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Sources of particulate organic matter at the ecosystem scale: a stable isotope and trace element study in a tropical coral reef

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ABSTRACT: Spatial and seasonal variability of sources of particulate organic matter (POM) were evaluated in a coral reef ecosystem. Reef water POM was sampled monthly along a south-north gradient. The passage of tropical cyclone Gamede, which crossed Reunion Island in February 2007, provided an ideal opportunity to examine the impact of high river discharge. Stable isotope composition (δ^{13} C, δ^{15} N) was determined in oceanic, riverine and reef water POM, sedimentary organic matter (SOM), benthic primary producers and detritus. Trace elements (Ti, Fe, Cr, Ni, Cu, Zn) measured in SOM were used as additional terrestrial tracers. Stable isotope analysis of reef water showed that POM was affected by anthropogenic non-point nutrient sources, water circulation patterns and residence time. During the cold and dry season, the southern end of the reef received organic matter input derived from ocean primary production, while the middle and northern reef water POM originated primarily from SOM, reflecting an important bentho-pelagic coupling process. During the hot and wet season, reef water was enriched in benthic detritus due to higher autochthonous production. We found important spatial variability in POM sources, highlighting the importance of small-scale (hundreds of meters) studies when investigating ecosystem functioning. Although coastal tidal currents transported some river discharge material to the south of the reef, riverine POM input was limited, even after cyclone passage. We hypothesized that the major effect of the cyclone was the export of SOM and benthic detritus out of the system and that persistent disturbances such as groundwater discharges can be of greater importance than a cyclone in long-term degradation of ecosystems.

KEY WORDS: Organic matter \cdot Stable isotopes \cdot Trace metals \cdot Coral reef \cdot Cyclone \cdot Benthopelagic coupling \cdot Seasonal variation

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INTRODUCTION

Coral reefs are highly diverse and complex ecosystems, capable of maintaining extremely high productivity in oligotrophic environments (Crossland 1983). Although nutrient supply is critical in supporting coral reef ecosystems, excess anthropogenic nutrient input such as sewage discharge, land-clearing operations and fertilizer application has been suggested as one of the major factors causing coral reef decline (Fabricius 2005). Transported via surface runoff or catchment drainage, nutrients can drastically impact the balance of coral reef production and consumption, even at concentrations as low as 1 μ M dissolved inorganic nitrogen (Bell 1992). Dissolved inorganic nutrients are rapidly converted into particulate form within hours to days (Furnas 2003). Inorganic nutrients and particulate organic matter (POM) are potentially the most important contaminants at regional and national levels (GESAMP 2001).

Reef water eutrophication is a process involving organic matter production and accumulation; it impacts the nutritional status of communities and leads to changes in ecosystem structure (Nixon 1995). As input increases, coral reef communities may shift from being dominated by nutrientrecycling corals to dominance by macroalgae and heterotrophic filter-feeders (Birkeland 1987). Many contemporary coral reefs increasingly fail to regenerate after natural or human impacts, and undergo a shift to an alternate ecological state (Done 1992, Scheffer et al. 2001). There is still debate as to how much coral reef decline is directly driven by excess organic enrichment as opposed to the numerous other factors known to be affecting them (e.g. sedimentation, thermal stress, over-harvesting of grazers and predators, storm damage; Szmant 2002). Hence, evaluation of terrestrial and anthropogenic organic matter inputs to coral reefs is an important prerequisite to understanding community structure.

Increased productivity of coastal benthic ecosystems caused by nutrients derived from land-based runoff has been demonstrated in various ecosystems (e.g. Maslowski 2003, DeCarlo et al. 2007). While such an effect has been hypothesized from groundwater seepages in Reunion Island's fringing reefs, located in the south-western Indian Ocean (Mioche & Cuet 1999, Taddei 2006), the sources and fates of increasing land-derived nutrient loading is still not well understood. Because this steep volcanic island is subject to intense short bursts of orographic events, with coastal delivery of terrestrial or anthropogenic material occurring on time scales of hours to days, erosion-derived nutrient inputs are difficult to measure in the reef area. More generally, the transfer of terrestrial matter into coral reef waters or sediments has not been well studied (Umezawa et al. 2002, Derse et al. 2007, Wolanski et al. 2009), especially in terms of spatial and temporal variability.

Stable isotope analysis (δ^{13} C, δ^{15} N values) has been used to trace the transfer of organic matter from different origins through estuarine and oceanic food webs (e.g. Riera & Richard 1996, Pinnegar & Polunin 2000, Vizzini & Mazzola 2006). Marine plants are ¹³C-enriched compared to most of their terrestrial counterparts, partly due to the fact that most photosynthetic producers in oceans use dissolved HCO₃⁻ which is ~7% enriched with respect to atmospheric CO₂, the carbon source for terrestrial plants. Terrestrial primary producers have typically lower δ^{13} C values than marine producers (from –20 to -30‰; Haines & Montague 1979, Fry 2002), allowing terrestrial inputs to be traced in coastal systems. Nitrogen isotopic values of seawater nitrate, the major nitrogen source for marine primary producers such as phytoplankton, is around 4.5% for deep water (Montoya et al. 2002, Reynolds et al. 2007). Moreover, it may become depleted (-2%) in surface waters due to N_2 fixation (Liu & Kaplan 1989, Reynolds et al. 2007), atmospheric deposition of isotopically light N (Paerl & Fogel 1994), or preferential export of ¹⁵N out of the upper water column through food web processes (Montoya et al. 2002). Systems affected by nitrogenous fertilizer inputs are expected to exhibit $\delta^{15}N$ POM values between -4 and 4‰, because most fertilizers are made by the fixation of atmospheric N_{2} , which has a $\delta^{15}N$ value of ~0‰ (Kendall 1998). Wastewater nutrients derived from septic tanks and other landbased sources are generally enriched, with higher δ^{15} N values (from 10 to 22‰) due to typical transformations involving loss of ¹⁴N, such as ammonia volatilization, denitrification and ammonia nitrification (Heaton 1986, Jordan et al. 1997).

Trace metal abundance has been widely used as an indicator of environmental conditions in coral reefs (e.g. Ramos et al. 2004). As Reunion Island soils are derived mainly from volcanic-detrital minerals (Louvat 1997), assessment of trace metal concentrations in reef sediments may provide an additional and valuable tool for investigating the fate of terrestrial materials due to erosional transport. Trace metals such as Ti, Fe, Ni and Cr are typical constituents of Reunion Island's basaltic terrain (Hoareau 2001). In addition, Cu and Zn are typical of the heavy metals found in sewage sludge, plumbing, roofing and enriched cattle feed, and are commonly used to detect human-generated contaminants in aquatic environments (e.g. Morse et al. 1993, Rhoads & Cahill 1999, Galay-Burgos & Rainbow 2001).

