

FRINGING REEFS OF REUNION ISLAND AND EUTROPHICATION EFFECTS. PART 1: LONG-TERM MONITORING OF TWO SHALLOW CORAL REEF COMMUNITIES

BY

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ABSTRACT

This study assesses changes in subtidal benthic communities on the largest reef flat in Reunion, *Saint-Gilles La Saline*, using several types of surveys. Temporal and spatial trends are documented over a 22 year period (1987-2009), thus spanning the 1998 and 2000s bleaching events. The most plausible explanations for the observed trends are proposed. We chose two sites that are characterized by two types of community and metabolism: (1) an oligotrophic site dominated by *Acropora* corals (Site-Toboggan), where sea-urchins are numerous and macroalgae rare and (2) a dystrophic site dominated by non-*Acropora* corals, mostly massive and submassive, where macroalgae abound and sea-urchins are almost absent (Site-Planch'Alizés). Results are presented in three parts : Part 1 : general trends of the communities, part 2 : primary producers, part 3 : living corals.

Part 1 presents three surveys. Survey 1 reports status and trends across the reef flats in 1993, 1996, and 2002, with all attached benthic components reported at the level of the species where possible. Survey 2 reports composition and changes in associated sedentary organisms such as sea urchins, holothurids, and the Pomacentridae fish *Stegastes*. Survey 3 focuses on the period 1998 to 2009 on permanent transects established in 1987 and monitored periodically, partly as a contribution to the Global Coral Reef Monitoring Network (GCRMN). In general, community structures at both locations remained stable, with primary producer coverage around 5% at Toboggan (T) and around 60% at Planch'Alizés (P). Living coral coverage averaged around 17% at both sites, but it was dominated by *Acropora* on Site-T (68%) and by massive corals on Site-P (88%). Regular echinoids were very abundant at T but almost absent from P, while the opposite was true for holothurids. The territorial damselfish *Stegastes* was of comparable abundance at both sites (<1 individuals per m²). There were large changes in coral cover in some zones, especially due to growth in *Acropora* from 1993 to 2002. On the two GCRMN permanent transects, 1999 and 2004 were turning points, so results are reported in three blocks: 1987-98, 1999-2003 and 2004-09. From 1987 to 1998 primary

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producers were inconspicuous on T transect but increased after that, suggesting abiotic conditions had become more favorable to algae. On the other transect (P-one), algae began to decline from 1999 and massive corals increased. Possible causes for these changes are discussed.

Key words: Coral reefs, benthic community, subtidal, stability, benthic primary producers, living corals, *Acropora*, sea urchins, holothurids, *Stegastes*.

INTRODUCTION

Forty years ago, reef workers and oceanographers claimed that the Indian Ocean was the least known of the tropical oceans (Behrman, 1981; Stoddart, 1973). A workshop held in Mombasa in 1997 put an end to this situation through releasing a synthesis of existing knowledge on major Indian Ocean coastal ecosystems (McClanahan *et al.*, eds, 2000). The widespread degradation of the coastal habitats and their associated ecosystem services was recently reported (Sheppard, 2000; Lindèn *et al.*, eds, 2002; Souter & Lindèn, eds, 2005; Obura *et al.*, eds, 2008; Wilkinson, ed., 2008; Burke *et al.*, 2011), especially as a result of previous bleaching events that occurred in 1998, 2000, 2005 and 2010.

In oceanic islands, highly dependent on coastal resources, increasing urbanization and economic development along the coastlines exacerbates ecological problems. The Mascarene Islands (e.g. Reunion, Mauritius and Rodrigues), belong to this category, suffering from fast human-derived disturbances, largely concentrated along their narrow coasts. It is difficult to estimate reef degradation since man's first arrival occurred in the 17th century. Gardiner (1936) collected corals from Mauritius and the St Brandon Bank during the Percy Sladen Expedition of 1905. Although some studies on specific taxonomic groups were undertaken in Mauritius in the intervening period, no further coral reef studies were made until the early 1970s. The studies by Pichon (1971), Faure & Montaggioni (1970, 1971a, 1971b, 1976), Faure (1974, 1975, 1977), Montaggioni (1978), Montaggioni & Faure (1980), Bouchon (1981, 1996), and Faure (1982) provided baseline data for the Mascarene coral reefs, appropriately just prior to the recent period of rapid demographic and economic development of these islands. The transformation of original coastal habitats for agricultural and urban use have accompanied these developments (Cheke, 1987) and contributed to reef degradation.

The mapping of the Mascarene reefs using satellite imagery indicates that the shallow reef ecosystems cover some 705 km² (Turner & Klaus, 2005). In Reunion, the fringing reefs are good test sites due to their small sizes (12 km² of shallow habitats) (Spalding *et al.*, 2001). Their study started from the 1970s, in particular the largest *Saint-Gilles La Saline* reef (See references herein). As a result of the increasing human population (1982: 515,814 inhabitants; 2010: 833,000 inhab., INSEE), urbanization and beach activities have greatly increased reef utilization, degradation and other impacts (Faure, 1994; Naim *et al.*, 2000). In addition, natural events, such as bleaching (McClanahan *et al.*, 2007) and extreme low tides, chronically affect the subtidal coral communities.

In Reunion, Guillaume *et al.* (1983) first recorded reef degradation. In some sectors of *Saint-Gilles La Saline*, *Acropora* assemblages died and macroalgae became dominant, and the reef degradation was attributed to water nutrient-enrichment *via* submarine groundwater discharge (Cuet *et al.*, 1988). Nowadays, in spite of local

degradation, the major part of the Reunion shallow reef flats are still dominated by *Acropora* populations (Bruggemann *et al.*, 2007; Faure, 2009), and Reunion still harbours original benthic communities mainly because it is often just outside the core area of major temperature anomalies (McClanahan *et al.*, 2007).

Phase-shifts from one persistent assemblage of species to another have become increasingly commonplace in many coral ecosystems. Coral reef science, monitoring and global assessments have focused mainly on producing detailed descriptions of reef decline, and continue to pay insufficient attention to the underlying processes causing degradation (Hughes *et al.*, 2010). Long term records on benthic assemblages are thus important to assess the resilience capacity of different communities and predict future changes (Done, 1997). Such data are rare. Using a combination of different datasets, this work focuses on the spatio-temporal evolution, from 1987 to 2009, of the major components of two major subtidal reef community structures, one classified as being in “good health” (ACR), one considered to be in “bad health” (MAS). These communities are respectively observed at Site-Toboggan (Site-T) and at Site-Planch’Alizés (Site-P).

The results will be presented in three distinct parts: (1) Part 1 (the present paper) discusses the spatio-temporal variation, from 1993 to 2002, and then the temporal variation from 1987 to 2009 experienced respectively by the two (ACR, MAS) community structures, in terms of zonation, patterns of primary producers, living and dead corals, echinoids, holothurids and sedentary species of fish; (2) Part 2 (Naim *et al.*, 2013a) deals with the temporal variation that affected the benthic primary producer community in ACR and MAS, in terms of dominant forms (cyanophytes, turfs, encrusting coralline, and macroalgae) and dominant species. The species composition, diversity and biomass of primary producers will be also analyzed at the two sites; (3) Part 3 (Naim *et al.*, 2013b) focuses on the temporal variation in coral abundance, diversity and coral species as bioindicators.

MATERIAL AND METHODS

General environmental setting and study sites

Island and climatic setting. Reunion (21°07'-19°40' S, 55°13'-61°13' E) is a steep volcanic island, regarded as not exceeding 2.1 mya in age (Bachèlery, 2000), and typified by a narrow shelf. Coral reef development is limited to the drier west and south coasts, forming a series of fringing reefs intersected by gullies that transfer terrestrial run-off during tropical storms (Montaggioni & Faure, 1980). Reefs are exposed to high wave energy conditions. During the cool season, from June to August, southeast trade winds (speed: 7-11 km.h⁻¹) generate southeast 1-2 m high swells that affect most of the coastline. During the hot season, from November to February, winds and swells are weak (wind speed: less than 6 km.h⁻¹; swell under 0.5 m high) but cyclones occur occasionally, generating whirlwinds of 120-250 km.h⁻¹ and swells of 4-11 m amplitude, although the west coast often escapes the harshest impacts. The reef is also affected by 3-5 m-high swells, mainly from the southwest, generated by polar depressions starting in the Marion Island region (in the Roaring Forties). Tides are semi-diurnal. The tidal range, greatly modified by swells, varies from 0.10 m (neaps) to 0.95 m (springs). Reunion held two world records for 3-days precipitation events: 3.24 meters that fell during January 1980 (cyclone Hyacinthe), and 3.93 m recorded in February 2007 (cyclone Gamède). Nevertheless, on the leeward side, mean annual rainfall is only 570 mm, and rain occurs mainly between

December and March. Mean costal sea surface temperature varies from 23.7 ± 0.3 °C in cold season to 27.7 ± 0.4 °C in hot season (Conand *et al.*, 2007), but can reach more than 31.0°C on the reef flats (Cuet, 1989a).

The *Saint-Gilles La Saline reef*, located on the west coast, is the most developed. It is typified by two subtidal reef flats of < 1.5 m depth, 250-550 m in width, and extending over 9 km. This nearly continuous reef rim is widest in the south and slightly deeper (**Fig.1**). Narrow passes occur where freshwater runoff periodically overflows the shoreline (Ermitage and Trois Bassins). Runoff occurs intermittently in the hot and wet season, but compared to other large Reunion reefs, such as those of Saint-Leu and Saint-Pierre, the *Saint-Gilles La Saline reef* can be considered to be moderately influenced by land-derived freshwater and sediment discharge, except when the island is crossed by the trajectories of strong cyclones, like Gamède (2007) (Kolasinski *et al.*, 2011). Sediments are predominantly of biogenic origin (Montaggioni, 1978, Gabrié & Montaggioni, 1982). From the coast seawards, the studied area refers to the inner reef flat. The outermost reef flat zone was not studied.

