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Chemical and biological characteristics of Albion reef in the South-West of Mauritius Island with special reference to primary production and N₂ fixation of benthic substrata

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Abstract

The role of heterotrophic bacteria, pico-cyanobacteria and benthic cyanobacterial mats was assessed in the cycling of organic carbon and nitrogen in the Albion lagoon, Mauritius. Surveys and sampling for biological and chemical parameters were undertaken at three locations along one northern (T1) and one southern (T2) transect perpendicular to the shore. Low levels of nutrients showing a typical oligotrophic condition promoted by a rapid water exchange with oceanic waters characterized this lagoon. A general trend in zonation was observed from the shore with seagrass beds followed by sand and rubble, with cyanobacteria forming mats. Coral cover increased towards the reef crest with dominating *Porites* spp. and *Acropora* spp. colonies, however coral cover was not higher than 20%. Heavy grazing of pico-plankton was detected in the middle of the lagoon between T1 and T2. *In situ* incubations on different substrata (coral rubble, cyanobacterial mats and surrounding seawater) revealed maximum primary production and nitrogen fixation rates of cyanobacterial mats, with respectively 1-2 and up to 2 orders of magnitude higher levels found than other substrata. This study showed that cyanobacteria mats and coral rubble substrata constituted an important source of new nitrogen for the whole lagoon.

Keywords: Coral reefs, cyanobacteria mat, picoplankton, primary production, nitrogen fixation

Introduction

The oxy-photosynthetic bacteria, commonly known as cyanobacteria, play an important role in coral reef ecosystems. They occur in the planktonic form in the water column (Charpy, 1996; Charpy & Blanchot, 1996; Casareto *et al.*, 2006; Sadally *et al.*, 2015). In the benthic realm they attach on the surface of sediments (Crosbie & Furnas, 2001; Tribollet *et al.*, 2006). They are also found attached to sedentary organisms anchored to the seafloor (Yamamuro, 1999; Iizuni & Yamamuro, 2000), as symbionts in reef-dwelling organisms (Thacker

& Starnes, 1993; Hinde *et al.*, 1994). They are mostly observed forming microbial mats in coral reef ecosystems worldwide, including Tikehau atoll (French Polynesia), New Caledonia, the western Indian Ocean in Zanzibar (Tanzania), La Reunion Island and Okinawa, Japan (Abed *et al.*, 2003; Charpy *et al.*, 2007; Bauer *et al.*, 2008; Charpy *et al.*, 2010, Charpy *et al.*, 2012).

Charpy *et al.* (2012) have reviewed the role of cyanobacteria in coral reef ecosystems. They occur as part of the reef (microbialites), inside (endoliths), and

above (epiliths and epiphytes) corals. Their functional roles include assistance in building and eroding the reef, contribution to primary production, provision of organic materials for planktonic and benthic heterotrophic organisms, and nitrogen enrichment in the ecosystem. Although cyanobacteria have been recognized to be important on coral reefs worldwide, very limited investigations (Réunion and Zanzibar islands) have probed the role of cyanobacteria mats on coral reefs of the western Indian Ocean islands, especially in a changing global climate scenario where coral reefs are facing drastic decline.

Mauritius is an island nation off the coast of the African continent in the southwest Indian Ocean, about 900 kilometers east of Madagascar. In addition to the island of Mauritius, the Republic includes several islands such as St. Brandon, Rodrigues and the Agalega Islands. Mauritius is part of the Mascarene Islands, with the French island of Réunion 200 km to the southwest, and the island of Rodrigues 570 km to the northeast. The richness of Mauritius in coral reefs was observed and a first survey indicated a high abundance of healthy and highly diversified coral reefs. This study aimed to assess the spatial distribution of fundamental physico-chemical parameters, and the biological distribution on a coral reef around Mauritius Island. The study focused mainly on the role of