In the present study we have characterized the sources of POM using isotopic composition (δ^{13} C, δ^{15} N values) and trace metals abundance (Ti, Fe, Mn, Ni, Cu and Zn) in sediments from Reunion Island's coral reef. Our method was designed to assess seasonal and spatial variability in reef water POM. Tropical cyclone Gamede, which crossed Reunion Island from 22 to 28 February 2007, provided an ideal opportunity to examine the impact of high river discharge in the reef area. Potential sources of POM in reef water (oceanic, terrestrial, reef benthic production) were quantified during the 2 main seasons, one cold-dry and the other hot-wet, representing the 2 extreme climatic conditions on Reunion Island.

MATERIALS AND METHODS

Study area

Reunion Island (21° 07' S, 55° 32' E) is located in the south-western Indian Ocean, 800 km east of Madagascar (Fig. 1a). Coral reefs fringe less than 10% of the coastline, being restricted to the dry leeward west coast (Fig. 1b). The cold-dry season extends from July to October and the hot-wet season from January to April, followed by transitional warming (November and December) and cooling (May and June) periods, respectively. Mean coastal sea surface temperature (SST) varies from 23.7 \pm 0.3° C in the cold-dry season to $27.7 \pm 0.4^{\circ}$ C in the hot-wet season (Conand et al. 2007). Mean west coast rainfall is 5.0 mm mo⁻¹ in the cold-dry season and 87.5 mm mo⁻¹ in the hot-wet season. Maximum rainfall recorded during the wet season ranges from 800 to 1400 mm mo⁻¹ (Météo-France database).

The study was carried out at 3 locations in the La Saline fringing reef (4 km long, 500 m maximum width; Fig. 1c). These locations were, from south to north, Petit Trou d'Eau (TE), Planch'Alizés (PA) and Club Med (CM). Within each location, 2 geomorpho-



Fig. 1. Location of La Saline fringing reef showing main current directions (Cordier 2007) and sampling stations

logical zones were considered: (1) the back-reef zone (BR), mainly comprising detrital sediments; and (2) the inner-reef flat zone (IRF), typified by transverse strips of branched corals, and associated with coarse sand and coral fragments. One sampling station was established in each of these zones, for a total of 6 sampling stations (Fig. 1c). Mean water depth over the reef varies from 1.0 to 1.5 m, depending on tidal level. Currents are mainly wind-driven, with water flowing from the reef front to the back reef zone, and returning to the open ocean through the Hermitage pass in the north and the Trois-Bassins pass in the south (Fig. 1c). Average current speed varies from 0.3 to 1.0 km h⁻¹, with tidal currents rarely exceeding 2 km h^{-1} (Chazottes et al. 2008). Mean reef water residence time is 10 h 30 min (Cordier 2007). On the land side, the reef is surrounded by La Saline city. One freshwater stream (Hermitage) empties near the north pass, and another (Trois-Bassins) near the south pass (Fig. 1c). The La Saline stream has been filled in and no longer discharges surface runoff. Stream discharge is characterized by extended periods of low or no flow, with sporadic periods of intense runoff associated with orographic events or tropical storms.

Reef water POM survey

Reef water POM was sampled monthly for elemental and isotopic measurements from June 2006 to June 2007 at TE, PA and CM back reefs and inner-reef flats. Reef water temperature was recorded hourly with 2 HOBO Water Temp Pro data loggers (accuracy, 0.2°C; Onset Computer Corporation), deployed at 1.2 m depth at TE and PA (inner-reef flat and backreef transition zone). Since monthly mean temperatures did not significantly differ between the 2 sites (Student's paired *t*-test, p > 0.05), the PA dataset was selected to represent reef water temperature for this study. SST and chl a concentrations were obtained from the SeaWIFS/MODIS database (NASA Giovanni satellite). The prospected area is about 850 km², located from 5 to 15 km west of La Saline reef. Rainfall data were obtained from the coastal Trois-Bassins Météo-France station (2 km south of the reef).

Potential POM sources

Two sampling campaigns were undertaken, one in August 2006 (cold-dry) and the other in March 2007 (hot-wet; 20 d after passage of cyclone Gamede). Oceanic water was sampled at a point 8 km from the coast, and river water was sampled from the Hermitage stream mouth. Sedimentary organic matter (SOM) and benthic detritus (organic matter deposited on macroalgae above the sediment-water interface) were sampled at each station and analyzed for their carbon and nitrogen isotopic composition. Isotopic composition of fresh benthic primary producers (macroalgae, seagrass and cyanobacteria mats) was also determined since these potentially represent a source of detrital organic matter in coral reefs. In March 2007, concentrations of Ti, Cr, Fe, Ni, Cu and Zn, as additional tracers of terrestrial input to the reef area, were measured in sediment samples.

Sample collection and analysis

POM samples were obtained by filtering 41 of oceanic and reef water and 500 ml of river water through precombusted (4 h at 450°C) GF/F filters (3 replicates per station). Macroalgae fragments and macrofauna (organisms >1 mm) were removed from sediment cores (\emptyset 3.5 cm, top 2 cm of sediment) to obtain SOM samples (n = 5). The non-living parts of the cyanobacteria mats were carefully removed and the samples (n = 5) rinsed with deionized water. Macroalgae (Caulerpa serrulata, Boergesenia forbesii and Dictyota sp.) and seagrass (Syringodium isoetifolium) were cleaned from their epiphytes and rinsed with deionized water. Detritus samples were obtained by centrifuging (6 min at 5000 rpm $[1680 \times g]$) organic matter contained in the macroalgae rinsing water (without the epiphytes). Microscopic analysis revealed that the organic matter fraction was composed of 80% amorphous organic matter, 20% undetermined vegetal and non-vegetal detrital fragments and <1% unicellular organisms and crustacean meiofauna.

POM samples were dried for 12 h at 60°C while all other samples were lyophilized. Reef SOM, benthic detritus and primary producers were ground to a fine homogeneous powder. Oceanic and riverine POM filters were analyzed according to Lorrain et al. (2003). Rich CaCO₃ reef water POM, SOM, detritus and cyanobacteria samples were acidified before δ^{13} C analysis. POM filters were reacted with 2 N HCl while all other samples were treated with 1 N HCl until no further fizzing was observed (Nieuwenhuyse et al. 1994). Since acid treatment can lead to a loss of nitrogenous compounds, untreated sub-samples were used to measure δ^{15} N values (Bunn et al. 1995, Kolasinski et al. 2008). All samples were weighed into tin capsules and analyzed in duplicate using isotope ratio mass spectrometry (IRMS).