Water energy and physico-chemistry.

Average current speed varies between 0.3 and 1.0 km.h⁻¹ and tidal currents rarely exceed 2 km.h⁻¹ (Chazottes *et al.*, 2002). At the two studied sites, Toboggan (Site-T) and Planch'Alizés (Site-P), the flow of oceanic waters is dependent on swell, tide, wind, and topography (Cordier, 2007). In the north, Site-T receives a strong flux of oceanic waters, while further south, at Site-P, a depression in the reef front serves as an outlet of reef flat waters. Thus, at Site-P, benthic communities are bathed in waters that have transited over the reef flat (Conand *et al.*, 2002a). In addition, submarine groundwater discharge occurs near shore during low tides, and is drained by the Site-P outlet (Cuet *et al.*, 1988). Thus, P waters display very variable salinities and silicate concentrations (Cuet, 1989a, 1989b). Moreover, P waters have slower flow rates, higher mean and more variable sea surface temperature (Denis *et al.*, 2009). Thus, physico-chemical parameters of waters at Site-P greatly differ from those measured at Site-T (see discussions in parts II and III, Naim *et al.*, 2013a, 2013b).

Background

Selection of Site-Toboggan and Site-Planch'Alizés is based on four previous studies carried out on the *Saint-Gilles La Saline* reef flat: (1) Cuet *et al.* (1988) mapped hydrographic conditions, silicate concentrations and reef degradation from data obtained along the 17 radial lines on the entire reef flat; (2) Naim (2006) described the *Saint-Gilles La Saline* reef community structure through the analysis of the benthic components along the same 17 radial lines. The benthic community structure appeared to be typified by two distinct assemblages: (a) a dominant assemblage, labelled ACR, made up of branching *Acropora* corals, with a very low primary producer coverage, abundant sea urchins and a low number of holothurids; (b) an assemblage, labelled MAS, dominated by massive or submassive coral species, together with abundant cyanophytes and soft macro-algae, few sea urchins and abundant holothurids. In 1987, ACR assemblages were observed in reef-flat sites subjected to ingoing oceanic water flow (*inflow sites*), such as Site-Toboggan (Site-T) and Site-Petit Trou d'eau, while the MAS assemblages characterized subtidal areas where the reef flat waters come back to the ocean, after having passed over the reef

flat (*outflow sites*). These MAS assemblages were only observed at Site-Planch'alizés (Site-P) and Site-Club Med; (3 & 4) Mioche (1998), Mioche & Cuet (2002) and Mioche *et al.* (2002), in two studies conducted in 1996 and 2002 on community metabolism, demonstrated that communities at Site-Toboggan and Site-Petit Trou d'eau (inflow sites, ACR) have an autotrophic functioning, thus indicating a "healthy" state for the reef ecosystem.

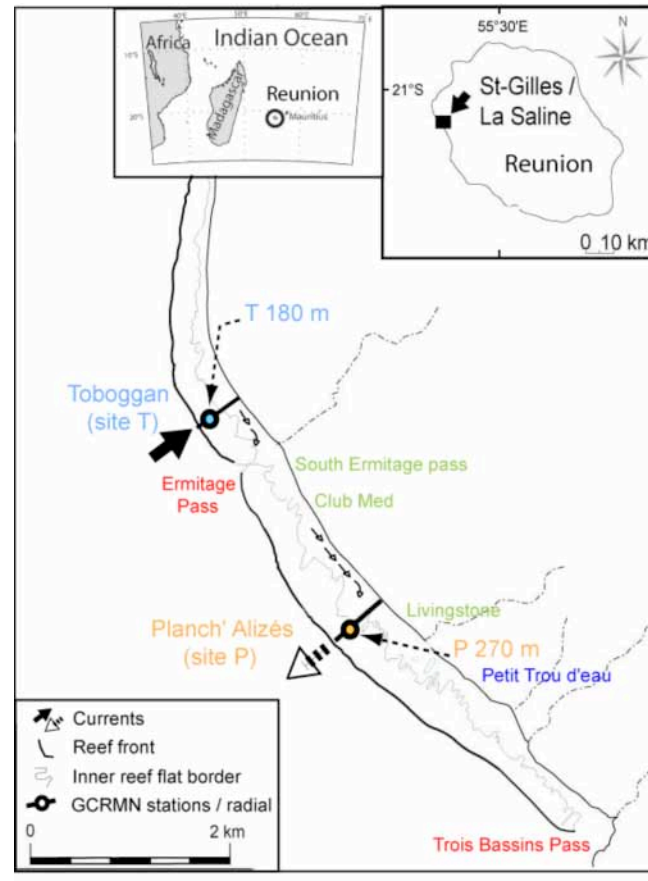


Figure 1: The *Saint-Gilles La Saline* reef. The two studied sites. T180 and P270 are the Global Coral Reef Monitoring Network (GCRMN) stations.

By contrast, communities at Site-Planch'Alizés and Site-Club Med (outflow sites, MAS) are significantly altered to heterotrophy, indicating depletion of oxygen and eventual anaerobic conditions at the end of the night. Further investigations on reef hydrology (Cordier, 2007) and on sediment metabolism at Site-P (Clavier *et al.*, 2008) were in accordance with these previous results and observations.

In 1987, according to the high amount of macroalgae (Naim, 1993) and the lack of sewage treatment along the west coast, MAS at Site-P was regarded as resulting from the nutrient-enriched submarine groundwater discharge onto the reef flat (Cuet, 1989a; 1989b; Naim, 1989).

Benthic community assessment

Three kinds of surveys have been performed at the two Sites-T and P (**Table 1**).

Survey 1: abundance of major benthic associations (1993, 1996, 2002).

Estimates of percent coverage and species composition of major benthic categories (including live and dead corals, primary producers, sand and rubble at each site) were made at a 1 centimeter resolution, using the Line Intercept Transect (LIT) method (Lucas & Seber, 1977; Loya, 1978). LITs, 50 m in length, parallel to the front of the reef, were run at fixed intervals of 30 m at each site from 30 m to 330 m off the beach in 1993, 1996, and 2002. At 360 m, analyses became too hazardous owing to strong waves and a reduction of the depth to 0.30 m or less. A ten meter-LIT is considered as a sample for mean calculation. The study was carried out during the hot season when algae are most fully developed (Semple, 1997). The terms “primary producers” refer to sea-grass, cyanophytes and benthic algae and the terms “bare dead corals” refer to dead substrates that are not covered by any living organism visible to the naked eye.

Survey 2: densities of echinids, holothurids and the territorial fish

***Stegastes* (Pomacentridae) (1993, 1996, 2002).** On Saint-Gilles la Saline, Cuet *et al.* (1988), Naim *et al.* (1997), and Naim (2006) showed that spatial distribution of sedentary fauna (echinids, holothurids and the territorial damselfish *Stegastes*) was correlated with the physico-chemistry of reef waters and reef degradation. Thus, their occurrence in a benthic assemblage may give also an indication of the health state of the reef.

Echinids. On the Saint-Gilles la Saline reef flat, sea urchins occur mostly on the coral zone. *Echinometra mathaei* is the dominant species, followed distantly by *Tripneustes gratilla*, *Diadema setosum*, *Toxopneustes pileolus* and *Stomopneustes variolaris*. *Heterocentrotus* spp and *Cidarids* were abundant in the 1980's on the outer reef flat but are now very uncommon.

Holothurids. On the Saint-Gilles la Saline reef flat, sea cucumbers occur mostly in the back reef area. *Holothuria leucospilota* is the dominant species, followed by *H. atra*, *Synapta maculata*, *Stichopus chloronotus*, *Actinopyga echinites*, *A. mauritiana*, *Stichopus chloronotus*, *H. impatiens* (hidden under blocks). *H. nobilis* and *Bohadschia vitensis* also occur but are uncommon.

The territorial damselfish, *Stegastes*. On the Saint-Gilles la Saline reef flat, *Stegastes* is a common damselfish in the inner coral zone. *S. nigricans* is the dominant species, followed by *S. lividus* and *S. limbatus*. Two other species, *S. fasciatus* and *S. pelicieri*, occur rarely.

Densities, at the specific level, were censused in belt-transects, 1 m strip on either side of each 10 m LIT in the back reef zone, or in 5 * 1 m²-quadrats for 10 m-LIT in the coral zone. All animals, visible from a vertical position as well as those hiding underneath ledges and in crevices, were counted. Animals cut by the upper and left boundaries of the belt-transects were not counted. Data from surveys 1 and 2 form a matrix of 127 variables (including fixed organisms, in cm per 10m-LIT and echinoderms and fishes, in number of individuals per 10 square meter), each species identified if possible, measured on 55 *(10m-LITs) per year at each site, *i.e.* a matrix made of 127 lines * 330 columns in total.

Survey 3: abundance of primary producers, living corals, abiotic coverage and *Stegastes* along two permanent transects T180m and P270m (1987, 1993, 1996, and each year from 1998 to 2009). In 1987, two 50 m-permanent transects,

incremented every 5 meters, were established on Sites-T and P, at a distance of 180 m and of 270 m seawards from the beach. These T180 and P270 transects were monitored in survey 1 (1993, 1996, 2002). In March 1996, 24 h-variation of sea urchin density was also measured along these two permanent 50 m-LITs.

Table 1: Summary of the 3 studies. "LIT"= Line Intercept Transect. "T180" means: a permanent transect, marked off every 5 meters at Site-T, distance from the shore line : 180 m).