heterotrophic bacteria, pico-cyanobacteria, benthic cyanobacterial mats and other microbes in organic matter cycling, nutrient dynamics, and the role of nitrogen fixation as a source of new production on a coral reef. For these purposes, a representative coral reef located in Albion (Northwest coast of Mauritius) was selected. In previous surveys at Albion, important areas covered by coral rubble were found, and mats of cyanobacteria of different sizes were frequently seen. It is well known that coral rubble constitutes a microhabitat for epilithic and endolithic algae, among which the filamentous cyanobacteria are dominant. For this study, two transect lines were established from the coast to the reef crest, and different physico-chemical parameters and biological zonation was assessed. Moreover, coral rubble, cyanobacteria mats, and the overlying seawater was incubated to measure their primary production and N_2 fixation rates. As N_2 fixation is a process that requires an anoxic environment for efficient functioning of Nitrogenase (the enzyme which mediates the N_2 fixation chemical reaction), high rates of N_2 fixation can be expected during the night. However, some cyanobacteria possess specialized cells called heterocysts, which are N_2 fixation sites and can fix N_2 even during the day. The study aimed to compare nighttime N_2 fixation rates with that of a 24h period in order to assess the rates of N_2 fixation during the light period. Moreover, using the C/N ratio, and

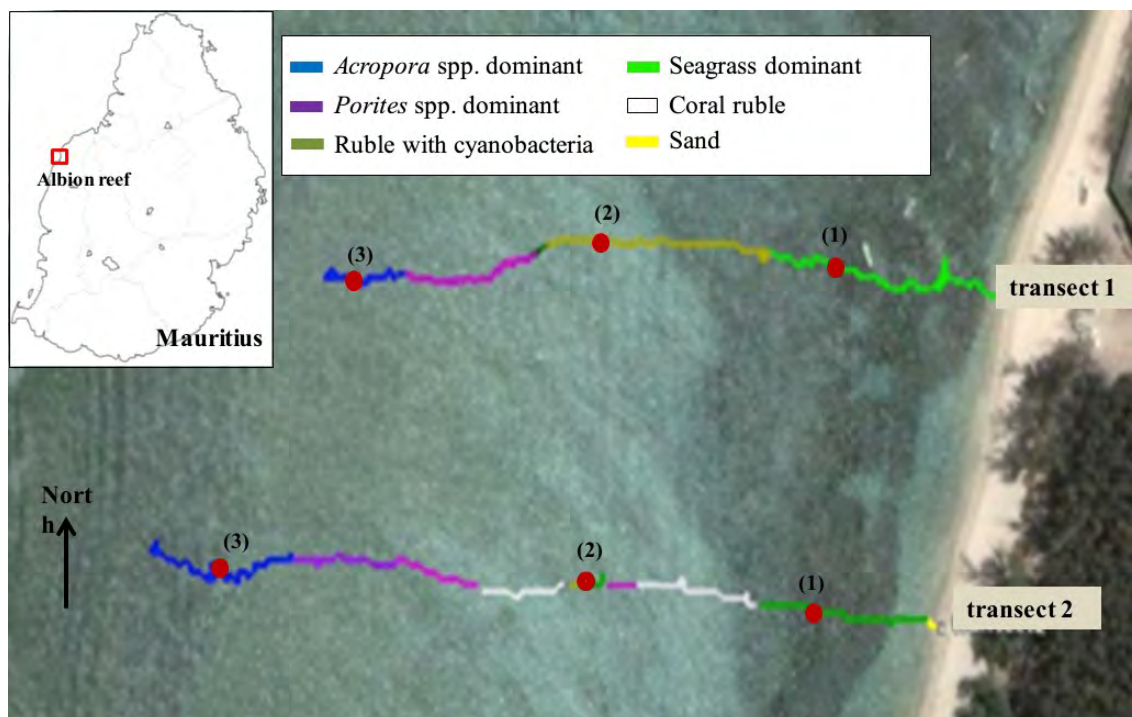


Figure 1. Transects 1 and 2 with substrate zonation and the position of sampling points (1), (2) and (3) along transects in Albion lagoon.

primary production rates, it was intended to calculate the amount of carbon which is possible to fix based on measured N_2 fixation rates. On the bases of these data, it was attempted to estimate which benthic community contributes more to the nitrogen supply at the selected reef site.