C and N content and isotopic composition were analyzed at the National Stable Isotope Laboratory, GNS Science, Lower Hutt, NZ, using a Europa Geo 20/20 isotope ratio mass spectrometer (PDZ Europa), interfaced to an ANCA-SL elemental analyzer (PDZ Europa) in continuous-flow mode (EA-IRMS). CO_2 and N_2 gases were separated on a GC column at 68°C, and analyzed for isotopic abundance.

The ¹³C/¹²C and ¹⁵N/¹⁴N isotope compositions are expressed in conventional delta notation as ‰, according to the following equation:

$$\delta X = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 1000 \tag{1}$$

where X is ¹³C or ¹⁵N and R is the ratio of heavy to light isotope ($^{13}C/^{12}C$ or $^{15}N/^{14}N$). All results are reported with respect to Vienna PeeDee Belemnite (VPDB) and N-Air, normalized to internal standards leucine (-22.7% for $\delta^{13}C$, 2.2% for $\delta^{15}N$), Montana Soil (-17.1% for $\delta^{13}C$, 7.6% for $\delta^{15}N$), Buffalo River Sediment (-19.8% for $\delta^{13}C$, 3.7% for $\delta^{15}N$), GNS Moa Bone (-21.0% for $\delta^{13}C$, 9.8% for $\delta^{15}N$) and caffeine (-8.0% for $\delta^{13}C$, -7.4% for $\delta^{15}N$). The analytical precision for these measurements is 0.2‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$.

Elemental concentrations in sediment core samples were determined by Proton Induced X-ray Emission (PIXE) at GNS Science, NZ. A few tens of mg of each dry sediment sample were pressed into pellet form with cellulose backing material. A force of 4 t was applied to produce a compact pellet. The pellets were then carbon-coated to avoid charging during PIXE analysis. A 2.5 MeV proton beam from a 3 MV particle accelerator was used to analyze the pellets under vacuum conditions (residual gas pressure below 10⁻⁶ mbar). The proton beam was focused to 1 mm diameter. A beam current of typically 30 nA was applied until 40 µC charge was accumulated. The X-ray signals were detected with a Si(Li) detector placed at a 135° backward angle. A 25 µm Be foil and a 50 µm Al foil were attached to the detector to reduce the dead time due to large numbers of X-rays from low-atomic-number elements such as Si and Ca. The standard used was USGS-G-2 granite. The PIXE spectra were analyzed with the peak-fitting program GUPIX (Maxwell et al. 1995).

Statistical analyses

Statistical analyses were undertaken with STATIS-TICA 7.0 software (StatSoft). Influence of environmental variables on reef water POM isotopic composition was first investigated using principal component analysis (PCA). POM isotopic composition (δ^{13} C, δ^{15} N) values were considered as active variables, while oceanic SST, chl a concentration, rainfall and rainfall from the previous month were used as supplementary variables. Results were illustrated in 2 types of diagrams: (1) the correlation between descriptors and the first 2 principal axes, and (2) the multidimensional plotting of the sampling months along the first 2 principal axes. Standard linear regressions (Pearson's correlation coefficients, ANOVAs) were used to assess the strength of relationships between environmental variables and reef water POM isotopic composition. (Rainfall data were log-transformed to account for extreme-precipitation events.) Significant groups of sampling months were tested using ANOSIM (Primer 5.0).

One- and 2-way ANOVA was used to assess spatial and temporal variability in isotopic composition of reef water POM and its potential sources. Spatial variability in levels of sediment trace metals were also investigated using variance analysis. Data were tested for homogeneity with Levene's test. Kruskall-Wallis (1-way) was used when data did not fulfill requirements. The Newman-Keuls post hoc test was used to identify homogeneous groups.

RESULTS

Seasonal trends in environmental variables

Open ocean and reef water temperatures were strongly correlated ($r^2 = 0.956$, p < 0.001) and were not significantly different (Student's paired *t*-test, t = 0.12, p > 0.05). Mean seawater temperature and rainfall depth were 24.0 ± 0.3°C and 2.5 ± 2.9 mm mo⁻¹, respectively, in the cold-dry season, and 28.2 ± 0.7°C and 51.9 ± 63.4 mm mo⁻¹, respectively, in the hot-wet season (Fig. 2). Oceanic chl *a* concentration was slightly higher during the cold-dry season (0.10 ± 0.01 mg m⁻³) than during the hot-wet season (0.07 ± 0.02 mg m⁻³). The latter was significantly correlated to water temperature ($r^2 = 0.734$, p < 0.001) but not to rainfall ($r^2 = 0.448$, p > 0.05) or to rainfall recorded a month before ($r^2 = 0.151$, p > 0.05). An increase in oceanic chl *a* of



Fig. 2. Monthly mean \pm SD of (a) reef and oceanic water temperature (*T*) and oceanic chlorophyll *a* (chl *a*) concentration, and (b) rainfall measured on island's west coast

about 80% was, however, observed between February and March 2007, corresponding to the cyclone Gamede event.

Spatio-temporal variation in reef water POM isotopic composition

Mean δ^{13} C and δ^{15} N values, as well as the C:N ratio of reef water POM collected during the monthly survey are presented in Fig. 3. The most striking feature was, about 10 d after the cyclone event (i.e. on 9 March 2007), the decrease in POM δ^{13} C values observed at CM stations (mean depletion of 2.1%), at the PA inner-reef flat (3.4%) and, to a lesser extent, at the PA back-reef (1.0%) and TE stations (0.6%). Elevated C:N ratios were observed at all stations



Fig. 3. (a,c,e) δ¹³C, δ¹⁵N values. (b,d,f) C:N molar ratios. All values are mean ± SD of 3 replicates per station from reef water particulate organic matter collected at 6 sampling stations at the 3 sampling sites: (a,b) Petit Trou d'Eau (TE), (c,d) Planch' Alizés (PA), (e,f) Club Med (CM). In (a,c,e) open symbols: back-reef (BR) stations; closed symbols: inner-reef flat (IRF) stations. In (b,d,f) open bar: BR stations; dark bar: IRF stations. C: cooling. Vertical grey lines show passage of the tropical cyclone Gamede

5 wk after the cyclone event (i.e. on 6 April 2007). C:N ratios increased by a factor of 7, 4 and 3 at the CM, PA and TE stations, respectively, and tended to decrease during the following months, except at the PA back-reef station where ratios remained high until June 2007. Monthly deviation from the annual mean of reef water POM δ^{13} C and δ^{15} N values is presented in Fig. 4. At the reef scale, variability in water POM isotopic composition was characterized by ¹³C enrichment and ¹⁵N depletion during the cold-dry and warming periods. The decrease in reef water POM δ^{13} C values observed in March 2007, after cyclone passage, was concurrent with ¹⁵N enrichment that went on through the following months.

