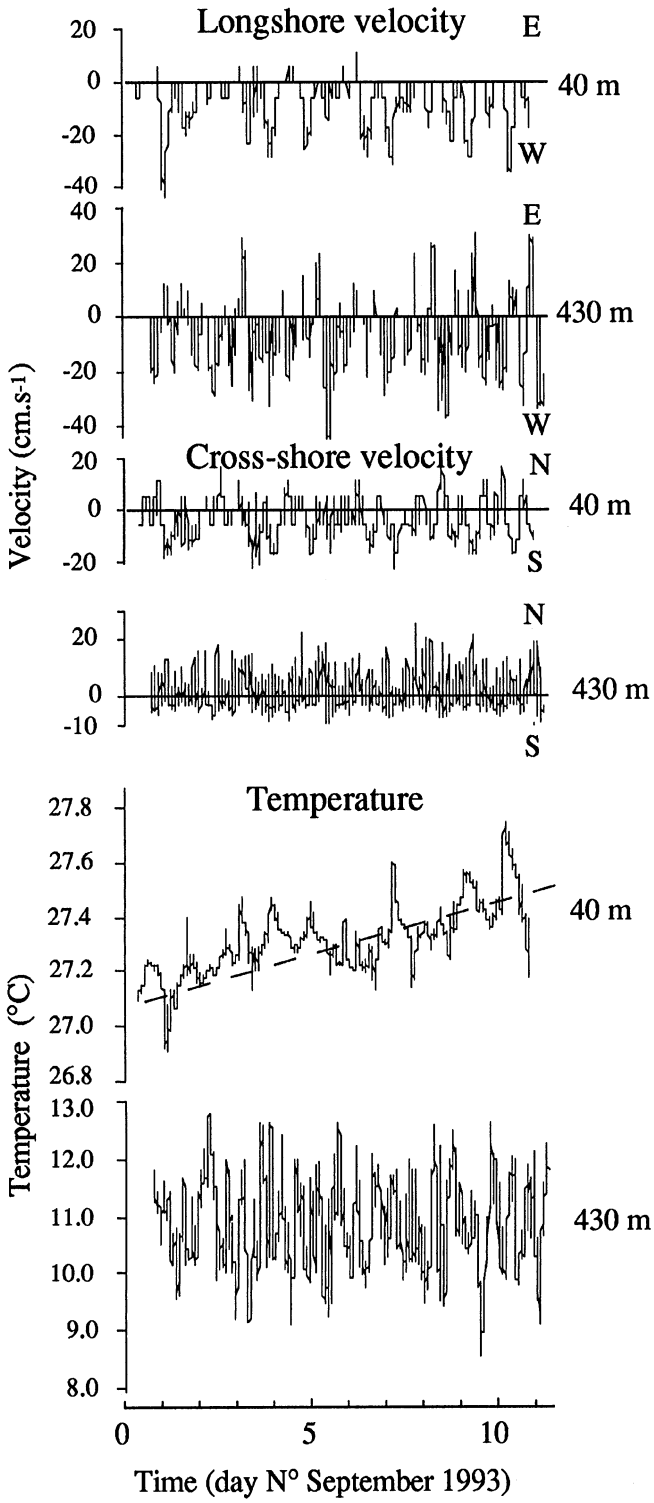

Fig. 3 Raw time-series plots of longshore and crosshore currents velocities and temperatures at 40 m and 430 m depth. Positive values indicate either eastward (longshore) or northward (cross-shore) flow

imum velocities of 40 cm s^{-1} and a noisy cross-shore northwards component of similar magnitude with maximum velocities of 25 cm s^{-1}.

Temperature over 11 days ranged between 26.9 and 28.4°C at 40 m and 8.5 and 13.0°C at 430 m depth. Temperatures at 430 m depth displayed pulsations similar to those of the currents and following the tidal frequencies, whereas temperatures at 40 m depth showed low frequency modes, with a positive long-term trend (Fig. 3).