Material and Methods

Study site and survey

Albion reef is located on the western side of Mauritius. It covers an area of about 1 km². The depth of the lagoon in the center is around 0.7 m during low tide. For this study, two transects lines were established on 19th March 2008; transect 1 (northern transect) (T1) and transect 2 (T2) (southern transect) from the coast towards the reef crest (Fig. 1). Moreover, in April of 2011, a detailed transect from near shore towards the reef crest covering 260m was performed. Using a quadrate of 1m², the distribution of the main substrates were recorded as sand and coral rubble, and benthic organisms as coralline algae, sea grasses, algae, and corals. Depth along the transects was also recorded. Samples for determination of chemical parameters including pH, total alkalinity (TA), nutrients, particulate organic carbon (POC), and biological parameters such as bacteria, cyanobacteria, autotrophic nanoflagellates (ANF) and heterotrophic nanoflagellates (HNF), were taken at three different locations along the transects (Fig. 1).

Sampling point 1 (closest to the beach) was characterized by seagrass beds, whereas point 2 (intermediate) and 3 (reef crest), were characterized respectively by rubble with cyanobacteria mats, and increasing coral coverage. A fixed station located between the transects was chosen to register physical parameters such as light, currents and temperature using loggers which were set-up *in situ*.

Sampling

Water samples for nutrients, alkalinity and particulate organic carbon (POC) were taken simultaneously at the three selected points along the transects. Samples for alkalinity were collected in 100ml polycarbonate bottles (detergent-washed) and kept cool until analysis after filtering with a syringe filter (0.45 μ m) to remove plankton and other particles. For nutrients, seawater was collected in acid-washed 100ml polycarbonate bottles and stored at -20 °C until analysis. For POC measurements, one litre of seawater was filtered through pre-combusted (500 °C during 4 h.) GF/F (Whatman) filters and kept at -20 °C until measurement. pH was measured immediately after water sampling. For bacteria, pico-cyanobacteria, HNF and ANF observation and counting, 50 ml seawater samples were taken in sterile 50 ml corning tubes and immediately fixed using glutaraldehyde solution (2% final concentration).

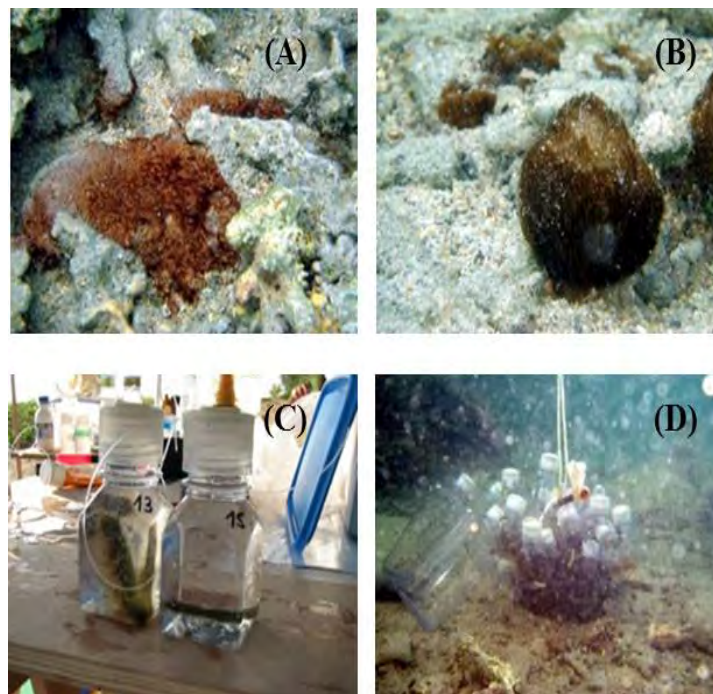


Figure 2. (A) Cyanobacteria mat from Transect 1 (*Lyngbya* spp dominated); (B) Cyanobacteria mats from Transect 2 (*Oscillatoria* spp dominated); (C) Coral rubble in the incubation bottle; (D) Aspect of *in situ* incubation at Albion lagoon.