The PCA performed on reef water POM δ^{13} C and δ^{15} N values is presented in Fig. 5. Together the 2 principal component axes (PC 1 and PC 2) explained 73% of the total variation, with 55.3% inferred from PC 1. PC 1 was highly correlated with rainfall from the previous month (r = 0.876), and, to a lesser extent, with oceanic SST (r = 0.575). PC 2 was best correlated with oceanic chl *a* (r = 0.406). Rainfall recorded during the sampling month was poorly correlated with either axis (r = 0.052 and 0.218 for PC 1 and PC 2,



Fig. 4. Monthly deviations (mean \pm SD) from annual mean of δ^{13} C and δ^{15} N values of reef water particulate organic matter (POM) calculated for each month from combined TE, PA and CM stations (see Fig. 1). C/D: cold-dry; H/W: hot-wet; C: cooling; W: warming

respectively). Hence, we used the rainfall dataset with a 1 mo time-lag for further analyses. Correlations of $\delta^{13}C$ and $\delta^{15}N$ active variables with PC 1 were generally strong (r values from 0.611 to 0.907) and showed a marked opposition between $\delta^{13}C$ and



Fig. 5. Principal component (PC) analysis performed on δ^{13} C and δ^{15} N values of reef water particulate organic matter (POM). (a) Correlation between variables and 2 first axes. SST: sea surface temperature; Active var.: active variables; Suppl. var.: supplementary variables. Site and zone abbreviations as in Fig. 3. (b) Distribution of sampling months onto 2-dimensional plot of principal components and analysis of similarity (ANOSIM) analysis (stress = 0.01). In the ANOSIM analysis, transitional cooling (May–June) and warming (November–December) periods (dashed lines) were added to hot-wet and cold-dry months (solid lines), respectively

 $\delta^{15}N$ values (boxes in Fig. 5a). PC 2 mainly separated TE stations from all others, based on POM $\delta^{13}C$ values, and reef-flat from back-reef stations (except at TE), based on $\delta^{15}N$ values.

Fig. 5b displays the distribution of sampling months onto the 2-dimensional plot of the principal components. Cluster analysis showed 3 separate groups (analysis of similarities [ANOSIM], R = 0.709). March 2007, during which time POM δ^{13} C values were slightly depleted and $\delta^{15}N$ values slightly enriched (see Figs. 3 & 4), was plotted independently of the other months. In hot-wet months (January to April) more ¹³C-depleted and ¹⁵N-enriched values were observed than in cold-dry months (July to October). In addition, transitional warming (November-December) and cooling (May-June) periods tended to be related to cold-dry and hot-wet seasons respectively (ANOSIM, R = 0.645). Statistical analyses were therefore performed using POM isotopic composition values from cold-dry/warming (CD/W) and hot-wet/ cooling (HW/C) periods to further investigate the influence of environmental parameters. POM δ^{13} C values significantly decreased with rainfall during the HW/C period at the PA back-reef station, and, to a lesser extent, at the CM stations (Table 1). POM δ^{13} C values significantly increased with oceanic chl a in the CD/W period at the TE stations and the PA innerreef flat. POM δ^{13} C values were better correlated with oceanic chl a than with oceanic SST. Significant positive correlations were observed between $\delta^{15}N$ values and rainfall at the PA back-reef station during the HW/C period (CD/W and HW/C periods, $r^2 =$ 0.717, p < 0.001), indicating a slight N enrichment with increasing rainfall. No significant relationships between environmental parameters and $\delta^{15}N$ values were observed at any other station (p > 0.05 in each case).

At the reef scale, POM δ^{13} C and δ^{15} N values varied inversely and seasonally (Fig. 4 and PC 1 in Fig.5a).

However, these variations are related to different factors depending on the station. Three main sources of variation were identified for reef water POM δ^{13} C and δ^{15} N values: (1) a seasonal influence of oceanic chl *a* concentration, resulting in a marked POM 13 C enrichment at the southern TE stations, and, to a lesser extent, at the PA inner-reef flat, during the CD/W period; (2) a specific effect of rainfall on POM δ^{13} C values (depletion) during the month following the cyclone Gamede event (i.e. March 2007), the effect being more marked at the northern PA inner-reef flat and CM stations (Fig. 3c,e); and (3) an annual positive effect of rainfall on POM δ^{15} N values at the PA back-reef station, also typified by a persistence of high C:N ratios after the cyclone event.

Reef water POM sources

Average δ^{13} C and δ^{15} N values of potential sources of POM in reef water (oceanic and riverine POM, SOM, benthic detritus and benthic primary producers) sampled in August 2006 and March 2007 are listed in Table 2. Riverine POM δ^{13} C values were more strongly depleted (<-30‰) than oceanic POM (mean of $-22.9 \pm 0.7\%$), reef SOM ($-15.6 \pm 1.6\%$) or detritus samples (-14.0 ± 3.4 %). Riverine POM samples were also more 15 N-depleted (-4.1 ± 0.5 ‰) than reef SOM $(3.5 \pm 1.1\%)$, oceanic POM $(5.0 \pm 0.8\%)$ or detritus (7.3 \pm 1.2‰). On average, benthic primary producers were the most ¹³C-enriched and ¹⁵Ndepleted reef samples, presenting a range of $\delta^{13}C$ values extending from $-12.4 \pm 2.9\%$ for macroalgae to $-7.2 \pm 2.5\%$ for cyanobacteria mats and $-4.7 \pm$ 0.5% for the seagrass Syringodium isoetifolium). $\delta^{15}N$ values were as low as $0.4 \pm 0.9\%$ for cyanobacteria mats, 1.3 ± 0.4 % for *S. isoetifolium* and 2.8 ± 0.6 % for macroalgae. Riverine and oceanic POM exhibited

Table 1. Linear regression coefficient (r^2) and ANOVA (p-value) analyses between reef water particulate organic matter (POM) δ^{13} C values and 3 environmental variables during 2 periods of the year. Variables: oceanic sea surface temperature (Ocean SST), oceanic chlorophyll *a* concentrations (Ocean chl *a*), rainfall (from previous month). Periods: cold-dry warming (CD/W), hot-wet cooling (HW/C). Sites: Petit Trou d'Eau (TE), Planch' Alizés (PA), Club Med (CM). Geomorphological zone: inner-reef flat (IRF), back-reef (BR). d: ¹³C depletion, e: ¹³C enrichment. Statistical significance: *p <0.05, **p <0.01, ***p < 0.001; ns: not significant