	Aim of the study	Stations	Method	Period
Survey 1	Estimate of coverage and species composition of major fixed benthic categories	At each site, T and P, LITs are parallel to the front, run at fixed intervals of 30m, from 30m to 330m off the beach	50 m-LIT separated in 10 m, 1 cm resolution	1993, 1996, 2002 hot season
Survey 2	Estimate of densities of sea-urchins, holothurids, and sedentary fishes	At each site, T and P, 5 belt-transects are located 1m apart each 50 m-LIT	Belt-transects (10m * 2 m)	1993, 1996, 2002 hot season
Survey 3	Estimate of coverage and species composition of major fixed benthic categories	T 180 and P 270	Permanent transects (2 * 20 m)	1987, 1993, 1996, 2002, and GCRMN each year from 1998 to 2009, hot season
	24 h-variation in sea urchin density	T180 and P270	30 quadrats of 1m ² thrown along a 50m-LIT	1996, hot season
	<i>Stegastes</i> density	T180 and P270	Belt-transects (50m * 2.0m)*1 (50m * 2.5m)*3	1987, 1993, 1996 GCRMN from 1998 to 2002, hot season

Since 1998, the Global Coral Reef Monitoring Network (GCRMN) (Wilkinson, ed., 2008) started in Reunion (Chabanet *et al.*, 2002), and 3 * 20m-LITs were monitored each year on each site. Two of these three 20m-LITs are located on the permanent transects T180 and P270, monitored from 1987. Then, temporal variation in abundance of primary producers, living coral and abiotic coverage was analyzed from 1987 to 2009 along the two same 20m-permanent transects. *Stegastes nigricans* density was also analyzed (3 belt transects, length: 50m, width: 2.5 m).

Data analysis

Due to the multi-species nature of the data and the design of the survey, the most appropriate analyses are multivariate (Clarke & Warwick 2001). To assess patterns in benthic data from all stations during all years of survey, we used non-metric multidimensional scaling (MDS). To assess temporal patterns in benthic variation, we used Kruskal-Wallis one-way analysis of variance by ranks: this non-parametric method tests equality of population medians among groups. It is identical to a one-way analysis of variance with the data replaced by their ranks and is an extension of the Mann-Whitney U test to 3 or more groups. Since it is a non-parametric method, the Kruskal-Wallis test does not assume a normal population, but it does assume an identically-shaped and scaled distribution for each group, except for any difference in medians.

Mean coral coverage and densities are given with standard deviation, SD (mean \pm SD). These are calculated as per the following example (shown only for mean calculation here): on Site-T, for a given parameter (e.g. the primary producer coverage), the mean in a subzone (e.g. the back reef, B), for a given-year (e.g. 1993) is denoted TB93, and is the average of the 20 "10m-samples" taken on the 50m-LITs located at 30m, 60m, 90m and 120m. Similarly, the TL93 mean is the average over the 25 "10m-samples" taken on the 150 to 270m LITs, and the TN93 is the average

over the 10 “10m samples” taken on the 300 and 330m LITs. The TB mean is the average over the 60 “10m-samples” taken in the back reef – 20 in each of 1993, 1996 and 2002; the T mean is the average of the 165 “10m-samples” taken – 55 in each of 1993, 1996 and 2002.

Nomenclature

Concerning the nomenclature used in the text, the « ACR » and « MAS » terms refer to *Acropora*-dominated and massive corals-dominated community structures. The morphological zones are noted as follows, from the beach seawards: the back reef zone T_B and P_B , respectively of Sites T and P; the inner coral zone made of « large coral strips »: T_L and P_L ; the outer coral zone made of « narrow coral strips »: T_N and P_N ; the inner reef flat including the two coral strip subzones: T_{L+N} and P_{L+N} . The living coral coverage can be noted as LCcv and the primary producer coverage as PPcv.

RESULTS

Survey 1: total reef flat, 50m LITs, 1993, 1996, 2002

Are ACR and MAS communities stable over time? Based on the mean abundance of species in the communities censused along each 50m-LIT across the reef flat, the MDS plot clearly shows that the data from Site-T and Site-P form two separate clusters (**Fig. 2**). Apparently, the community structure of ACR at Site-T and MAS at Site-P remained different during the nine years covered by this survey. A stress of 0.15 corresponds to a potentially useful ordination.

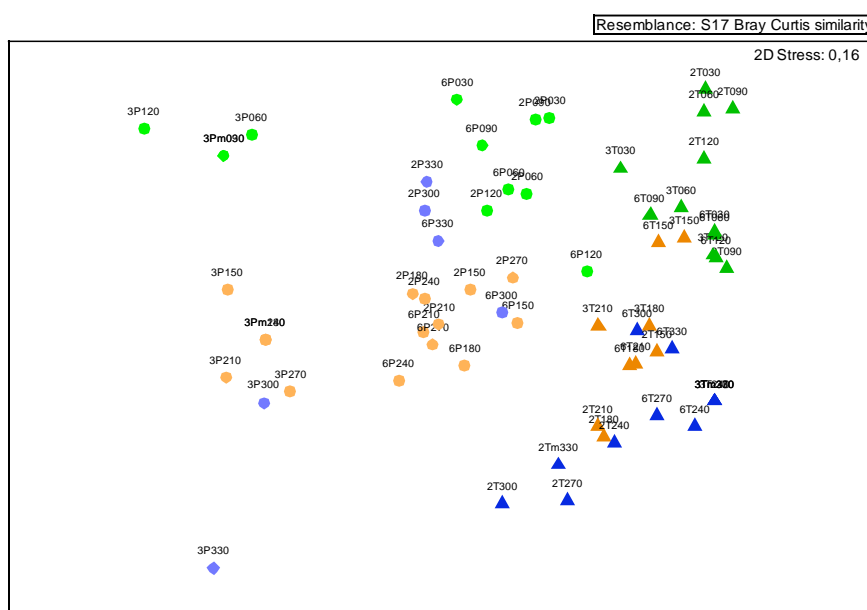


Figure 2: Two dimensional-MDS configuration (T: triangles, P: circles; Back reef in green, L-zone in orange and N-zone in blue), obtained with a hierarchical clustering of the 66*(50m-LIT) (all benthic data: corals, algae, etc., echinoderms and territorial fishes included) using group-average linking of Bray-Curtis. "LIT 3P330" means: year 1993, Site-P, 330 m off the beach; similarly, "LIT 6T60" means: year 1996, Site-T, 60 m off the beach, 2P50: year 2002 etc.

Bubble plots, overlaying percent cover of benthic variables without the detail of species, further highlight these trends (**Fig. 3**). Bubble plots of living *Acropora* and sea-urchins, characterizing ACR, overlay Site-T LITs (reef flat and back reef LITs), while bubble plots of primary producers, non-*Acropora* corals, holothurids, characterizing MAS, overlay Site-P LITs (only back reef LITs for holothurids). These results show that from 1993 to 2002, ACR and MAS have kept the characteristics described previously in Naim (2006). Thus, in the following results, we will consider separately the two sites and their spatio-temporal evolution.

Geomorphology of the reef flat. A cross-check with a hierarchical clustering was performed based on the same data (not shown). Cluster analysis separates each site into 3 distinct groups (depth value refers to fairweather conditions): (1) LITs 30, 60, 90, 120 m group together in Site-T and Site-P clouds and highlight the *Back reef* (**B-zone**), where depth reaches 1.50 m maximum and coral coverage is low; (2) LITs 150, 180, 210, 240, 270 m, grouping in separate T and P clouds, highlight the deeper zone (0.8 m) of the coral zone, where depth allows corals to organize in *Large strips* of a meter-wide or more (**L-zone**), often anastomosing shoreward where the swell decreases. (3) LITs 300 and 330m grouping together, in T and P clouds, are located in the shallow (0.2-0.4 m deep) coral zone where corals can only form *Narrow* (inframetric) *strips* (**N-zone**). L+N zones form the “inner reef flat” or the “coral zone”.

Primary producers (Cyanophytes and benthic algae). The benthic algae form a very complex community (see part 2, Naim *et al.*, 2013a for further details). Algal coverage at Site-P is about 10 times higher than at Site-T (T: $5.3 \pm 11.4\%$; P: $61.3 \pm 26.6\%$) (**Fig. 3a**). Marine phanerogams are rare and not recorded in the survey.