Turbidity profiles

Turbidity profiles revealed persistent features in the Tiahura area with some spatial and temporal variation at a scale of 7 days. The turbidity varied locally in relation to seabed morphology and depth as well as with sediment input (Fig. 2).

In front of the pass, a layered system with surface and bottom layers was identified. The surface layer was restricted to the near reef portion of the study area and was mainly related to direct lagoonal flushing from the pass. The general trend was a decrease of the surface suspended particle content from the pass offshore to the west. Profiles recorded close to the pass showed a thin (2–10 m thick) surface layer and a distinct bottom boundary layer, respectively associated with the warm and saline surface water of lagoonal origin and the colder and less saline oceanic water.

Over the sandy plain, below a clear water layer, turbidity patterns reflected a highly turbid benthic layer in front and immediately west of the pass. At the other stations the transmission did not decrease near the seabed which indicates that, under calm conditions, significant resuspension on the sandy plain is restricted to the vicinity of the pass.

An intermediate turbidity layer was observed along the slope of the northern coast at most of the offshore stations, at the boundary (120 m) between the two water masses, marked by a strong density gradient (Fig. 2).

Concentration and composition of suspended particulate matter

The mean ($\pm$ SE) total suspended particulate matter (SPM) concentration was 0.5 ± 0.4 mg l^{-1} ($n = 14$) in the lagoon and 0.11 ± 0.05 mg l^{-1} ($n = 21$) on the outer slope down to 150 m depth. An intermediate value of 0.3 ± 0.1 mg l^{-1} ($n = 3$) in front of the Taotoi pass reflects the outflow of lagoonal waters. In the lagoon, the mean concentration of particulate organic carbon (POC) was 46.0 ± 6.7 µg l^{-1} (mean $\pm$ SE, $n = 9$) excluding the extremely high (> 100 µg l^{-1}) near shore values (Table 1). POC was significantly lower (32.5 ± 3.2 µg l^{-1}, $n = 15$, $P = 0.05$) on the outer slope. The mean inorganic particulate carbon (PIC) concentration was of the same order of magnitude as POC in the lagoon and on the outer slope (respectively,

Table 1 Composition of the suspended particulate matter (SPM) in the lagoon and on the outer slope (subsurface and near-bottom waters). POC, PIC and chlorophyll-a concentrations ($\mu g l^{-1}$), ratios of POC and PIC to SPM, % of active chlorophyll and POC/chl-a ratios. Samples on the outer reef are arranged according to the sampling and maximum depths and to the transect number defined in Fig. 1

Site/transect	Sampling (maximum) depths m	POC $\mu g l^{-1}$	POC/SPM %	PIC $\mu g l^{-1}$	PIC/SPM %	Chl-a $\mu g l^{-1}$	Active chl %	POC/chl-a
Lagoon								
Nearshore	0.5 (5)	73	13	115	9	0.17	64.2	400
Nearshore	7.5 (8)	146	11.5	78	16	0.21	62.7	557
Back reef	0.5 (1.5)	30	10	9	4	0.17	47.4	367
Channel	0.5 (2)	18	10	21	8.5	—	—	—
Channel	0.5 (3)	33	14	23	9	—	—	—
Channel	0.5 (6)	38	5	97	15.5	—	—	—
Channel	0.5 (6)	36	10	55	8.5	—	—	—
Papetoai	0.5 (2)	76	7	84	5	—	—	—
Taotoi Pass	0.5 (10)	58	12	87	8.5	—	—	—
Taotoi Pass	8.5 (10)	52	12	70	15	—	—	—
Nearshore	0.5 (5)	106	12	25	12	—	—	—
Nearshore	0.5 (2)	107	14.5	48	8	—	—	—
Sandy plain								
T1	3 (25)	30	16	19	11	0.18	60.5	169
T1	3 (50)	46	11	30	9	0.20	73.7	230
T6	3 (60)	34	13	56	31	0.20	87.6	170
T3	15 (21)	17	17	13	5	0.28	77.5	60
T3	20 (25)	24	19	6	3.5	0.18	86.5	152
T1	38 (50)	32	16	19	10	0.26	80.9	122
T6	45 (60)	18	9	8	2.2	0.18	47.6	102
Drop off								
T3	5 (100)	21	10	56	31	0.13	68.7	161
T1	3 (200)	33	18	42	17	0.21	67.5	159
T3	3 (200)	35	13	63	23.4	0.15	60.6	239
T6	3 (210)	43	15	39	19	0.15	64.4	294
T3	65 (100)	34	21	5	2.5	0.41	97.6	83
T1	85 (200)	65	24	26	13.5	0.35	77.7	184
T3	110 (200)	30	18	10	6	0.48	88.9	76
T6	111 (210)	25	15	41	33	0.39	61.7	64