Sampling	Sampling	Ocean SST		Ocean c	hl a ———	Rainfall		
site	zone	CD/W	HW/C	CD/W	HW/C	CD/W	HW/C	
TE	IRF	0.799 (*, d)	0.489 (ns)	0.941 (***, e)	0.007 (ns)	0.002 (ns)	0.366 (ns)	
	BR	0.661 (*, d)	0.037 (ns)	0.838 (**, e)	0.426 (ns)	0.048 (ns)	0.204 (ns)	
PA	IRF	0.432 (ns)	0.004 (ns)	0.784 (*, e)	0.547 (ns)	0.129 (ns)	0.456 (ns)	
	BR	0.226 (ns)	0.379 (ns)	0.641 (ns)	0.038 (ns)	0.020 (ns)	0.964 (***, d)	
CM	IRF	0.579 (ns)	0.024 (ns)	0.442 (ns)	0.292 (ns)	0.058 (ns)	0.558 (*, d)	
	BR	0.702 (ns)	0.075 (ns)	0.460 (ns)	0.210 (ns)	0.057 (ns)	0.658 (*, d)	

Samplos	Sampling	Sampling	August 2006 (cold-dry)			March 2007 (hot wot)		
Samples	site	zone	$\frac{\delta^{13}C}{\delta^{13}C}$	δ^{15} N (%)	C:N	$\delta^{13}C$ (%)	$\delta^{15}N$ (‰)	C:N
Reef water POM	TE	IRF	-19.7 ± 0.2	4.9 ± 0.2	10.7 ± 0.1	-20.7 ± 0.2	6.2 ± 0.2	14.5 ± 2.2
		BR	-17.8 ± 0.2	4.4 ± 0.2	10.4 ± 0.1	-19.3 ± 0.1	5.5 ± 0.2	13.1 ± 0.5
	PA	IRF	-17.3 ± 0.2	4.2 ± 0.4	10.0 ± 0.1	-20.3 ± 0.3	5.1 ± 0.2	16.7 ± 2.8
		BR	-16.6 ± 0.2	4.3 ± 0.2	10.2 ± 1.3	-17.8 ± 0.3	5.9 ± 0.1	15.4 ± 0.6
	CM	IRF	-16.8 ± 0.1	4.7 ± 0.4	10.6 ± 0.8	-19.3 ± 0.2	5.4 ± 0.2	17.6 ± 0.2
		BR	-16.1 ± 0.1	4.6 ± 0.2	7.8 ± 0.1	-19.6 ± 0.1	5.0 ± 0.1	13.7 ± 0.7
	Mean		-17.4 ± 1.3	4.5 ± 0.3	10.4 ± 1.1	-19.5 ± 1.1	5.5 ± 0.5	15.2 ± 1.7
Reef SOM	TE	IRF	-16.4 ± 0.7	3.4 ± 0.2	6.6 ± 0.2	-17.2 ± 0.1	3.3 ± 0.3	7.9 ± 0.3
		BR	-15.1 ± 0.6	$3.4 \pm 0.3)$	3.7 ± 0.5	-16.4 ± 0.5	3.1 ± 0.7	7.5 ± 1.0
	PA	IRF	-14.7 ± 0.4	3.2 ± 0.2	9.6 ± 1.3	-15.8 ± 0.6	3.0 ± 0.2	10.5 ± 0.7
		BR	-13.5 ± 0.2	3.9 ± 0.2	11.7 ± 3.8	-14.4 ± 0.6	3.9 ± 0.1	15.6 ± 2.5
	CM	IRF	-15.9 ± 0.4	3.3 ± 0.2	6.5 ± 0.3	-16.3 ± 0.1	3.2 ± 0.2	7.0 ± 0.5
		BR	-15.2 ± 0.4	3.1 ± 0.3	6.5 ± 0.8	-16.1 ± 0.5	3.5 ± 0.3	7.7 ± 1.6
	Mean		-15.1 ± 1.0	3.4 ± 0.3	7.4 ± 2.8	-16.0 ± 1.0	3.3 ± 0.3	9.4 ± 3.3
Benthic detritus	TE	IRF	-9.3 ± 2.3	7.6 ± 2.4	19.6 ± 6.9	-16.9 ± 2.0	8.9 ± 3.3	15.6 ± 4.6
		BR	-7.6 ± 1.3	5.2 ± 3.4	19.5 ± 9.5	-17.1 ± 1.8	6.4 ± 3.6	17.4 ± 7.2
	PA	IRF	-13.1 ± 2.7	7.7 ± 1.9	22.7 ± 10.5	-18.2 ± 3.6	6.5 ± 3.8	13.9 ± 6.3
		BR	-12.7 ± 4.2	9.4 ± 2.2	26.4 ± 12.3	-13.8 ± 3.7	8.7 ± 2.6	20.7 ± 4.4
	CM	IRF	-11.6 ± 1.6	6.5 ± 1.8	19.6 ± 2.1	-17.3 ± 2.9	7.4 ± 2.2	16.4 ± 8.7
		BR	-13.4 ± 2.6	6.3 ± 2.8	24.8 ± 8.7	-16.8 ± 2.0	6.8 ± 3.2	17.6 ± 5.6
	Mean		-11.3 ± 2.3	7.1 ± 1.4	22.1 ± 3.0	-16.7 ± 1.5	7.5 ± 1.1	17.0 ± 2.3
Cyanobacteria mats			-7.4 ± 2.7	0.5 ± 1.2	8.5 ± 1.0	-6.9 ± 2.3	0.3 ± 0.8	9.9 ± 0.6
Syringodium isoetifolium			-4.9 ± 0.5	1.4 ± 0.5	20.6 ± 4.5	-4.5 ± 0.7	1.2 ± 0.3	21.2 ± 3.9
Caulerpa serrulata			-8.7 ± 1.0	1.6 ± 0.9	19.3 ± 3.1	-9.2 ± 1.8	0.3 ± 0.8	18.2 ± 4.0
Boergesenia forbesii			-13.2 ± 1.7	4.5 ± 1.0	48.5 ± 10.3	-15.4 ± 1.5	3.5 ± 0.6	44.6 ± 15.7
Dictyota sp.			-14.6 ± 1.1	2.9 ± 0.8	24.2 ± 5.6	-13.3 ± 1.3	2.7 ± 0.4	22.5 ± 6.6
Oceanic POM			-22.2 ± 0.2	4.7 ± 0.3	6.5 ± 0.3	-23.5 ± 0.4	5.2 ± 0.4	8.8 ± 0.7
Riverine POM			-32.5 ± 0.4	-3.4 ± 0.7	6.3 ± 0.4	-33.9 ± 0.5	-4.6 ± 0.6	7.5 ± 0.5

Table 2. Isotopic composition (δ^{13} C, δ^{15} N values) and C:N molar ratio (all mean values ± SD) of various sources of organic matter during 2 periods of the year. POM: particulate organic matter, SOM: sedimentary organic matter. Sampling sites and geomorphological zones as in Table 1

the lowest C:N ratios $(6.9 \pm 1.2 \text{ and } 7.6 \pm 1.1, \text{ respectively})$ out of all potential POM sources. C:N ratios were highest in macroalgae (means from 18.2 to 48.5), detritus (19.5 ± 3.7), cyanobacteria mats (9.2 ± 0.9) and SOM (8.4 ± 0.9).