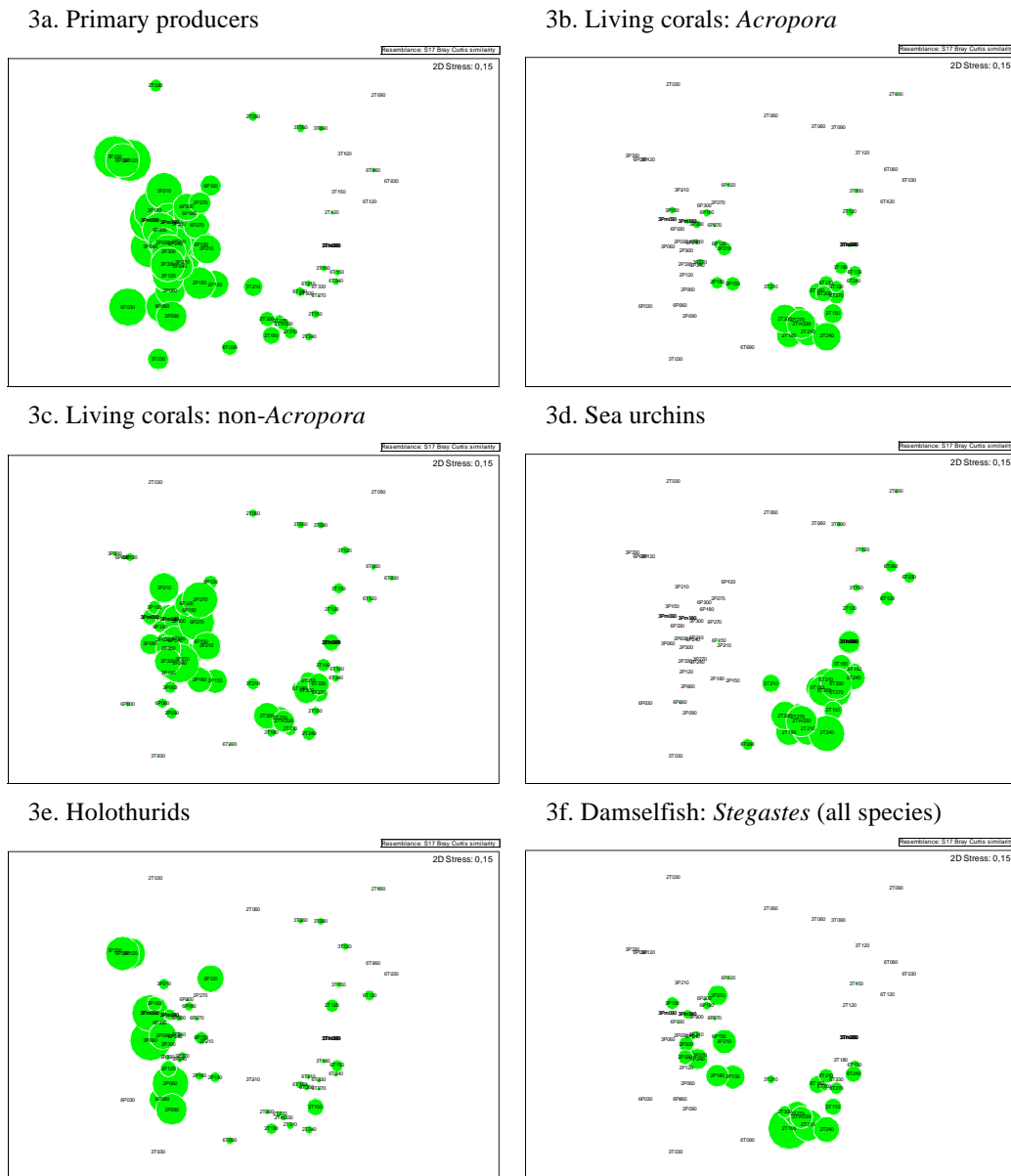


Figure 3a to 3f: Bubble plots, overlaying LITs from figure 2 (benthic variables without the detail of species).

At Site-T, the primary producers coverage -PPcv-, which was very low in 1993, increased significantly to 2002 (**Fig. 4a, Table 2**). However, the values remained low (mean < 10%). The increase was mostly obvious at TN outer subzone where the primary producers, barely visible in 1993 ($0.9 \pm 2.0\%$), increased to $9.1 \pm 10.2\%$ in 2002 (**Fig. 4b**). At Site-P, the highest coverage was recorded in 1993 ($81.6 \pm 19.3\%$). Between 1993 and 1996, and between 1996 and 2002, the primary producers declined significantly (**Table 2**), but still covered $49.0 \pm 18.2\%$ of the substrate in 2002. PB and PL-subzones showed the same trend as the entire site. At PN subzone, although the PPcv also significantly declined between 1993 and 1996, it stabilized at $63.7 \pm 9.0\%$ in 2002.

Living corals, *Acropora* and non-*Acropora*. Between 1993 and 2002, although the living coral coverage -LCcv- was similar at both sites (T: $17.4 \pm 20.7\%$;

P: $16.2 \pm 16.9\%$), the genus *Acropora* (*Acr*) dominated the T-coral community ($11.9 \pm 17.4\%$) and the "non-*Acropora*" corals (*NAcr*) dominated to an even greater extent at Site-P ($14.2 \pm 15.8\%$).

Species richness and diversity of corals is treated in part 3 of the paper (Naim *et al.*, 2013b). At Site-T, 11 *Acropora* species formed 68.4% of the coral coverage, while at Site-P, only two species of *Acropora* accounted for 12.6% of cover. *Acropora muricata* was the dominant species at both sites (T: 76.4% of *Acropora* corals; P: 99.2%).

Among non-*Acropora* (*NAcr*) species, both *Montipora circumvallata* and *Porites* (*Synaraea*) *rus* dominated (T: 60.8% of *NAcr*; P: 89.0% of *NAcr*).

Considering spatio-temporal variation, the living coral coverage was relatively stable at Site-P while increasing at Site-T (**Table 2**). The Site-T increase was due to an intense growth of *Acropora* from $1.9 \pm 3.3\%$ in 1993 to $25.8 \pm 22.4\%$ in 2002 (**Fig. 4c**) while non-*Acropora* coverage remained stable through time at this site (**Fig. 4e**). In the T-coral zone (TL + TN), the LCcv increased from 1993 to 2002 (**Fig. 4d**) while remaining relatively stable in the P-coral zone (PL + PN), except for a slight increase from 1996 to 2002 in PL (**Fig. 4f**). *Acropora* growth was particularly spectacular in the outer TN zone, where the coverage, reduced to $1.2 \pm 1.6\%$ in 1993, recovered to $46.2 \pm 14.4\%$ in 2002. In the back reef areas, due to the rarity of coral patches and the associated high variance, the LCcv did not vary significantly.

At Site-P, *Acropora* and non-*Acropora* coverages did not vary significantly over time. At both sites, non-branching corals showed a remarkable stability over time.

Bare dead corals. The bare dead corals were locally abundant at Site-T but were exceedingly rare at Site-P (coverage: T: $13.5 \pm 16.9\%$; P: $1.2 \pm 3.1\%$). Considering spatio-temporal variation, their coverage remained stable through time, except in TN, where it dropped from $36.1 \pm 8.3\%$ in 1993 to $12.4 \pm 8.8\%$ in 2002 (**Fig. 4g, 4h, Table 2**). In the same subzone, TN, considering the {living corals/(bare substrates + living corals)} ratio, it increased continually, from 20% in 1993, to 44% in 1996, and to 83% in 2002, meaning that young coral colonies settled preferentially on bare substrates.

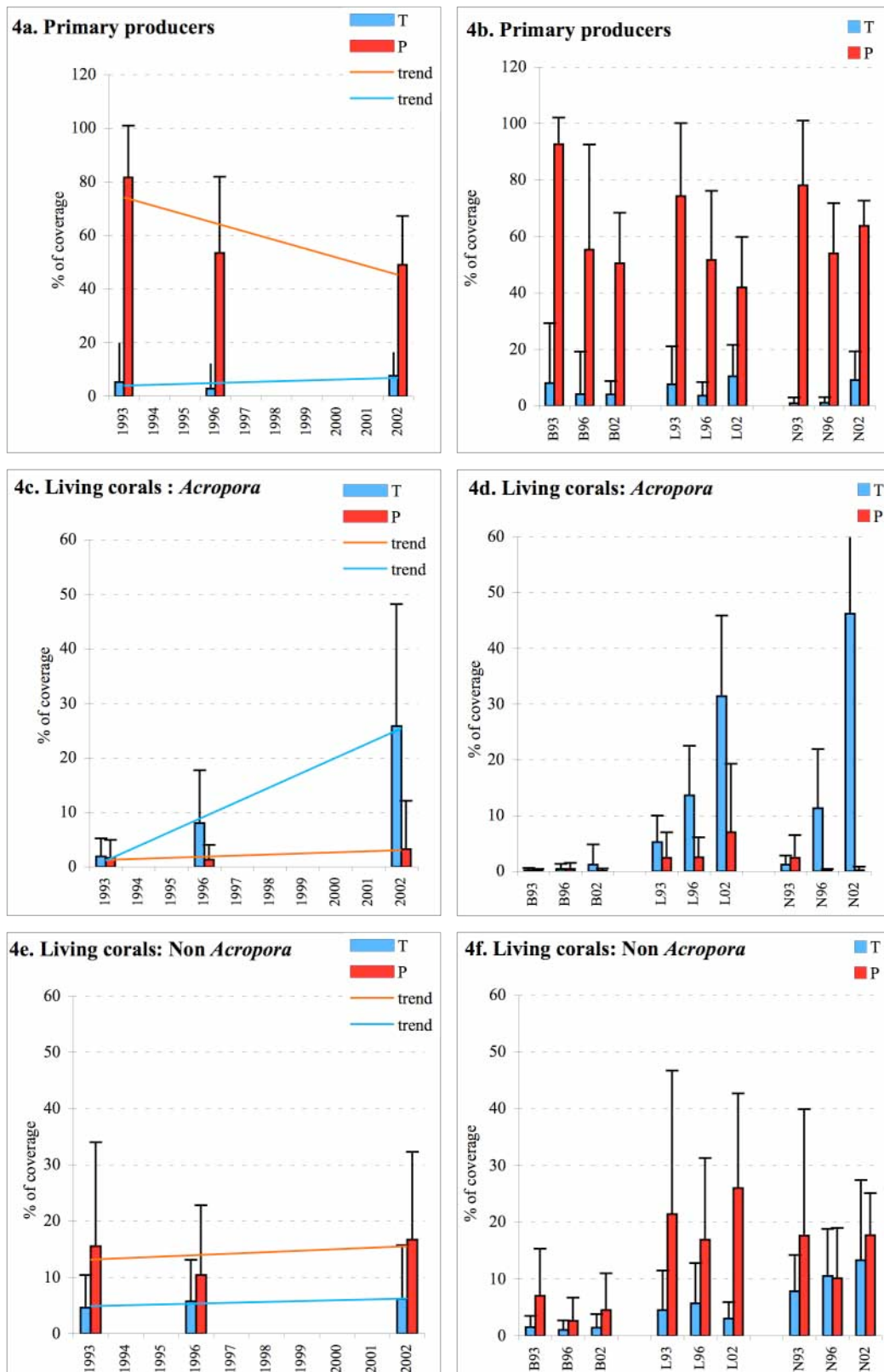


Figure 4a to 4f: Spatio-temporal variation from 1993 to 2002 of the coverage of primary producers, living corals, *Acropora* and non-*Acropora*. Left : over the total site, right: in the three geomorphological zones, B= back reef, L= inner zone of Large coral strips, N= outer zone of Narrow coral strips. Error bars are standard deviation.