$59.3 \pm 9.9\ \mu g l^{-1}$ and $28.9 \pm 5.1\ \mu g l^{-1}$). In the lagoon, POC and PIC represented $10.9 \pm 0.8\%$ and $9.9 \pm 1.1\%$ of the SPM respectively. On the outer slope, they reached $15.6 \pm 1.1\%$ and $13.8 \pm 2.8\%$ of SPM respectively. The POC/SPM ratios in deep water ($19.5 \pm 3.9\%$, $n = 4$) were significantly higher ($P < 0.005$) than in surface water ($13.8 \pm 2.8\%$, $n = 7$).

Chlorophyll-a concentration was 0.19 ± 0.03 mg m^{-3} (mean $\pm$ SE; $n = 3$) in the lagoon (Table 1). Outside the reef, the chlorophyll-a concentration was similar to the lagoon in surface water (0.17 ± 0.03 mg m^{-3}; $n = 7$) but was significantly higher (0.41 ± 0.06 mg m^{-3}; $n = 4$, $P < 0.001$) between depths of 65 m and 200 m. The percentage of active chlorophyll showed similar pattern of variation. It did not differ between lagoon and surface oceanic waters ($58 \pm 9\%$ versus $69 \pm 10\%$, $P > 0.1$) but increased significantly below 65 m ($83 \pm 17\%$, $P < 0.001$).

The organic carbon/chlorophyll-a ratio was very high (441 ± 58; $n = 3$) in the lagoon waters and in the pass, whereas it never exceeded 300 in oceanic waters. Moreover, the ratios in surface water were twice those of deep water (201 ± 19, $n = 7$ versus 105 ± 28, $n = 4$; $P < 0.01$). Phytoplankton thus represented the major part of organic carbon in deep waters. The phytoplankton composition was identical to that of previous studies in the same area (Delesalle et al. 1993). At all depths, dinoflagellates and coccolithophorids dominated the oceanic microphytoplankton, whereas diatoms and cyanophytes were most abundant in the lagoonal waters.

Particulate fluxes

Fluxes of particulate organic and inorganic carbon measured using the two types of sediment traps are shown in Table 2. It must be noted that, owing to possible resuspension flux values could have been overestimated in the small benthic traps since these traps were deployed only 1.5 m above the bottom. However, it was assumed that resuspension affected all the traps similarly.

Table 2 POC and PIC concentrations (% dry weight), total, POC and PIC fluxes (mg m^{-2} d^{-1}) and organic matter, carbonates and residual fluxes (mg m^{-2} d^{-1} and % of the total flux) collected by benthic (M1 to M4) and time-series sediment traps. M fluxes are integrated over 12 days whereas each time-series cup is given separately. Each cup was sampled for 3 days, except for the first one at 430 m depth in order to compensate for the 1-day delay in the mooring of the two traps