Differences in δ^{13} C values of potential autochthonous POM sources were observed between the 2 sampling periods, corresponding to a generalized ¹³C depletion in March 2007 (Table 2). The most conspicuous changes were seen in benthic detritus samples with a mean ¹³C depletion of 5.4‰. Reef SOM δ^{13} C values were depleted by 0.9‰, and a mean depletion of 1.4‰ was observed for both allochthonous oceanic and riverine POM (Mann-Whitney, *Z* = 1.96, p = 0.049). In contrast, no radical changes in δ^{15} N values were observed between the 2 sampling periods for SOM or benthic detritus. No general trend was seen for the other sources, with an increase in oceanic POM δ^{15} N values, and a decrease in riverine POM and primary producers in March as compared to August (Table 2). While reef SOM C:N ratios remained the same (Kruskal-Wallis, H = 2.08, p > 0.05), benthic detritus C:N ratios were significantly higher in August (22.1 ± 3.0) than in March (17.0 ± 2.3; F = 14.82, p < 0.01). The trend was similar for macroalgae (slightly higher C:N ratios in August than in March), but the opposite for oceanic and riverine POM, cyanobacteria mats and seagrass (i.e. slightly higher C:N ratios in March than in August).

Since δ^{15} N values of reef water POM and potential benthic sources both presented small variations, reef



Fig. 6. δ^{13} C values and C:N ratios of reef water particulate organic matter (POM) and potential sources sampled in (a) August 2006 (cold-dry season) and (b) March 2007 (hot-wet season). Mean values (symbols) for reef water POM, sedimentary organic matter (SOM) and benthic detritus are presented for each station (1–6). Site and geomorphological zone abbreviations as in Table 1. cyanob.: cyanobacteria. Boxes: SD; boxes with dotted lines are reef primary producers. Black verticle box illustrates typical range of phytoplankton (7:1 Redfield ratio)

water POM origin in August 2006 and March 2007 was investigated using a combination of δ^{13} C values and C:N ratios (Fig. 6). Benthic detritus associated with living macroalgae was seen to contribute little to reef water POM in August 2006 (Fig. 6a). Major reef water POM sources were reef SOM and oceanic POM. The reef SOM contribution was much lower in March 2007 than in August 2006. In March 2007 benthic detritus generally dominated reef water POM composition. Interestingly, reef SOM spatial patterns were similar in both August 2006 and March 2007. The benthic detritus contribution to SOM was always higher at PA stations, especially at the PA back-reef station in March 2007 (Fig. 6b). The highest contribution of allochthonous oceanic material to reef water POM was observed at the TE inner-reef flat station in both seasons. Riverine POM showed no significant contribution to reef water POM during either sampling session.

Trace metal abundance in SOM

Sediment trace-metals distribution determined in March 2007 at the TE, PA and CM inner-reef flat and backreef stations is presented in Figs. 7 & 8. Metals selected as erosional input tracers (Fe, Ti, Cr, Ni) showed a generally south to north trend, with higher levels in southern TE stations than in the middle and northern PA and CM stations (Fig. 7). This trend was more noticeable on reef flats, where significantly higher Fe, Cr and Ti concentrations were measured at TE than at CM. Considering the entire reef area, Fe and Ti abundances were also significantly higher at the TE inner-reef flat station than at any other station. Correlations between organic-matter δ^{13} C values and metals abundance in sediment cores were observed at the TE stations (pooled inner-reef flat and back-reef samples; Fig. 8a). The linear relationships between SOM δ^{13} C values and

Ti $(r^2 = 0.914, p = 0.003, n = 6)$, Cr $(r^2 = 0.840, p = 0.010, n = 6)$ and Fe $(r^2 = 0.876, p = 0.006, n = 6)$ concentrations, respectively, had negative slopes, with SOM δ^{13} C values decreasing (from -16.3 to -17.7%), inversely with trace metals levels. Such relationships were not observed at the other stations.



Fig. 7. Trace metal (Fe, Ti, Cr, Ni) levels in reef sediments sampled in March 2007. Black bars: mean ± SD of 3 replicates per station; grey bars: limit of detection (LOD). ANOVA (*F*, p-value) and Kruskal-Wallis (*H*, p-value) tests for spatial effect. Statistical significance: *p <0.05, **p <0.01, ns: not significant. Stations labeled with same letters belong to homogeneous groups. Site and geomorphological zone abbreviations as in Table 1





Fig. 8. (a) Linear regression analysis between δ^{13} C values of sediment organic matter (SOM) and Fe, Ti and Cr levels in reef sediment samples. Ti (r² = 0.914, p = 0.003, n = 6), Cr (r² = 0.840, p = 0.010, n = 6) and Fe (r² = 0.876, p = 0.006, n = 6). (b) Spatial distribution of Cu and Zn levels (mean ± SD, 3 replicates per station) on the La Saline reef. Grey bars: limits of detection (LOD). Site and geomorphological zone abbreviations as in Table 1

Anthropogenic input tracers (Cu, Zn) did not show a similar south to north trend (Fig. 8b). Cu and Zn concentrations were of the same order of magnitude (ANOVA, F = 0.05, p = 0.832) and were highly correlated ($r^2 = 0.996$). Since an influence of rainfall was detected only at the PA and CM stations (with an effect on both POM δ^{13} C and δ^{15} N values; see 'Spatiotemporal variation in reef POM isotopic composition') we investigated any possible geomorphological effect at these stations (e.g. back-reef versus innerreef flat). Significantly higher Cu and Zn concentrations were found in the back-reef than in the inner-reef flat in the northern part of the reef (Kruskal-Wallis, H(1, N = 24) = 4.38, p = 0.036).