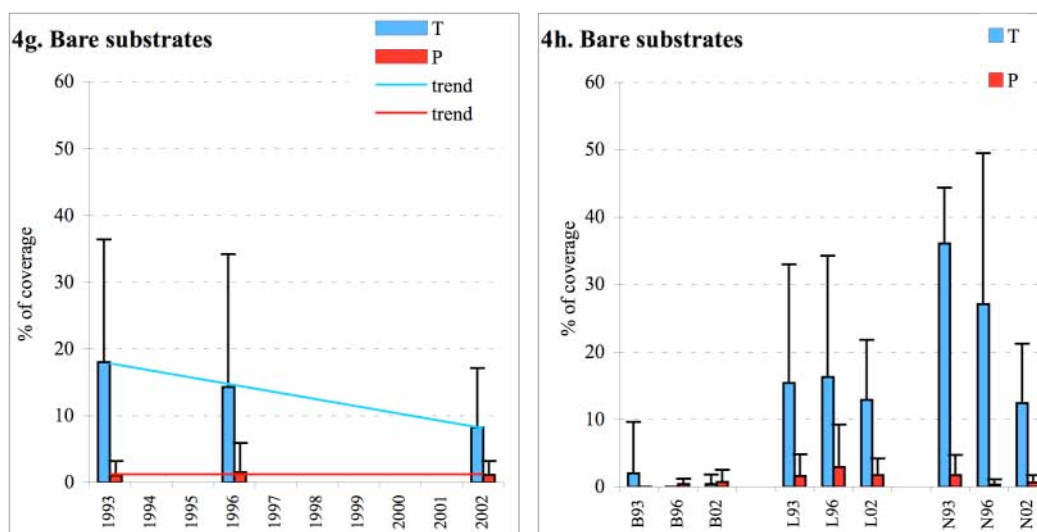


Figure 4g, 4h: Spatio-temporal variation from 1993 to 2002 in the coverage of bare substrate, the density of sea urchins and holothurids. Left : over the total site, right: in the three morphological zones, B= back reef, L= inner zone of Large coral strips, N= outer zone of Narrow coral strips.

Survey 2: sedentary fauna

Sea urchins. At Site-T, from 1993 to 2002, sea urchin densities were 100 times higher than at Site-P (T: 70.4 ± 69.6 number of individuals (ind.) per 10 m^2 ; P: 0.6 ± 1.2). *Echinometra mathaei* is the dominant species, averaging 99.7% of the echinoid community at Site-T, and 77.7% at Site-P.

Looking at spatio-temporal variation, the densities varied at Site-T and remained stable at Site-P (mean always <1 ind. per 10 m^2) (**Table 2**). At Site-T, the lowest density was observed in 1993 (42.9 ± 46.8 ind. per 10 m^2). Then the density increased in 1996, to reach in 2002 89.9 ± 86.7 ind. per 10 m^2 (**Fig. 4i, 4j**). Sea urchin density increased on TL and TN, but in the back reef zone, TB, density and distribution were highly variable through time as follows: very low density and regular distribution in 1993 (3.5 ± 4.1 ind. per 10 m^2), high density and random distribution in 1996 (27.9 ± 10.0 ind. per 10 m^2), and again low density but aggregated distribution in 2002 (7.6 ± 19.4 ind. per 10 m^2).

Holothurids. Unlike sea urchins, sea cucumbers were abundant at Site-P, but rare at Site-T (T: 1.8 ± 2.6 ind. per 10 m^2 ; P: 12.5 ± 19.2). Considering the subzones, no significant differences appeared at Site-T, while at Site-P, holothurids were mostly located in the back reef (PB: 27.8 ± 21.2 ind. per 10 m^2).

Considering spatio-temporal variation (**Fig. 4.k, 4.l, Table 2**), holothurid density did not vary significantly from site to site. However, in TL and TN, their numbers increased significantly in 1993-96 and 1993-2002 periods. But, due to low densities in L and N-zones (≤ 5 ind. per 10 m^2), these results prove not to be highly significant. In contrast, in PL and PN, the density decreased between 1993 and 2002. In PB, density declined just as much (on average) but the variance was too great for this decrease to be significant.

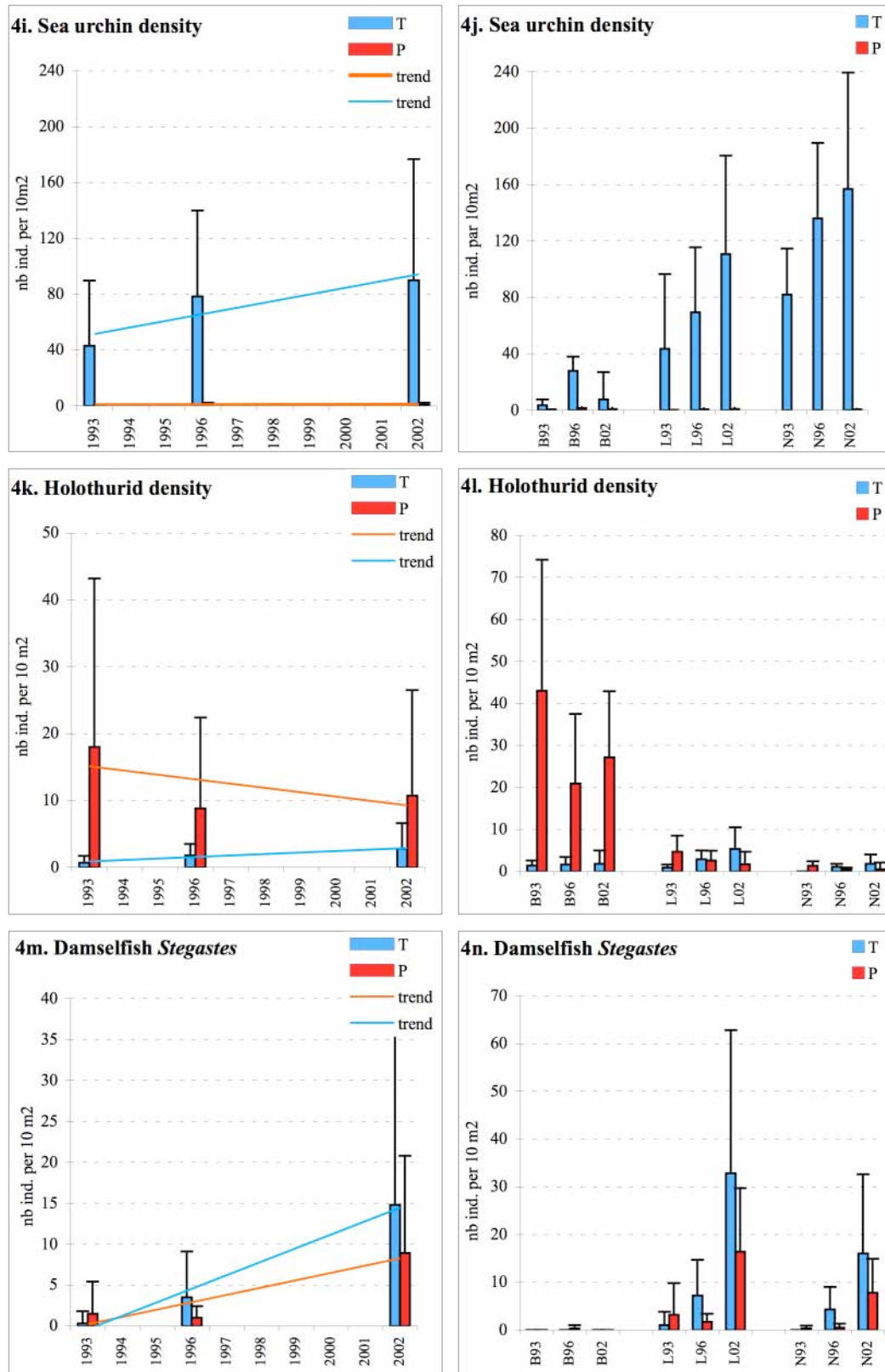


Figure 4j to 4n: Spatio-temporal variation in the coverage of bare substrate, the density of sea urchins and holothurids from 1993 to 2002. Left : over the total site, right: in the three geomorphological zones, B= back reef, L= inner zone of Large coral strips, N= outer zone of Narrow coral strips.

Table 3: Surveys 1 & 2 (whole sites, 1993, 1996, 2002): Kruskal-Wallis test between means (μ) of the variables in the 3 different years, at the two sites (T= “Toboggan”, P= “Planch’Alizés”). B= back reef, L= zone of large coral strips, N= zone of narrow coral strips). (>: significant increase, <: significant decrease, Ns: non significant).