Site/samples	POC % d.w.	PIC % d.w.	Total flux mg $m^{-2}d^{-1}$	POC flux mg $m^{-2}d^{-1}$	PIC flux mg $m^{-2}d^{-1}$	Organic matter flux mg $m^{-2}d^{-1}$	%	Carbonates flux mg $m^{-2}d^{-1}$	%	Residual flux mg $m^{-2}d^{-1}$	%
Shelf											
40 m											
M1	3.04	8.90	2253.0	68.5	200.5	123.3	5.5	1671.0	74.2	458.7	20.3
M2	1.89	10.40	3878.0	73.3	403.3	131.9	3.4	3360.9	86.7	385.1	9.9
M3	1.71	10.40	2878.0	49.2	299.3	88.6	3.1	2494.3	86.7	295.1	10.2
M4	1.75	10.30	1953.0	34.2	201.2	61.5	3.2	1676.3	85.8	215.2	11.0
Mean	2.10	10.00	2740.5	56.3	276.1	101.3	3.8	2300.6	83.3	338.5	12.9
SE	0.21	0.24	283.5	6.0	32.2	10.8	0.4	268.6	2.0	35.3	1.7
Shelf/slope											
40 m											
Cup 2	3.75	8.60	81.5	3.1	7.0	5.5	6.8	58.4	71.7	17.6	21.5
Cup 3	8.66	10.00	25.0	2.2	2.5	3.9	15.6	20.8	83.3	0.3	1.1
Cup 4	6.58	10.50	30.5	2.0	3.2	3.6	11.8	26.7	87.5	0.2	0.7
Mean	6.33	9.70	45.7	2.4	4.2	4.3	11.4	35.3	80.8	6.0	7.8
SE	1.23	0.49	15.6	0.3	1.2	0.5	2.2	10.1	4.1	5.0	3.9
430 m											
Cup 1	2.23	8.80	105.5	2.4	9.3	4.2	4.0	77.4	73.3	23.9	22.7
Cup 2	1.68	9.20	197.5	3.3	18.2	6.0	3.0	151.4	76.7	40.1	20.3
Cup 3	1.82	9.40	270.5	4.9	25.4	8.9	3.3	211.9	78.3	49.7	18.4
Cup 4	2.67	8.90	265.0	7.1	23.6	12.7	4.8	196.5	74.2	55.8	21.0
Mean	2.10	9.08	209.6	4.4	19.1	7.9	3.8	159.3	75.6	42.4	20.6
SE	0.15	0.09	25.6	0.7	2.4	1.2	0.3	20.1	0.8	4.6	0.6

Shelf sites (40 *m*)

The total particulate flux at 40 m ranged between 1953 and 3878 mg m^{-2} d^{-1} (mean $\pm$ SE 2740 $\pm$ 283 mg m^{-2} d^{-1}, $n = 4$, Table 2). The trapped material was sandy-silt sediment (mean grain size = 103 $\pm$ 15 μm, $n = 4$) composed mainly of skeletal structures and biogenic detritus. The flux was highest (3878 mg m^{-2} d^{-1}) off the Taotoi Pass and decreased both to the east and to the west. Mean ($\pm$ SE, $n = 4$) organic and inorganic carbon concentrations were respectively 2.1 $\pm$ 0.2% and 10.0 $\pm$ 0.2%. The highest organic carbon (3.0%) but lowest inorganic carbon (8.9%) concentrations were found in the easternmost trap located upstream of the pass, whereas they were respectively 1.7–1.9% and 10.3–10.4% in front and west of the pass.

Nitrogen concentration showed a similar pattern to organic carbon with the exception that the highest value (0.27% dry weight) was found in front of the pass (Table 3). Resulting C/N ratios, however, were higher in the easternmost trap (11.8) than in the other traps (7.0 to 8.6).

The shelf-slope

The mean mass fluxes measured by the two time-series traps positioned at the shelf site (40 m depth) and at the slope site (430 m depth), were respectively 45.7 $\pm$ 15.6 mg m^{-2} d^{-1} and 209.6 $\pm$ 25.6 mg m^{-2} d^{-1}, i.e. four times higher at the deeper site (Fig. 4). The organic and inorganic carbon contents differed (Table 2), resulting in a significant increase of the flux of inorganic carbon (from 4.2 $\pm$ 1.2 at 40 m to