DISCUSSION

Spatio-temporal variability in reef POM sources

Sinking or suspended POM is often heterogeneous, originating from different sources (e.g. fecal pellets, algal cells, SOM), and it is difficult to trace the origin and fate of this organic matter as it traverses the water column. According to Wissel et al. (2005), δ^{13} C values and C:N ratios are an efficient way to determine the main origin of water POM. Since coral reef phytoplankton production is considered negligible compared to that of other primary producers (Charpy-Roubaud et al. 1988), water POM in La Saline reef mainly comprised oceanic phytoplankton, autochthonous SOM and detritus (found at the sediment-water interface). The annual trend in isotopic composition of reef water POM revealed marked spatio-temporal variations. Cold-dry and warming periods were characterized by a general ¹³C enrichment and ¹⁵N depletion. During those cold periods, reef water POM δ^{13} C values were strongly correlated with oceanic chl a concentration at southern TE stations, and, to a lesser extent, at the PA inner-reef flat (Table 1). POM δ^{13} C values increased with chl a concentration, reflecting the ¹³C enrichment of long-term phytoplankton growth (Goericke et al. 1994, Laws et al. 1995) and a significant contribution from oceanic phytoplankton to reef water POM at southern stations. No relationship between reef water POM δ^{13} C values and oceanic chl *a* concentration was found at the PA back-reef and northern CM stations, showing that, as water residence time on the reef increases, the contribution of oceanic phytoplankton to reef water POM decreases, probably due to rapid oceanic POM removal by consumers such as coral polyps, sponges and actiniarians

(Sorokin 1993, Lesser 2006). In the northern part of the reef, the main source of reef water POM was reef SOM (Fig. 6), where the δ^{13} C value was enriched by ~2.3‰. This suggests important bentho-pelagic (sed-iment-water column) coupling processes inside this reef area, and shows that factors driving the ¹³C seasonal variability greatly differed between reef sites.

While oceanic POM and SOM were major contributors to the reef water POM composition in the colddry season, an important generalized increase in benthic detritus contribution was observed in the hot-wet season, based on both $\delta^{13}C$ values and C:N ratios. This higher detrital contribution was concurrent with the increase in benthic community productivity and respiration observed in reef sediments at that time of year (Taddei 2006), and is therefore likely to occur throughout the entire hot-wet season. A similar spatial pattern was observed in the hot-wet season, with POM isotopic and elemental composition at middle and northern stations being more influenced by the benthic compartment. Reef POM δ^{13} C values at southern stations were slightly depleted as compared to the other stations, but $\delta^{13}C$ values were not driven by oceanic phytoplankton input, probably due to both low biomass (mean chl a of 0.07 mg m^{-3}) and low advective flow, which is due in turn to low swell amplitude affecting the island shelf at this time (Gabrié & Montaggioni 1986).

Seasonal variations in reef water POM $\delta^{15}N$ values also reflected the differing sources over the spatiotemporal scale. Detritus that dominated reef water POM composition in March 2007 is the most ¹⁵Nenriched of all potential sources $(7.5 \pm 1.1\%)$, explaining the positive deviation from annual mean in reef water POM δ^{15} N values observed during the hotwet and cooling periods. The $\delta^{15}N$ value of oceanic POM, which contributed significantly to reef water POM composition at southern stations in August 2006, was lower $(4.7 \pm 0.3\%)$, explaining the decrease in reef water POM $\delta^{15}N$ values observed during the cold-dry and warming periods. The southern part of the reef therefore benefits from newly fixed or recycled N inputs from oceanic primary production during the cold-dry and warming periods. This is not the case in the northern part of the reef, where the water column is enriched in benthic organic matter in either season.

Tracing allochthonous inputs to the reef

Severe rainfall associated with tropical cyclone Gamede provided an ideal opportunity to investigate intense river discharge effects on La Saline reef. Trace metals derived from volcanic-detrital minerals (Ti, Fe, Cr and Ni) showed a general decrease from the southern TE inner-reef flat to the northern CM inner-reef flat in sediments sampled in March 2007. Significantly higher concentrations of Ti and Fe (2.1 ± 0.4 and 13.7 \pm 1.2 mg g⁻¹ of dry sediment, respectively) were measured at the TE inner-reef flat than at the other stations (1.0 \pm 0.4 and 6.9 \pm 2.7 mg g⁻¹ of dry sediment, respectively), including the TE backreef. This suggests that an erosion-derived sedimentary input occurs in the southern part of the reef, probably from the Trois-Bassins stream (tidal currents along the reef slope have a dominant component to the north-west), and obviously most strongly during the rainy season. Inhibited acetylcholine esterase (AChE) activity levels were detected in the tissue of the benthic deposit-feeder Holothuria leucospilota (Echinodermata) at TE during the hot-wet season, but were not detected elsewhere in the reef (Kolasinski et al. 2010), further supporting that hypothesis. Indeed, lower AChE activity levels indicate a possible presence of insecticides, probably from land-based market-gardening operations. Ti, Fe and Cr abundances were observed to increase with decreasing SOM δ^{13} C values at the TE stations, suggesting ¹³C-depleted riverine POM input. The combination of these elements may therefore be useful as a further small-scale tracer to quantify inputs of terrigenous matter to the coastal environment.

A significant decrease in POM δ^{13} C values with rainfall was noted at the PA back-reef and, to a lesser extent, at the CM stations during the hot-wet and cooling periods, suggesting input of organic matter of terrestrial origin or a higher contribution of benthic detritus. The decrease in POM δ^{13} C values with rainfall in the PA back-reef was concurrent with an increase in $\delta^{15}N$ values. Due to submarine groundwater discharge, nitrate pulses up to $1.5 \,\mu\text{M}$ are frequently detected at this station during the hot-wet season (Taddei 2006). The δ^{15} N of groundwater nitrate was measured in March 2009 in the coastal area of La Saline. Values were higher than 7.2‰ (P. Cuet unpubl. data), reflecting contamination by human or animal waste (Wassenaar 1995, Aravena & Robertson 1998) that originates at a higher altitude in the reef watershed (Payet et al. 2010). The trend in POM $\delta^{15}N$ values at the PA back-reef therefore presumably reflects a nitrate input from ¹⁵N-enriched groundwater.

The 2 PA stations, based on SOM isotopic and elemental composition in both seasons, and characterized by a relatively high contribution from benthic detritus, were identified as outliers (Fig. 6). These characteristics were particularly marked in the backreef zone where the SOM reservoir presented the most elevated δ^{13} C values (-13.5 ± 0.2 and -14.4 ± 0.6% in August 2006 and March 2007, respectively) and C:N ratios (11.7 \pm 3.8 and 15.6 \pm 2.5 in the same 2 mo, respectively), as well as the highest δ^{15} N values $(3.9 \pm 0.2\%$ and $3.9 \pm 0.1\%$ in the same 2 mo, respectively). Groundwater influence has been previously suggested to enhance benthic primary production in the northern back-reef sections (Mioche & Cuet 1999, Taddei 2006). Enriched δ^{15} N values in primary producers measured in both wet and dry seasons in other coral reef environments have been attributed to larger volumes of soluble anthropogenic-derived nutrients (Lapointe et al. 2004, Derse et al. 2007, Lin et al. 2007).