		$\mu 1993-\mu 1996$	$\mu 1993-\mu 2002$	$\mu 1996-\mu 2002$		$\mu 1993-\mu 1996$	$\mu 1993-\mu 2002$	$\mu 1996-\mu 2002$
Primary Producers	T	Ns	Ns	>>>> p=0.0000	P	<<<< p=0.0000	<<<< p=0.0000	Ns
	TB	Ns	Ns	Ns	PB	<< p= 0.0074	<<< p= 0.0007	Ns
	TL	Ns	Ns	Ns	PL	< p= 0.0200	<<< p= 0.0009	Ns
	TN	Ns	>> p= 0.0060	> p= 0.0201	PN	< p= 0.0247	Ns	Ns
Living corals	T	Ns	>>> p= 0.0001	Ns	P	Ns	Ns	Ns
	TB	Ns	Ns	Ns	PB	Ns	Ns	Ns
	TL	Ns	>>>> p=0.0000	Ns	PL	Ns	Ns	> p= 0.023
	TN	Ns	>>>> p=0.0000	>>>> p=0.0000	PN	Ns	Ns	Ns
<i>Acropora</i>	T	> p=0.0233	>>>> p=0.0000	Ns	P	Ns	Ns	Ns
	TB	Ns	Ns	Ns	PB	Ns	Ns	Ns
	TL	Ns	>>>> p=0.0000	> p=0.0205	PL	Ns	Ns	Ns
	TN	Ns	>>>> p=0.0000	>>> p= 0.0001	PN	Ns	Ns	Ns
Non- <i>Acropora</i>	T	Ns	Ns	Ns	P	Ns	Ns	Ns
	TB	Ns	Ns	Ns	PB	Ns	Ns	Ns
	TL	Ns	Ns	Ns	PL	Ns	Ns	Ns
	TN	Ns	Ns	Ns	PN	Ns	Ns	Ns
Bare dead corals	T	Ns	Ns	Ns	P	Ns	Ns	Ns
	TB	Ns	Ns	Ns	PB	Ns	Ns	Ns
	TL	Ns	Ns	Ns	PL	Ns	Ns	Ns
	TN	Ns	< p= 0.0103	Ns	PN	Ns	Ns	Ns
Sea urchins	T	>>>> p=0.0000	>> p= 0.0092	Ns	P	Ns	Ns	Ns
	TB	>>>> p=0.0000	Ns	<<<< p=0.0000	PB	Ns	Ns	Ns
	TL	Ns	>> p= 0.0073	Ns	PL	Ns	Ns	Ns
	TN	Ns	> p= 0.0440	Ns	PN	Ns	Ns	Ns
Holothurids	T	Ns	Ns	Ns	P	Ns	Ns	Ns
	TB	Ns	Ns	Ns	PB	Ns	Ns	Ns
	TL	> p= 0.0408	> p= 0.0280	Ns	PL	Ns	< p= 0.042	Ns
	TN	> p= 0.0384	> p= 0.0343	Ns	PN	Ns	< p=0.0221	Ns
<i>Stegastes</i> (all species)	T	> p=0.0162	>>> p= 0.0002	Ns	P	Ns	Ns	Ns
	TB	absent	absent	absent	PB	Ns	Ns	Ns
	TL	Ns	>>>> p=0.0000	Ns	PL	Ns	>>> p= 0.0004	>>> p= 0.0009
	TN	Ns	>> p= 0.0026	Ns	PN	Ns	>> p= 0.0075	> p=0.0213

***Stegastes*.** *Stegastes* is a territorial damselfish, that colonizes dead corals. Thus, this Pomacentridae is rare or absent from back reef areas. The density of *Stegastes* was not significantly different between Sites T and P (T: 6.2 ± 14.5 ind. per

10 m²; P: 3.8 ± 8.1), but its spatio-temporal distribution was more variable at Site-T (**Table 2**). In 1993, *Stegastes* density was very low at both sites (<2 ind. per 10 m²) (**Fig. 4m**). At Site-T, a significant increase in density was recorded between 1993 and 2002 to 14.8 ± 22.1 ind. per 10 m². This increase mainly concerned the TL area where the density increased from 1.0 ± 2.8 to 32.8 ± 30.0 ind. per 10 m² (**Fig. 4n**). In contrast, at Site-P, between 1993 and 2002, the density also significantly increased in PL and PN, but to a lesser extent.

Survey 3: the permanent transects T180m, P270m from 1987 to 2009

Do ACR and MAS structures remain stable until 2009? The primary producer coverage -PPcv- was lower on average and more variable at T180 than at P270 (T180: $23.9 \pm 15.1\%$; P270: $40.3 \pm 13.5\%$) whereas the living coral coverage -LCcv- was relatively stable at the two sites (T180: $36.8 \pm 13.3\%$; P270: $42.0 \pm 9.8\%$). Among corals, the genus *Acropora* remained dominant at T180 while scarce at P270 (relative %: T180: $73.5 \pm 8.4\%$ of LCcv, P270: $3.6\% \pm 5.5$ of LCcv).

Considering temporal variations: (1) at **T180**, from 1987 to 1998, the primary producer coverage remained below 10%. From 1999, it clearly increased, stabilizing in the range of 20-50% (**Fig. 5a**). For living corals, the total living coral coverage (as well as the *Acropora* and non-*Acropora* coverage), did not vary significantly (**Fig. 5a, 5c, 5d**). The *Acropora* coverage went through cycles of demise (1987-1993, 1999-00, 2003-06) followed by a rapid recovery (1993-98, 2000-03, 2006-09) while the non-*Acropora* coral coverage remained remarkably stable; (2) at **P270**, from 1987 to 1998, the primary producer coverage was high (range of 40-60%). In 1999, it clearly decreased, stabilizing then in the range of 20-40% until 2008 (**Fig. 5b**). In 2009, the algal coverage increased again to 60%. The living coral coverage was not significantly different in the 1987-98 and 1998-2003 periods (28-40%). Later, it increased to 40-60%, but markedly decreased in 2009 to 26.5%, with the lowest LCcv ever measured (**Fig. 5b**). Massive corals remained dominant over time and *Acropora* represented less than 10% of the benthic coverage (**Fig. 5c, 5d**).

In conclusion, (1) at **T180** (**Fig. 5a**), from 1987 to 1999, the living corals dominated, while primary producers remained inconspicuous, the 1987 coverage (70%) being no longer achieved. Then, from 1999 to 2009, living corals and primary producers dominated alternately: the 2001-2003 period was favorable to coral development, the 2004-2006 interval was favorable to primary producers, while from 2008, the conditions were again favorable to corals. This suggests that a critical shift occurred in 1999 in the functioning of the community structure, and a lesser shift happened in 2004;

(2) at **P270** (**Fig. 5b**), in contrast to T180, from 1987 to 1998, the algal coverage was higher than living coral coverage, the year 1987 being the worst period. In 1999, living corals became dominant over primary producers, and from 2004, the situation improved further. In 2009, there was a sharp decline in living corals and related increase in primary producers, thus once more inverting the dominance ratio. In terms of living coral coverage, 2009 appears to be the worse year of the 2000s.

Considering living coral and primary producer relative dominance, two 'turning points' occurred at both transects, one in 1999 in one direction and the other in 2004 in the opposite direction. Therefore, we divided the monitoring period into 3 blocks (1987-98, 1999-2004 and 2004-2009) and compared the mean coverages of the three periods.

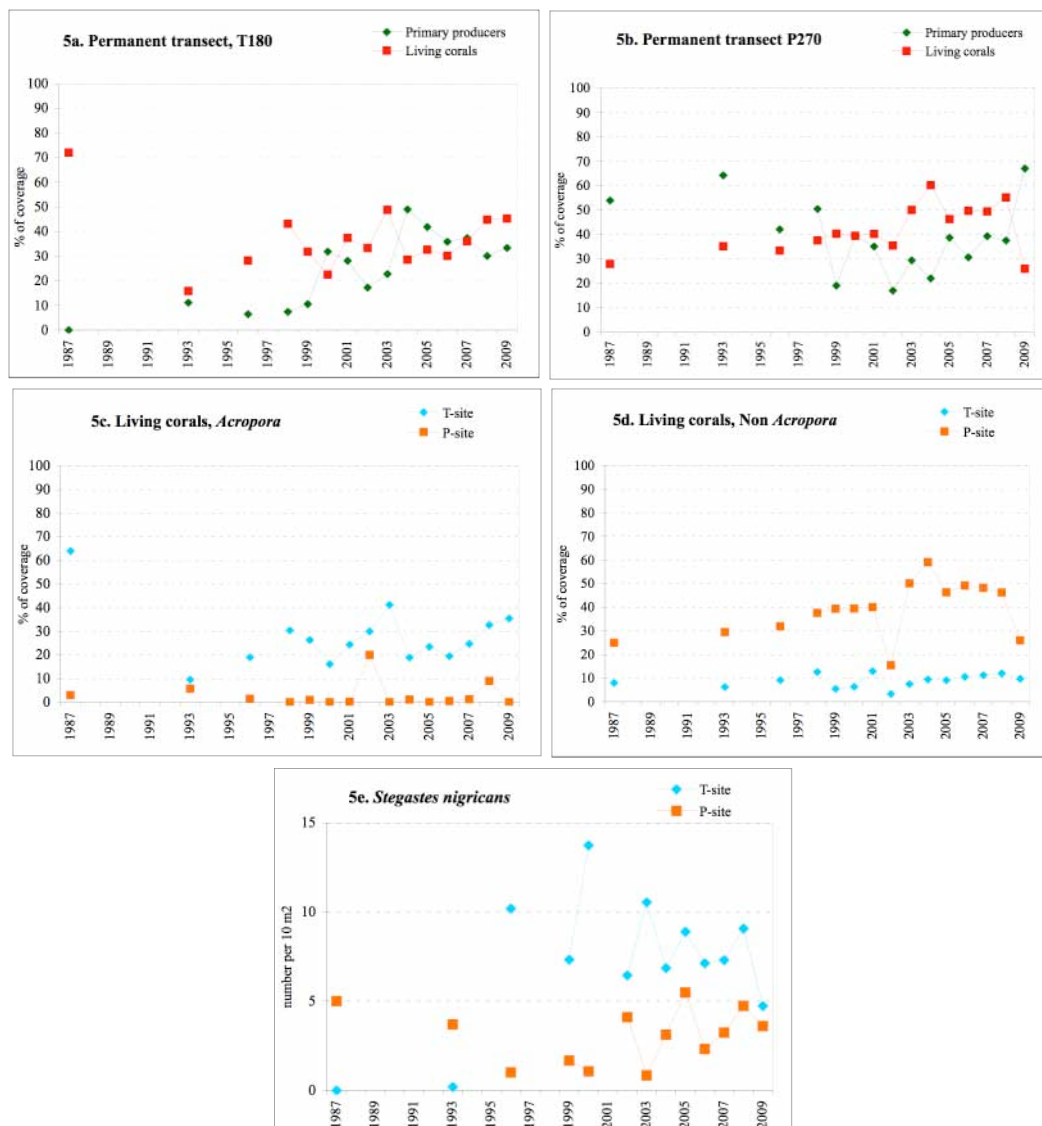


Figure 5: Yearly variation of primary producers, living corals, *Acropora* and non-*Acropora* at the two permanent transects T180 (Site-T) and P270 (Site-P).