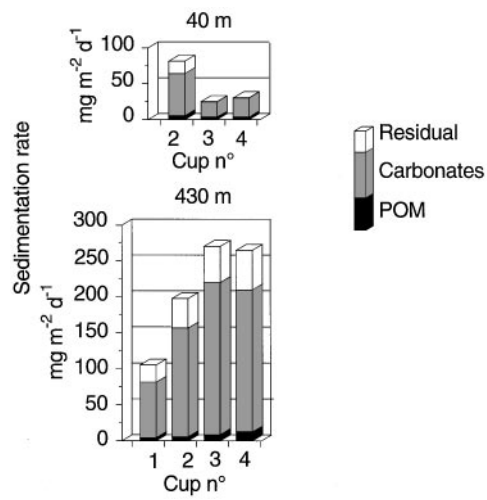

Fig. 4 Mass fluxes and particles composition (organic matter, carbonates and residual) in the time-series sediment traps at 40 and 430 m depth. The horizontal axis represents the sequential cups which were sampled over 3 days, except for the first cup at 430 m depth (1 day)

Table 3 Comparison of the organic composition between the benthic traps (40 m depth) and the corresponding surface sandy plain sediments. Averaged results are also compared with the lagoon sediments. Meiofauna data from A. Dinet, bacteria data from L. Guidi-Guilvard (personal communication)

	Organic carbon % d.w.	Carbonates % d.w.	N % d.w.	C/N	Amino acids		Sugars		Meiofauna	Bacteria
					mg g^{-1}	% TOM	mg g^{-1}	% TOM	individuals 10 cm^{-2}	Nb 10^{8} ml^{-1} wet sediment
Trap 1	3.04	74.5	0.255	11.8	–	–	–	–	–	–
Sediment 1	0.29	94.5	0.029	10.0	1.9	32.8	0.45	7.75	1364	2.2
Ratio	*10.5*	*0.8*	*8.8*	*1.2*	–	–	–	–	–	–
Trap 2	1.89	86.7	0.270	7.0	–	–	–	–	–	–
Sediment 2	0.17	95.4	0.021	8.1	1.2	34.7	0.44	12.8	713	1.7
Ratio	*11.1*	*0.9*	*12.8*	*0.9*	–	–	–	–	–	–
Trap 3	1.71	86.7	0.200	8.5	–	–	–	–	–	–
Sediment 3	0.24	94.3	0.027	8.0	1.0	20.2	0.71	15.0	4113	4.5
Ratio	*7.1*	*0.9*	*6.6*	*1.0*						
Trap 4	1.75	85.7	0.210	8.6	–	–	–	–	–	–
Sediment 4	0.22	94.7	0.023	9.5	1.0	22.7	0.45	10.2	1245	2.9
Ratio	*8.0*	*0.9*	*9.1*	*0.9*	–	–	–	–	–	–
mean ± SE										
Traps ($n = 4$)	2.10 ± 0.21	83.4 ± 2.0	0.234 ± 0.017	9.0 ± 0.7	–	–	–	–	–	–
Sandy plain sediment ($n = 4$)	0.23 ± 0.02	94.7 ± 0.2	0.025 ± 0.002	8.9 ± 0.3	1.3 ± 0.2	27.6 ± 2.6	0.51 ± 0.05	11.4 ± 1.2	1859 ± 602	2.8 ± 0.5
Lagoon sediment ($n = 5$)	0.22 ± 0.01	95.0 ± 1.3	0.015 ± 0.002	15.3 ± 2.3	1.4 ± 0.4	32.2 ± 7.9	0.73 ± 0.09	16.7 ± 1.9	–	–

19.1 ± 2.4 mg m^{-2} d^{-1} at 430 m, $P < 0.05$) but a non-significant increase of the flux of organic carbon (from 2.4 ± 0.3 to 4.4 ± 0.7 mg m^{-2} d^{-1}, $p > 0.1$). Moreover, the proportion of non-carbon (residual) material was greater at 430 m depth (21% of the total flux) than at 40 m (7%) (Fig. 4). Finally, considering the sampling interval (3 days), a high temporal variability was recorded. The mass flux varied between 25 and 82 mg m^{-2} d^{-1} (i.e. more than 3 times) at 40 m depth and increased from 105 to 270 mg m^{-2} d^{-1} during the 12 days of sampling at 430 m depth.