Higher combined Cu and Zn concentrations were recorded in the back-reef zone (mean $109 \pm 87 \mu g g^{-1}$ of dry sediment) than on the reef-flat (40 \pm 18 µg g⁻¹ of dry sediment) at the CM and PA stations. Concentrations tended to be highest at the PA back-reef, further supporting the idea of a groundwater discharge of anthropogenic material at the PA backreef. Although no POM δ^{15} N increase with increasing rainfall was observed at CM, groundwater influence at the CM back-reef showed a significant decrease in POM δ^{13} C values, and increased Cu and Zn concentrations, with rainfall. It is obvious that groundwater discharging at PA must further affect the CM backreef due to the northward current along shore. This provides an explanation for the strong sediment community heterotrophy observed by Taddei (2006) in CM back-reef sediments. Heterotrophy, also observed on the PA inner-reef flat, was explained by the presence of a natural channel at the PA reef front (Mioche & Cuet 1999), which temporarily drives POM-enriched back-reef waters to the open ocean depending on swell amplitude (Cordier 2007, their Fig. 2.1). Such changes in the distribution of water POM have been previously related to hydrodynamic seasonal changes in the reef and offshore waters (Umezawa 2004).

Effect of cyclone Gamede

Nitrogen availability and light intensity have been suggested as the main factors controlling phytoplankton abundance in oceans (Kana & Glibert 1987, Moore et al. 1995). Chl *a* concentration recorded at ~10 km offshore of Reunion Island's west coast was higher during the cold-dry and low-irradiance season (from July to October, mean 0.10 mg m⁻³), and increased with decreasing water temperature. Upwelling of nutrient-rich water due to seasonal upward displacement of the thermocline is a wellknown factor influencing ocean productivity; it may have stimulated phytoplankton communities during the cold-dry season (Falkowski et al. 1991, McGillicuddy et al. 1998). Tropical cyclone Gamede (22 to 28 February 2007) significantly impacted oceanic phytoplankton biomass, as an increase of 80% in chl a concentration was recorded the following month. Chl a enhancement, frequently observed following cyclone events, is generally linked to both terrestrial material delivery (Davies & Hughes 1983, Fabricius 2005) and the upwelling caused by evaporative heat loss from the water to the atmosphere during the thermal evolution of weather systems (Babin et al. 2004, Walker et al. 2005).

We measured a small depletion in δ^{13} C (-1.4‰) and $\delta^{15}N$ (-1.2‰) values in riverine POM 20 d after the cyclone event. This can be attributed to an increased contribution of C3 terrestrial plant debris and soil organic matter mobilized via surface waters. Oceanic water POM exhibited similarly depleted δ^{13} C values (-1.3%), suggesting a possible influence of ¹³C-depleted terrestrial input into coastal waters. However, oceanic POM ¹³C depletion may also reflect isotopic changes in phytoplankton community structure associated with early-blooming populations of diatoms and cyanobacteria that preferentially fix the lighter isotope (France 1995, Rissik et al. 2009). Unlike riverine POM, the $\delta^{15}N$ values of ocean-water POM were slightly higher in March 2007 than in August 2006 (5.2 \pm 0.4‰ and 4.7 \pm 0.3‰, respectively). Both values are typical of pelagic particulate N derived from phytoplankton (Sachs et al. 1999). We conclude that upwelling of ¹⁵N-enriched deep-water masses (Montoya et al. 2002, Reynolds et al. 2007) during cyclone passage was the major factor benefiting phytoplankton communities.

The distribution of trace elements inside the reef showed that the southern reef flat (TE) was the area most affected by runoff. Hence, the more important decrease in water POM δ^{13} C values observed at the more northerly CM stations (-2.1‰) as compared to the TE stations (-0.6‰) 10 d after cyclone Gamede could not be attributed to a significant input of terrestrial organic carbon. The contribution of terrestrial organic matter to reef organic matter reservoirs (water POM and SOM) remained minimal at TE in March 2007, the month following the cyclone event (Fig. 6). This result is not surprising with respect to reef water POM, considering the short residence time of the water in the reef ecosystem (10 h 30 min; Cordier 2007) and the hydrodynamic circulation in the open ocean surrounding Reunion Island, which rapidly exports water masses northward (Gabrié & Montaggioni 1986). Umezawa et al. (2008) also observed only a minor terrestrial POM contribution from an adjacent river to SOM reservoirs in the Shiraho fringing reef (Japan). This may reflect rapid organic matter turnover and incorporation into benthic food webs.

The significant decrease in water POM δ^{13} C values observed in April 2007, about 10 d after the passage of cyclone Gamede, at the PA inner-reef flat (-3.4 ‰) and CM stations (-2.1%), was therefore most likely due to export of SOM and benthic detritus from the system during the cyclone event. Lapointe et al. (2006) observed that physical removal or burial of macroalgae was the most pronounced ecological effect of 2 hurricanes on Florida's reefs. We hypothesize that the sources of water POM in these northern areas of the reef had temporarily switched from recently formed macroalgae-derived detritus to oceanic plankton, whose biomass was twice as high as it is usually during that time of year. These strong climatic events may be important to coral reef functioning, as a pathway for evacuating residual organic matter accumulated during high productivity periods. However, this effect was less pronounced in the mid back-reef section, which was subject to groundwater discharge and benthic detritus accumulation. The reef water POM C:N ratio increased by factors of 3, 4 and 7 at the TE, PA and CM stations, respectively, 1 mo after cyclone passage, and decreased throughout the reef afterwards, except at the PA back-reef station. We have not yet determined the source of this significant input at this station, as POM C:N ratios were up to 75, much higher than those measured in living macroalgae (≥ 40).

Overall, the Gamede cyclone effects on reef water POM were brief, as POM stable isotopic and elemental composition tended to return to normal 3 mo later at most sites. Previous studies on the impacts of hurricanes on coral reef substrate and benthic communities have documented either immediate consequences of high magnitude and speed, or minimal and inconspicuous impacts (e.g. Bythell et al. 1993). The variability of effects of such weather events has been associated with either natural variability in reef structure, presence of other stressors or the scale of observation (Bythell et al. 2000, Gardner et al. 2005). We suggest that high turnover of organic matter, low biomass of animals (Taddei 2006) and rapid watermass circulation probably make this geologically young system fairly resistant to physical disturbances.

The short-lived nature of the response to the cyclone perturbation suggested that extreme events are not always the principal factor in causing the long-term degradation of ecosystems. Nutrient enrichment of coastal ecosystems from human sources has been suggested as factor that can interfere with recovery of reefs from physical perturbation (Bell & Elmetri 1995, Connell 1997, Gardner et al. 2005). The present study highlights the possible impact of chronic groundwater discharge at the PA mid-reef section, rather than any event-derived point source (riverine input) during the rainy season. The anthropogenic influence upon the PA back-reef is of serious concern. Since additional organic matter produced at this station does not appear to be exported out of the reef ecosystem, as it was in other parts of the reef during the intense climatic event, this ongoing influence may permanently alter community structure and biodiversity over time.

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