Comparison of 1987-98, 1999-2003, and 2004-2009 periods. The primary producer coverage increased significantly at T180 between 1987-98 and 2004-09, and decreased significantly at P270 between 1987-98 and 1998-2003 (Fig. 6a, Table 3). The living coral coverage, as well as *Acropora* coverage, did not vary significantly at T180 from 1987-98 to 2004-09 (Fig. 6b, 6c, 6d, Table 3). By contrast, at P270, the massive coral coverage increased significantly between 1987-98 and 2004-09 (Fig. 6d, Table 3). At T180, *Stegastes* density significantly increased while it remained stable at P270 (Fig. 6e, Table 3).

Regarding PPcv and LCcv temporal trends, T180 and P270 seem to vary in opposite directions: (1) from 1987 to 1998, at T180, living corals dominate primary producers while at P270 living corals are heavily overgrown by algae (see part 2, Naim *et al.*, 2013a), then (2) since 1999, at T180, a period less favorable for coral growth began (alternate dominance of PPcv and LCcv), while at P270, a period more favourable to coral growth started. Then, in 2009, P270 provided the worst PPcv/LCcv ratio in the whole monitoring period, indicating a sharp decline in the coral health on the transect, while at T180, 2009 still was a prosperous period for

coral life. The *Acropora* coverage did not vary significantly (high variance) while the non-*Acropora* increased significantly at P270 between 1987-98 and 2004-2009.

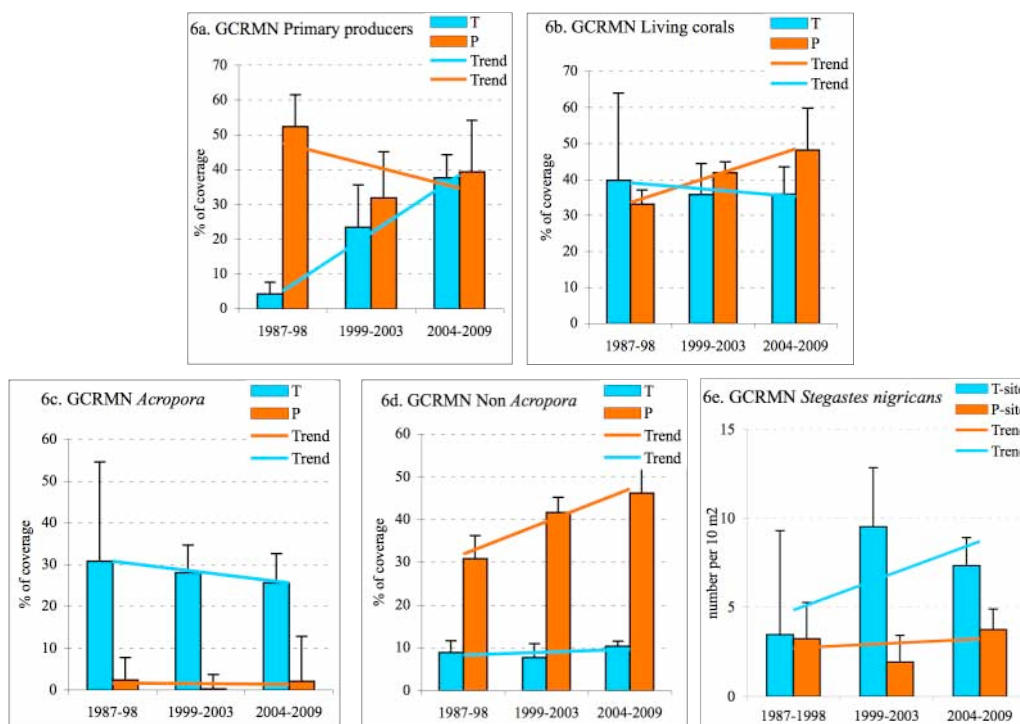


Figure 6: Temporal variation of primary producer, living *Acropora* and non-*Acropora* coverages between 1987-98, 1999-2003 and 2004-2009 "year-blocks".

Table 3: Survey 3: Kruskal-Wallis test between means (μ) of the variables in the 3 "year-blocks", at the two permanent transects (T180= "Toboggan" 180m off shore, P= "Planch'Alizés", 270 m off shore). *N.b.* For *Stegastes*, 2001 densities are not included. (>: significant increase, <: significant decrease, Ns: non significant).

		μ (1987-1998)	μ (1999-2003)	μ (1987-1998)	μ (1987-1998)	μ (1999-2003)	μ (1987-1998)
		μ (1999-2003)	μ (2004-09)	μ (2004-09)	μ (1999-2004)	μ (2004-09)	μ (2004-09)
Primary Producers	T180	Ns	Ns	>>	P270	<	Ns
				p= 0.0019		p= 0.0373	
Living corals	T180	Ns	Ns	Ns	P270	Ns	Ns
							p=0.0391
<i>Acropora</i>	T180	Ns	Ns	Ns	P270	Ns	Ns
Non- <i>Acropora</i>	T180	Ns	Ns	Ns	P270	Ns	Ns
							p=0.0361
<i>Stegastes</i>	T180	>	Ns	Ns	P270	Ns	Ns
		p=0.0298					

Concerning sea urchins, at T180 and P270, their density was measured only in 1987, 1993, 1996 and 2002 (survey 1) and 2011. In 1987, at T180, the density was the highest ever measured: 180.2 ± 52.1 ind. per 10 m^2 , while at P270, no sea urchin was recorded. In 2011, the sea urchin density is still 27.1 ± 3.6 ind. per 10 m^2 on T180 and 0.5 ± 0.6 ind. per 10 m^2 on P270.

The measurement of the nycthemeral variation in the density of sea urchins showed that at T180, the density at midnight is three times higher than at noon, while at P270, no sea urchin was observed (**Table 4**).

Table 4: Nycthemeral variation in the density of sea urchins on T180 and P270, in March 1996 (in number of individuals per 10 m² \pm standard deviation).

Sea urchin density	6 am	12 am	6 pm	12 pm
T180	30.1 \pm 10.9	20.5 \pm 22.2	30.3 \pm 32.5	62.9 \pm 32.9
P270	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0

DISCUSSION

Spatio-temporal variation of benthic communities: ACR and MAS are stable over 25 years

To our knowledge (the quantitative studies started in 1985), the Site-T and Site-P communities, labelled ACR and MAS, have preserved their principal characteristics until now, although the MAS components remain much more stable than the ACR ones.

Primary producers. From 1993 to 2002, at Site-T, the primary producer coverage remained stable and inconspicuous, except in the TN-subzone where it increased significantly. However, the average coverage never exceeded 10%. At Site-P, in 1993, algae were dominating the substratum (60-100% cov.) (see details in part 2). But from 1993 to 2002, their coverage steadily decreased and stabilized around 50% in 2002, except in the outer PN-subzone where the coverage remained stable. Outer N-subzones had the highest algal coverage at both sites, revealing then a greater fragility in relation to environmental factors, due certainly in part to their shallowness (0.4 m maximum depth).

From 1987 to 2009, a significant change in the amount of primary producers occurred at the two sites: at Site-T, the algal coverage increased while at Site-P it decreased. These results will be further developed and discussed in Part 2 (Naim *et al.*, 2013a).

Living corals. Between 1993 and 2002, the mean living coral coverage was relatively low, and not significantly different between sites (T: 17 \pm 21%); P: 16 \pm 17%). This might reflect a carrying capacity in living corals of the *Saint-Gilles La Saline reef* flat in extreme conditions (pure autotrophic, pure heterotrophic).

In the 1993-2002 period, the coral coverage was stable at Site-P and very unstable at Site-T. Instability observed at Site-T is linked to the dominance and fluctuations in the *Acropora* coverage. Conversely, the massive coral cover showed a remarkable 10 year-stability at both sites. The same trends were observed in the 1998-2009 GCRMN data, although massive coral coverage increased significantly at Site-P in the 2004-2008 period.

Before the creation of the marine reserve (2007), the T-coral zone (TL + TN) was a hotspot for visitors, either by snorkelers during the day, and/or by poachers at night. The great coral vitality and the fish richness (Letourneur, 1992; Chabanet, 1994; Chabanet *et al.*, 1997; Tessier *et al.*, 2008) probably explain the high touristic pressure it has suffered. In 2007, the area became a sanctuary, and such a new status may modify the coral as well as the fish carrying capacity in the future.

Acropora, stenoecious corals, ruderals (*r-strategists*), sensitive but rapidly growing, structuring the ACR community. Outer shallow coral zones (N-zones) develop on the large Reunion reef flats (La Saline, Saint-Leu, Saint-Pierre). At these particular zones, *Acropora* can form what Montaggioni and Faure (1980) and Faure (1982) called "fields of branching *Acropora*", that approach 100% coverage and in which rare sandy channels do not exceed some decimeters in width. These dense bushes appear to be the most vulnerable to environmental factors that chronically affect the reef flats (extreme low tides, bleaching events, etc.), and mortality can reach almost 100% of the coverage in one episode (Naim, pers. obs.). In this study, at TN, *Acropora* bushes were least in 1993 (1%), and recovered to more than 40% over 9 years, in spite of two small *Acropora* "declines" in 1998 and 1999.