Composition of sediments

Table 3 shows the detailed results concerning four sediments cores on the sandy plain at 40 m and the comparison with benthic traps at the same location. As expected, sediment cores in the Tiahura lagoon and on the sandy plain showed high carbonate concentrations (95% dry weight) and low concentrations of organic carbon (0.2% dry weight) because of the dilution of the organic matter in the carbonate matrix (Table 3). The organic carbon content was 7 to 11 times lower in the surface sediments than in the traps and the nitrogen content was 7 to 13 times lower (Table 3).

The surface sediments of the sandy plain were richer in nitrogen compounds than lagoon sediments (0.025 versus 0.015%, $P < 0.005$) whereas the organic carbon concentration did not differ markedly. Consequently, C/N never exceeded 10 on the sandy plain whereas it reached 15 in the lagoon. Amino acids concentrations are identical in both lagoon and sandy plain sediments whereas sugars are more abundant in lagoonal sediments.

There was spatial variation in the organic content of the sandy plain sediments. Highest values of organic carbon (0.29%) and nitrogen (0.03%) were observed east of the pass whereas lowest values (0.17% and 0.02% respectively) occured in front of the pass. The western sites showed intermediate values. The abundance of meiofauna and bacteria in sediments showed quite similar spatial variation. The meiofauna ranged from 713 to 4113 individuals 10 cm^{-2} whereas the concentration of bacteria ranged from 1.7 to 4.5 10^{8} bacteria ml^{-1} of wet sediment (Table 3). Lowest values were observed in front of the pass whereas the highest values were found west of the pass.

Discussion

The multidisciplinary approach which was followed in this study has allowed the investigation of all aspects (organic and inorganic, pelagic and benthic) of carbon outflowing from the reef system.

Transport of suspended particulate matter

The physical mechanisms responsible for the vertical transport of suspended particulate matter through the adjacent deep-ocean water column are still poorly understood on continental margins, as underlined by Pilskaln et al. (1989). Obviously, the transport of particulate matter from the lagoon is linked with the current velocity in the pass. The multilayer pattern observed in front of the Taotoi Pass is similar to those described for estuaries (e.g. Aloisi et al. 1982). The distribution of turbidity layers is strongly correlated with the distribution of density and with the water mass dynamics. A 0.2–0.3 FTU transmission reduction is observed in the surface layers, due to planktonic particles produced in the upper water column, and enrichment with particles exiting from the lagoon.

Benthic turbidity layers over the sandy plain in front and near the pass are indicative of the settling of particles drifting from the pass, and of the possible resuspension of bottom sediments by waves and coastal currents. The considerable difference between the fluxes at 1.5 m and 10 m above the seabed (2000 versus 40 $mg\,m^{-2}\,d^{-1}$) indicate that resuspension is a significant component of the outer slope hydrodynamics, although the presence of a benthic turbidity layer was only seen near the pass. In fact, this near-bottom horizontal transport is suspected over all the study area, but a direct confirmation could not be obtained because the rugosity of the bottom and the steepness of the dropoff below than 80 m precluded safe CTD-nephelometry investigations and water sampling in the vicinity of the bottom.

Intermediate turbidity layers along the slope, observed at all offshore stations, were particularly well-developed along the strong density gradient interface (at 120 m), where internal waves can appear and develop (Wolanski and Delesalle 1995). Several authors (e.g. McCave 1986) have noted the existence of resuspended surface sediments to depths of a few hundred meters along continental slopes, under the combined influence of topography and internal waves linked to the tides. On the outer reef slope, these internal waves could potentially remobilise and transport suspended material along isopycnals. This phenomenon indicates the predominance of horizontal advection of fine particles compared to vertical exchanges. Because current velocity is high on the sandy plain (up to 40 $cm\,s^{-1}$), this advective transport is relatively fast.