Chemical and biological measurements

pH was measured using a pH meter (ORION 290 A plus ion meter and 9172BNWP electrode) calibrated with NIST (NBS)-scaled buffer solutions (Mettler pH 6.865 and 4.008 buffers) at 25°C in a temperature-controlled water bath (Yamato Coolnics circulator CTA400). Total alkalinity was measured by potentiometric titration (Radiometer TIM850 and GK2401C pH electrode) with computation using the Gran plot method (Stumm & Morgan, 1981). Reproducibility of the TA measurement was $\pm 2 \mu\text{mol kg}^{-1}$ (1σ , $n = 10$). A working seawater standard was used for the calibration of the TA measurement. This seawater was taken from the East China Sea (26° 40.660'N, 127° 04.200'E) where there was no effect of coastal contamination, and analyzed precisely for TA with certified reference material for oceanic CO₂ measurement (CRM Batch # 50), distributed by A. Dickson of the Marine Physical Laboratory, University of California, San Diego. Nutrients were determined using an autoanalyzer (TRAACS-2000: BRAN+LUBE) according to Hansen & Koroleff (1999). Nitrate was determined by subtracting the values of nitrite from nitrate + nitrite. The detection limits were 0.052 μM for NO₃ + NO₂, 0.01 μM for NO₂, 0.020 μM for NH₄ and 0.020 μM for PO₄. Reproducibility of nutrient analysis was $\pm 0.5\%$. For POC measurements, GFF filters were dried prior to analysis, acidified by HCl fumes to remove inorganic carbon, and dried again

before analysis. The measurement was done using an N/C analyzer (Sumi-GraphNC-90A). The analytical precision (standard deviation) for POC measurements was less than 3%. Bacteria and pico-cyanobacteria were collected onto black 0.2 μm polycarbonate filters (Millipore) by filtering 5 to 10 ml aliquots previously stained with DAPI (Porter & Feig, 1980). Filters were mounted on glass slides. Bacteria were counted under ultraviolet excitation, and pico-cyanobacteria were counted under blue excitation with an epifluorescence microscope (Nikon, Eclipse). For HNF and ANF, 10 ml samples were filtered onto 0.8 μm black polycarbonate filters, mounted on a slide glass and observed under blue excitation on the same epifluorescence microscope.

In situ incubation experiment for measurements of primary production and N₂ fixation on coral rubble, cyanobacterial mats and seawater

Coral rubble and cyanobacterial mats were collected along the two transects and brought back to the shore where incubation bottles were prepared. Bottles were filled with seawater collected at the same points and incubated together with the substrates, or with only seawater (for control). For coral rubble, two small branches of similar size were placed into the incubation bottles (polycarbonate Nalgene bottles of 180 ml with septum cup). For cyanobacterial mats, aliquots of approximately 1 cm² of mats were placed into the