Gardner (1989) showed that periplatform environments are primarily influenced by the transport of suspended particulate matter with along-slope reworking by slope shape and bottom currents. This mode of resuspension and lateral advection does not explain, however, why the particle fluxes, as measured in the sediment traps, increased four fold from 40 to 430 m deep, while the particle concentrations evaluated using nephelometer profiles decreased by 2–3 times under the same hydrological conditions. Obviously, due to the existence of the thermo-halocline and of probable internal waves, the velocity of settling particles cannot be assumed to be constant throughout the water column. However, these hydrodynamic structures would slow down the settling velocity and, thus, the flux of particles would have been reduced rather than increased as observed. Furthermore, the "freshness" of the material either captured in the 430 m sediment trap or collected in the 120 m depth intermediate turbidity layers, was rather good, i.e. high percentages of active chlorophyll and high POC percentages when compared to surface waters values. Another source of particles and/or another mechanism of transport has to be invoked to account for this increasing flux with depth. During our investigations, this point could not have been completely elucidated by water sampling or with the nephelometer. Gardner and Walsh (1990) have shown that particle concentration measurements which are traditionally made with nephelometers and transmissiometers, while being adequate to quantify small particles, do not efficiently estimate large particles or aggregates, such as zooplankton and fish fecal pellets, which may significantly contribute to vertical particle fluxes (Fowler and Knauer 1986). Moreover, if fecal pellets, whose settling velocity can be more than 100 $m\,d^{-1}$ (Fowler and Knauer 1986), are involved in the fluxes of particles, it must be kept in mind that most of zooplankton have nocturnal activity whereas the nephelometer profiles were conducted only during the daytime. Zooplankton concentrations in shelf surface waters off the Tiahura reef system are twice as high during the night than during the day (Renon personal communication). It thus can be assumed that the mass flux between the 40 and 430 m sediment traps has to be related firstly to the horizontal advection of particulate originating from the outer reef slope and, secondly, to the settling of large particles derived from the pelagic system. Passing through the intermediate 120 m depth, carbon- and chlorophyll-rich particles are probably subjected to process of scavenging.

Organic carbon in settling particles and in sediments

The organic carbon content was lower in particles settled in sediment traps than in suspended particulate matter. Several mechanisms are involved in this organic carbon decrease. Firstly, a rapid degradation of the particulate organic carbon may arise because of the high sea surface temperature ($> 27\,^{\circ}C$) as outlined by Buscail et al. (1995) together with oxydising conditions favoured by the hydrodynamics. Secondly, the organic-rich settling particles may be consumed by zooplankton. Thirdly, advection processes could account for downslope transport of inorganic (carbonate and

refractory) material exported from the reef and the volcanic island.

Particles exiting from the lagoon settled rapidly as revealed by the lower fluxes in the western sites, where settling particles showed a 50% lower organic carbon concentration compared to the easternmost site. This might indicate that most of the particles outflowing from the lagoon are carbonate, with a low organic content resulting from recycling processes (Arias-González et al. 1997). However, the organic content collected in the time-series trap at 40 m depth seems to contradict this assumption because concentrations of POC in this trap were higher (ranging from 3.8 to 6.6%) than POC concentrations in the benthic traps. Obviously, due to the composition of sediment, the resuspension which occurred on the sandy plain mainly involved inorganic particles, leading to a lower organic content of the trapped particles. But if we assume that the resuspension affected all the benthic traps similarly, the difference between the easternmost trap and the other ones confirms that mainly carbonates particles exit from the lagoon. Further, the mixing of lagoonal water, poor in organic carbon, with richer nearshore water leads to a dilution of organic matter. Mixing resulted in a low particulate organic carbon (32.5 μg l^{-1}) concentration for a shelf environment, which lies in the lower bound of near reef oceanic values (10–71 μg l^{-1}) reported from the literature (Marshall et al. 1975; Reswig 1981). A mean value of 70 μg l^{-1} has been measured on the continental shelf of the NW Mediterranean between 30 and 200 m depth, i.e. twice that on Moorea's outer slope or in the oligotrophic offshore Mediterranean waters of the Gulf of Lions (40 μg.l^{-1}) (Buscail unpublished data).