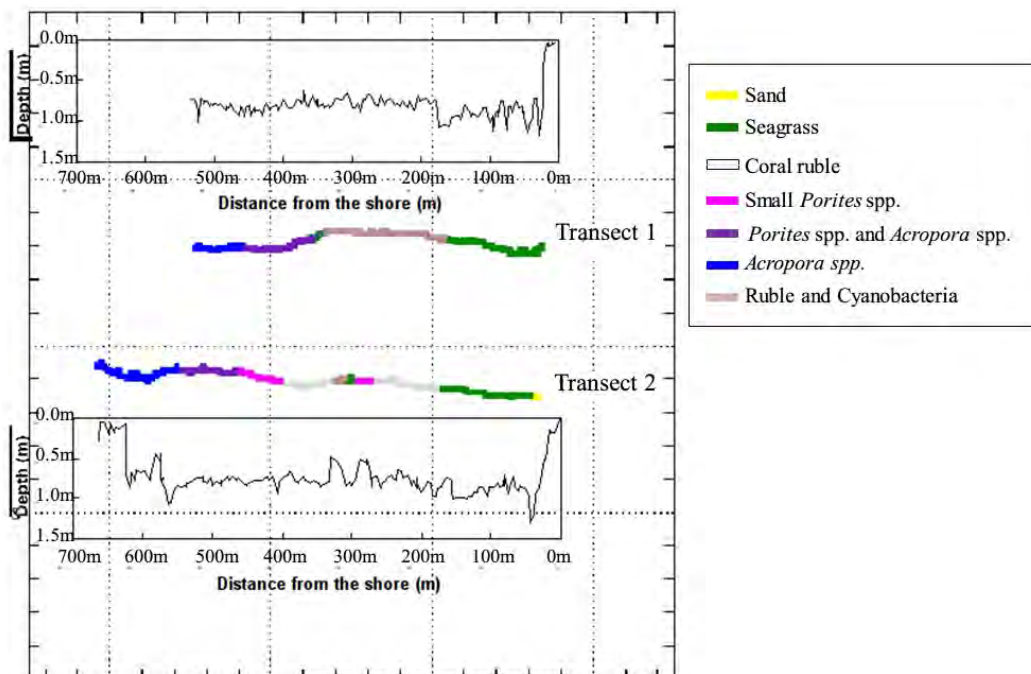


Figure 3. Transects 1 and 2 with substrate zonation and depth profile in Albion lagoon.

Table 1. Salinity, Alkalinity and nutrients measured along the two transects (T1 and T2) at the three selected sampling points (1), (2) and (3).

Transect	Salinity	Total alkalinity ($\mu\text{mol kg}^{-1}$)	POC ($\mu\text{g l}^{-1}$)	NO_3 (μM)	NO_2 (μM)	NH_4 (μM)	PO_4 (μM)	SiO_2 (μM)
1 (1)	34.506	2197.7	49.8	0.06	0.03	0.08	0.03	1.47
1 (2)	34.525	2200.2	43.6	0.09	0.02	0.12	0.03	2.16
1 (3)	34.535	2204	48.7	0.03	0.01	0.06	0.04	2.17
2 (1)	34.523	2201.5	50.6	0.06	0.03	0.11	0.03	1.72
2 (2)	34.529	2198.9	47.4	0.14	0.04	0.08	0.03	1.67
2 (3)	34.54	2206	37.6	0.05	0.01	0.06	0.03	2.08

incubation bottles (Fig. 2). Control incubations using only seawater from the sampling points were carried out using 2.3 L polycarbonate Nalgene bottles. All incubation bottles were enriched with ^{15}N and ^{13}C . For ^{13}C , ^{13}C -labelled sodium bicarbonate ($\text{NaH}^{13}\text{CO}_3$ – 100mg in 10 mL of deionized water – 99.9% ^{13}C) was added to the incubation bottles to obtain an enrichment of 11.5%. Subsequently, $^{15}\text{N}_2$ gas (99.8 atom %, Shoko Co. Ltd, Tokyo, JAPAN) was added with a gas-tight syringe to obtain an enrichment of 6.8%. Incubations were done *in situ* at ambient temperature and light conditions that were monitored using in situ loggers (MDSMkV/T and MDS-MkV/L, Alec Electronics). Incubation started at 18:00 and sampling was done at 06:00 (12 h dark incubation) and 18:00 (24 h) on the next day. Results were normalized per surface area (cm^2) and time (12 h or per day). Measurements of delta ^{13}C , delta ^{15}N , POC and PON were done using a mass spectrometer (DELTA plus Advantage, Thermofinigan Co.) equipped with EA1110 for measurements of POC and PON. Primary production was calculated according to Hama *et al.* (1993), and N_2 fixation rates were calculated using a modified method (Casareto *et al.*, 2008) based on Montaya *et al.*, (1996).

Results

Substrate zonation

Figure 1 shows the observed zonation along T1 and T2. A general trend of different types of substrate zonation along transects was observed: starting from the shore line, a seagrass bed was observed followed by an area of sand and coral rubble with some cyanobacterial mats and small patches of seagrass. Small colonies of *Porites spp.* alternated with rubble and/or small patches of seagrass. At 150m from the shore, the seagrass bed disappeared, and corals became dominant with *Acropora spp* colonies being the most dominant towards the reef crest. The coral coverage increased rapidly near the reef crest. Towards the reef crest, extensive colonies of *Porites spp.* forming micro-atolls, and small but abundant *Acropora spp.* colonies were observed. The presence of sand characterized T1 but at T2 coral rubble covered most of the central part of the lagoon.

Depth was measured along both transects by dragging sensors along with a GPS. The depth profiles are shown in Fig. 3. The average depth of T1 and T2 at the time of the survey (low tide) was 0.71 ± 0.13 m and 0.65 ± 0.25

Table 2. Abundance of microorganism determined along the two transects (T1 and T2) at the three selected sampling points (1), (2) and (3). Abundance is expressed in cells. ml^{-1} .

Transect	Heterotrophic Bacteria	Pico-cyanobacteria	HNF (heterotrophic nanoflagellates)	ANF (autotrophic nanoflagellates)
1 (1)	6.9×10^5	18.1×10^3	791	603
1 (2)	4.5×10^5	7.5×10^3	678	565
1 (3)	3.2×10^5	5.8×10^3	640	339
2 (1)	6.1×10^5	1.9×10^3	452	603
2 (2)	3.5×10^5	3.7×10^3	301	452
2 (3)	3.3×10^5	3.0×10^3	1696	1093

Table 3. Primary production and N₂ fixation (12h dark period, and 24h) of coral rubble, cyanobacterial mats and seawater at Albion reef.

	Site	Primary Production ($\mu\text{g C cm}^{-2}\text{ day}^{-1}$)	N ₂ fixation 12h (dark) (nanograms N $\text{cm}^{-2}\text{ day}^{-1}$)	N ₂ fixation 24h (nanograms N $\text{cm}^{-2}\text{ day}^{-1}$)	C/N	Organic carbon production by N ₂ fixation ($\mu\text{g C cm}^{-2}\text{ day}^{-1}$)	Contribution of N ₂ fixation to Primary Production (%)
<i>Coral rubble</i>	Transect 1	11.5	57.8	207.2	8	1.7	14.8
	Transect 2	11.6	145.3	237.1	11	2.6	22.4
<i>Cyanobacterial mats</i>	Transect 1	212.5	2712.8	9698.1	16	155.2	73.0
	Transect 2	278.2	6414.3	9481.7	14	132.7	47.7
<i>Seawater (plankton)</i>	Transect 1	7.8	nd	0.05	3	0.0002	0.002
	Transect 2	7.9	nd	0.03	5	0.0002	0.002

m, respectively. Seagrass beds were mainly observed in the deeper zone near the shore line whereas the highest coral coverage, dominated by *Acropora* spp. was observed near and on the reef crest at very shallow depth. Cyanobacteria mats were located mainly in the shallow zone in the middle of the transects attached to rocks and coral rubble. At the fixed station, the water current recorded between 15:00 and 17:00 on 19th March 2008 showed an average velocity of $1.3 \pm 0.3 \text{ cm.s}^{-1}$ in a southwest ($220^\circ \pm 24$) direction. Average light and temperature were $980 \pm 420 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and $28.3 \pm 1^\circ \text{C}$, respectively.

Chemical characteristic in the lagoon at Albion

Alkalinity ($2200 \pm 181 \mu\text{mol/L}$), pH (8.2-8.3) and salinity (34.5‰) did not differ from usual data for fringing reefs, or between the two transects during our short observation period (2 hours). It was difficult to detect differences in chemical signals in the water column caused by the coral reef community because of the rapid water flow. During the study, currents were relatively strong and there was no stagnant period even at low tide. Water exchange between the open waters outside of the reef and the lagoon seemed to be high at Albion. Total inorganic nitrogen ($\text{NO}_3 + \text{NO}_2 + \text{NH}_4$) varied from 0.1 to $0.26 \mu\text{M}$. PO_4 was also very low with less than $0.04 \mu\text{M}$, and Si showed the usual low levels found in coral reefs (Table 1). POC concentrations were also the same as the levels of other coral reefs, ranging from 37.6 to $50.6 \mu\text{g C l}^{-1}$.

Abundance of bacteria, picocyanobacteria, HNF and ANF

Results for abundance of microorganisms are shown in Table 2. T1 showed significantly higher abundance of pico-cyanobacteria, especially in the nearshore region. At T2, HNF and ANF showed higher abundance values near the reef crest. Overall, observed abundance of microbes in this study was similar to other fringing coral reefs (Casareto *et al.*, 2006).