The organic carbon concentrations measured in the lagoon or sandy plain sediments (0.2% dry weight) is at the lower bound of the values (0.1 to 0.8%) reported in the literature (e.g. Gordon 1971; Smith and Jokiel 1978). An active degradation of organic matter clearly occurred at the sediment-water interface, as revealed by the 7 to 11 times lower organic content of surface sediments when compared to sediment trap samples. In temperate coastal environment, similar coefficients at 30 m depth were 1 to 6 for the organic carbon and 3 to 13 for nitrogen (Buscail et al. 1990). However, the abundance of meiofauna is similar to Mediterranean coastal silts (1200–5600 individuals per 10 cm^{-2}), where the organic carbon concentration is twice that of Moorea's sandy plain (Guidi-Guilvard and Buscail 1995). It could be assumed that the lower organic matter content of the sediment-water interface is the consequence of its consumption by the benthic fauna. Labile organic matter (mainly amino acids and carbohydrates) at the sediment-water interface represent an important source of energy for the benthos (e.g. Parsons et al. 1984). The intensity of the degradation processes of the organic matter (C and N) could also be linked to environmental factors (e.g. reworking processes, oxygenation caused by hydrodynamism, physico-chemical conditions).

Intensity of export processes

Results reported here must be considered as the very lowest bound of export as (1) sampling took place during calm weather and thus did not adequately reflect the influence of major climatic events, either seasonal (e.g. high swells or strong winds) or aperiodic and catastrophic (e.g. storms or cyclones), and (2) several aspects of carbon export were not considered: mainly export towards the shore and the export of macroscopic particles such as drifting macroalgae.

Strong winds or large swells mainly induce a quick filling of the lagoon. This results in a strong surface jet exiting from the pass, visible far from the reef because of the milky colour given by suspended carbonate particles. Aperiodic events like cyclones result in the export of huge amounts of reefal material either downslope in the ocean or onshore. The effects of such catastrophic disturbances were reviewed by Scoffin (1993) and Harmelin-Vivien (1994). In French Polynesia where fore reef slopes are narrow, the destruction occurs not only on the upper part of the reef slope but also on the lower part which, although protected from direct wave action, is devastated by avalanches of colonies broken in upper areas which roll downwards (Harmelin-Vivien 1994). Onshore transport of reef sediments represents another mode of export from the reef ecosystem that should be taken into account in carbon and carbonate budgets.

The export of macroscopic debris is assumed to be significant on Tiahura reef because large accumulations of drifting brown macroalgae, *Turbinaria ornata* and *Sargassum mangarevense*, are commonly observed in the sheltered areas of the lagoon of Moorea Island. Depending on the changes in the wind strength and direction, these accumulations can be partly dissociated and exported through the pass. Accumulation of drifting algae on a fringing reef is reported by Killar and Norris (1988). The exported biomass (dry weight) ranged from 29 to 580 kg mo^{-1} for a reef flat covering about 1 ha, i.e. 0.1 to 1.9 g m^{-2} d^{-1}. In Kaneohe Bay (Hawaii), Morrissey (1985) estimated the export of organic carbon in drifting algae to be 2.2 to 29.3 g m^{-2} d^{-1} dry weight. Assuming that organic carbon was 29% of dry weight, the mean export of organic carbon was estimated as 0.7 gC m^{-2} d^{-1}. Similar obervations have been made on the Great Barrier Reef where significant quantities of carbon are exported, ranging from 0.3 to 3.8 gC m^{-2} d^{-1} (Morissey and Pichon unpublished data).

Finally, the estimated rates of organic carbon and carbonates export reported here for Tiahura reef have been included in a general carbon model, together with previous measurements of reef organic production/res-

piration and carbonate precipitation/dissolution (Gattuso et al. 1993, 1996). This preliminary model shows that exports represented 47% and 21% respectively of the organic (net excess production) and inorganic production of the reef. The model has now to be completed by obtaining a precise estimation of the inputs in the reef system mainly in term of organic, dissolved and particulate, carbon.

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