Primary production and N₂ fixation of coral rubble, cyanobacterial mats and seawater

Table 3 shows the primary production and N₂ fixation rates measured during the *in situ* incubation experiment. Among the three studied substrata, the maximum primary production rates were found in cyanobacteria mats, being one order of magnitude higher than that of coral rubble and seawater. N₂ fixation rates were also up to 2 orders of magnitude higher for the cyanobacteria mats than that of coral rubble. On the other hand, N₂ fixation rates in sea water were very low and near negligible when compared to those of cyanobacteria mats, but may be important due to the vast area covered with reef waters compared to the small areas covered by cyanobacteria mats. N₂ fixation occurred at night but continued during the day with higher fixation rates during the day (24 h minus 12 h night). Based on the C/N ratio measured from each of the incubated substrates, the amount of carbon that can be fixed by new nitrogen (from N₂ fixation source) was calculated. Results indicate that endolithic

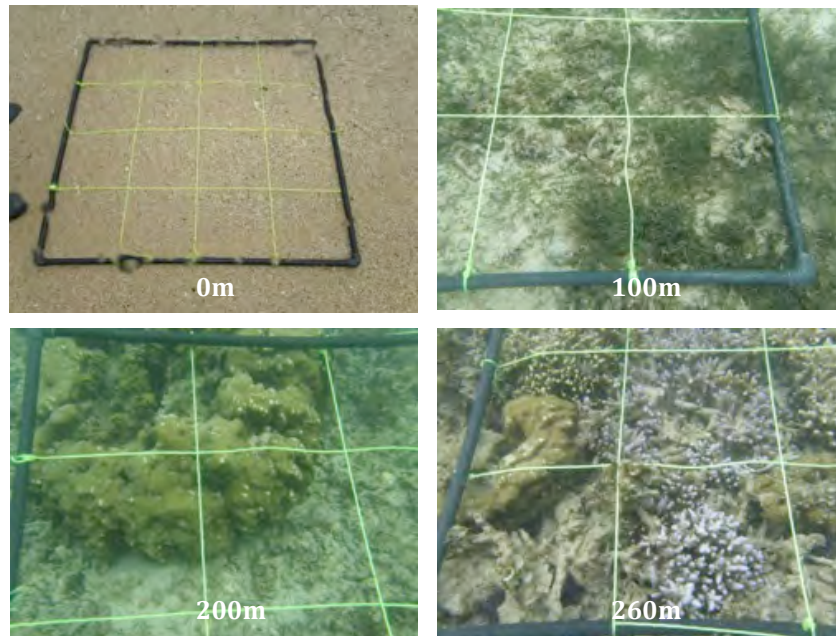


Figure 4. Aspects of benthic community at different points along the main transect in Albion lagoon. Distance from the shore line (in meters) is indicated for each quadrat image.

algae in coral rubble can supply from 15 to 22 % of their nitrogen requirements through N_2 fixation. However, in the case of cyanobacterial mats this rate is higher, and up to 73% of the nitrogen requirements can be supplied by N_2 fixation. These results indicate that such benthic substrata covered by cyanobacteria mats and coral rubble constitutes an important source of new nitrogen (production based on allochthonous nitrogen rather than recycled nitrogen).

Distribution and abundance of different substrates and benthic organisms at Albion reef from the shore to the reef crest

In April 2011, a detailed transect from the nearshore towards the reef crest of Albion covering 260m was

carried out. Using a quadrat of $1m^2$ (Fig. 4) the degree of cover (%) of 6 different benthic substrata (sand, coral rubble, coralline algae, sea grasses, algae, and corals) was recorded (Fig. 5). Sandy bottom dominated near the shore, followed by an area of high abundance of seagrass up to 100m from the shore. An area dominated by turf algae extended up to 120 m from the shore. Coral heads could be observed at 60 to 80m from the shore. However, the substrate was dominated by coral rubble with coverage ranging between 60 to 80% from 80 m towards the end of the transect. Coral coverage remained lower than 20% throughout the transect, and coralline algae was particularly scarce. Overall, a zonation ranging from seagrass- dominated towards algal- and rubble-dominated, with some coral heads present,

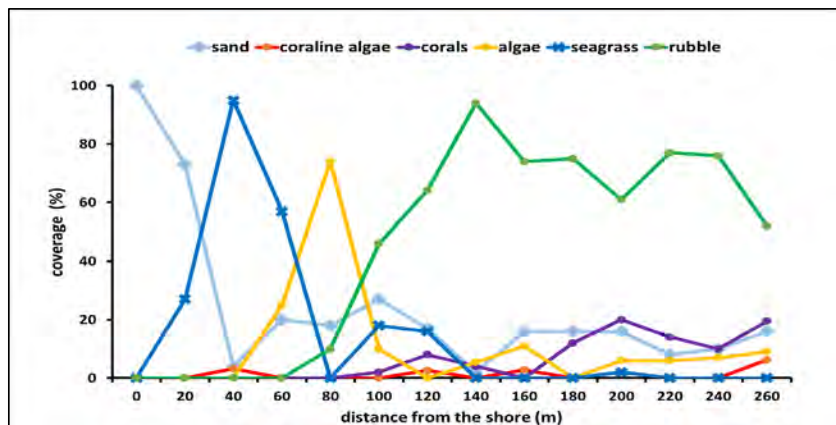


Figure 5. Percentage coverage of different benthic substrata and organisms along the main transect in Albion lagoon

increasing from the middle of the lagoon toward the reef crest, was observed at Albion.

Discussion and Conclusion

Clean oligotrophic waters characterize Albion lagoon. Until now very few data from this area were available. Pillay *et al.* (2011) studied coral culture adaptations at Albion providing a brief characterization of this reef. During the present survey, nutrient concentrations were slightly lower than other fringing reefs (Casareto *et al.*, 2006; Casareto *et al.*, 2008; Cuét *et al.*, 2011). At St-Gilles La Saline fringing reef in Réunion Island, total inorganic nitrogen (TIN) showed relatively higher concentrations varying from 1.07 to 1.24 μM in comparison to 0.1 to 0.26 μM values measured at Albion. This is due to important inputs of groundwater at La Saline reef (Cuét *et al.*, 2011). In Bora Bay of Miyako Island, and Sesoko reef, Sesoko Island, Japan, TIN was also slightly higher than at Albion (Casareto *et al.*, 2006; Casareto *et al.*, 2008). It seems that the open ocean waters influence Albion lagoon with a rapid water exchange rate, therefore no effect of ground water or fresh water could be detected. This is also supported by the salinity values that were higher than in other reefs. Other chemical parameters such as total alkalinity and POC fell well within values measured at similar reefs. Microbe abundance was also comparable to other reefs. An important difference between the abundance of pico-cyanobacteria at Albion (higher in T1 than in T2, and higher abundances of flagellates in T2 than in T1) was observed, indicating that significant grazing on picoplankton may occur between T1 and T2 resulting in increasing abundance of nanoflagellates that are picoplankton grazers. The prevailing water current from northeast to southwest also supports the conclusion that heavy grazing may occur between T1 and T2 in the near shore and mid-lagoon regions. Benthic primary production seems to be a very important feature on this reef. Production rates in coral rubble and cyanobacterial mats are very important and, considering the vast areas covered by coral rubble, it might be an important source of organic matter. N_2 fixation is also a very important feature to take into account in this lagoon. N_2 fixation can support the production of around 20% of endolithic algae associated with rubble and more than 70% of the production of cyanobacterial mats. Moreover, N_2 fixation was observed to occur over a 24 h period indicating that some cyanobacteria forming mats and living as endoliths in rubble may possess heterocysts and/or use other strategies to create an anoxic environment to protect the functioning of the Nitrogenase enzyme complex. N_2 fixation in this

reef may play a crucial role for the supply new nitrogen, as DIN is very scarce in the lagoon waters. Therefore, most of the lagoon organisms may depend on the new nitrogen supply from these two substrates. Distribution and abundance of benthic organisms and substrate in the lagoon showed that coral coverage is lower than 20%, being concentrating from the middle of the lagoon towards the reef crest. On the other hand, a vast area of coral rubble was observed. This result indicates that high coral mortality may occur in Albion mainly due to coral bleaching and/or diseases. However, the reef may have the potential to recover to some extent, since water exchange in the lagoon is rapid enough to prevent the formation of stagnant waters. Water heating may therefore not occur. The oligotrophic characteristics of this lagoon, together with the new nitrogen supply from N_2 fixation might be beneficial for coral health. This may help coral resilience if no new disturbances affect this reef.

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