In the inner L-coral zones, which are deeper than N-zones, *Acropora* form large colonies or coral strips that often merge shoreward. These coral formations are generally less affected by bleaching events and extreme low tides, as deeper parts of the colonies/strips remain alive. Nevertheless, at TL, between 1993 and 2002, *Acropora* coverage displayed, as in TN, a rapid recovery (5% to 30%). The GCRMN data showed that recovery can be quite rapid, increasing by up to 5-10% cover per year from 2000 to 2003, but the *Acropora* community did not reach 64% of coverage as reached in 1987 on the same permanent transect. Either this is due to lack of recovery time before a next disturbance affects the *Acropora* population, or this indicates an ecological change on the reef flat at Site-T.

The sensitivity of *Acropora* to environmental factors, as well as its ability to quickly recolonize the space, is demonstrated here. Similarly, on the Saint-Leu ville reef flat (ACR community, west Reunion coast), the *Acropora* assemblages recovered through 10 years following the impact of cyclone Firinga (Naim *et al.*, 2002; Scopélitis *et al.*, 2009). The rapid recovery of *Acropora* populations indicates that the Site-T and Site-Saint-Leu ville environments remained favorable enough for *Acropora* resettlement and survival. Similarly, in the Caribbean, after a serious degradation, reefs of the Florida Keys recovered rapidly (Shinn, 1976), but by contrast the Carysfort reef did not (Dustan & Halas, 1987).

Many studies over the past 30 years have been interested in the coral composition and distribution on the largest reef units at Reunion, including Saint-Gilles la Saline, Saint-Leu and Saint-Pierre (Faure & Montaggioni, 1970; Montaggioni, 1978; Faure, 1982; Naim, 1989; Naim *et al.*, 2002; Bruggemann *et al.*, 2007; Tessier *et al.*, 2008) and particularly on the *Saint-Gilles La Saline reef* (Bouchon, 1981, 1996; Guillaume, 1988; Naim, 2002, 2006). All show that *Acropora* is usually dominant on Reunion reef flats. Classified as ruderal, or *r-strategist* by Edinger and Risk (2000), *Acropora* still dominates the healthy parts of reef flats in Reunion, with both high coverage and high diversity. **Figure 5b** shows that except in 1985 and 2009, the T180-living coral coverage is still lower than the P270 one. The *Acropora* growth periods (1993-98, 2000-03, 2006-08) apparently do not compensate for periods of decline (1985-93, 1998-2000, 2003-04), some of which are very fast. Events that may cause *Acropora* degradation will be discussed further.

At Site-P, between 1993 and 2002, *Acropora* coverage did not exceed 2% (± 5.7). At P270, the *Acropora* coverage was always less than 4% between 1987 and 2009, except in 2008 when it reached 9% of the total coverage.

Massive and submassive corals, euryoecious, stress-tolerators (s-strategists), structuring the MAS community. From 1993 to 2002, in the PN shallow outer zone,

the flattened upper part of corals was generally invaded with macroalgae. The outer “ring pad” and the small (0.3 m max) vertical walls of coral colonies were the only parts alive. At PL, in 1993, the flat subtidal top of corals was also invaded by macroalgae. Exposure appears to be an important factor of degradation at the PL and PN subzones, but does not explain the abundance of primary producers.

Massive and submassive corals are considered as stress-tolerators (s-strategists) by Edinger and Risk (2000). In this study, they show a high spatial and temporal stability over time. From 2004 to 2008, their coverage increased at Site-P, certainly due in part, to the reduction of competition for space with primary producers (see part 2, Naim *et al.*, 2013a).

Bare dead substrates. Measurements of bare dead coral coverage are interesting because a bare substrate indicates, because of the total absence of primary producers, a high grazing pressure. Bare substrates were rare on the reef, except at TN where the sea-urchin *Echinometra mathaei* lived in nearby sites, either hidden in the cavities or at the base of these substrates. From 1993 to 2002, the significant decrease in bare dead corals at TN can be related to the increase of *Acropora* coverage since *Acropora* juveniles colonized -and extended beyond- these dead substrates over the 9 year-period, but also to the sea-urchin bioerosion (see below). As no bare substrate was found on the two GCRMN transects, temporal evolution was not documented after 2002.

Sea urchins. From 1993 to 2002, the density of sea urchins was 100 times higher at Site-T than at Site-P, as confirmed by Conand *et al.* (1998) in the coral-zones, TL and TN. Minimal in 1993 the urchin density increased significantly until 2002. *Echinometra mathaei* formed more than 99.7% of the community at Site-T.

In the T back reef, the density and distribution patterns of sea urchins were highly variable over years, partially due to animal movements but mainly to swell action. Density of sea-urchins was not monitored after 2002, but a 2011 monitoring confirms that the general trends did not change (GCRMN, not published). Chazottes *et al.* (2002) found significant variations in bioerosion among ACR and MAS sites.

Circadian census performed at the TL coral subzone revealed that the sea urchin density was three times higher at night than during the day. This very high nocturnal density shows how the *Echinometra mathaei* pressure on the reef may be underestimated by measures of the day-time densities.

Echinoids and algae. Inconspicuousness or dominance of algae at the T and P sites were obviously linked to nutrient concentrations and/or the quantity of nutrient regeneration through organic matter depletion (Cuet *et al.*, 1988; Mioche, 1998). However, regular echinoid grazing is also a major factor determining the dominance of primary producers (for instance, see Hughes *et al.*, 1987; Littler *et al.*, 2009). So, at both sites, the abundance (or rarity) of sea urchins provides a strong (or very weak) feedback on algal biomass (See part 2, Naim *et al.*, 2013a).

Echinoids and living corals. In September 1992, *Echinometra mathaei* and *Acropora* were similarly affected by a high rate of mortality and from 1993 to 2002, *Acropora* coverage and *Echinometra mathaei* densities increased significantly in the same way. It is interesting to note that the 1993-2002 increase in echinoid densities has not hampered the settlement of corals, as reported by Hardman *et al.* (2007). It

has to be noted that in 1987, when *Acropora* populations were at their best (64% of the coverage), the sea urchin density was the highest measured on Site-T (180 ind. per 10 m²).

Cover & Potts (2008) documented the direct impact of *E. mathaei* on living coral fragments (mostly *Montipora* and *Porites*): most fragments of all coral species placed in plots where *E. mathaei* occurred were grazed down, often resulting in a complete removal of coral tissue and corallites.

By contrast, Sammarco's experiments in Jamaica (1982) showed that percent-cover of adult corals was enhanced in relation to the presence of *Echinometra viridis*, and greatly reduced in the absence of echinoid grazing, as a result of massive overgrowth by algae. In the same way, this author showed that the presence of *Echinometra viridis*, even at the high densities naturally present on the reef, did not deter coral settlement. He showed also that as echinoid species composition and density were altered, the species composition of benthic algae and associated invertebrates shifted.

Therefore, are echinoids coral safe or not? This is a very debatable subject. Sea urchins are very often considered as reef pests, occurring in nutrient-enriched areas (Horrill *et al.*, 2000). From our point of view, it may depend on the species considered. At Site-P, *E. mathaei* is rare in the back reef zone and totally absent from the inner and outer reef flat. More generally, in Reunion as well as in the nearby island of Mauritius, the species seems to avoid freshwater or nutrient-enriched areas (except in strong current areas): the more oceanic are the reef flat conditions, the more abundant is *E. mathaei* (Naim, 2006). In Reunion, this species was considered to be grazing on turfs and microflora and eroding the dead corals (Conand *et al.*, 1998). But *E. mathaei* is an opportunistic species: at night, it has been observed to gnaw on living polyps and their corallites located at the base of *Acropora* branching colonies, while during the day, it has also been observed out of its hole, eating rice and corn from the dirty dishes of the beach users (Prigent & Naim, pers. obs.).

In september 1992, at TN, when *Acropora* colonies were almost all terminated, the last *E. mathaei* were hiding in the remaining coral framework (20-40 cm high). During the 1993-2002 recovery, young *Acropora* colonies settled despite the increase in *E. mathaei* density and did not seem to suffer from sea urchin grazing, suggesting that *E. mathaei* found enough « non coral-food » and/or had not exactly the same micro-niche as *Acropora* juveniles. Such contradictory results between different studies suggest that echinoid impact on living corals may depend on very diverse factors, including sea urchin species, density, food availability, coral forms (massive, branching, corymbose, etc.), accessibility of the corals, spatial competition with other organisms such as *Stegastes* (Naim *et al.*, 1997) and the exact overlapping of the coral and echinoid micro-niche.

Echinoids and bare substrates. At TN, *Echinometra mathaei* density increases from 1993 to 2002 (1993: 8.2 ind.m⁻²; 1996: 13.6 ind.m⁻²; 2002: 15.7 ind.m⁻²; **Fig. 4j**). At Reunion (Petit Trou d'eau, south Saline reef, **fig.1**), Conand *et al.* (1997) showed that one *Echinometra mathaei* adult grazes 113 g CaCO₃.y⁻¹ (in mean) on the N-zone of the reef flat.

Then, if we assume (1) that *E. mathaei* has a similar behavior at TN than at Petit Trou d'eau, and (2) that at TN, the population density increases *linearly* from 1993 to 1996 (1.8 ind. more per year), and from 1996 to 2002 (0.35 ind. more per year) the total bioerosion of the *E. mathaei* population can be estimated:

$$\int_0^3 0.113(1.8x + 8.2).dx + \int_0^6 0.113(0.35x + 13.6).dx = 13.6 \text{ kg.m}^{-2}$$

This approximative value of 13 kg.m^{-2} (that corresponds to the amount of CaCO_3 grazed by the *E. mathaei* population in 9 years), allows us to better understand how the *E. mathaei* population contributes to the decrease of dead coral coverage in this outer zone of the reef flat.

Holothurids. Sea cucumbers, as deposit-feeders, collect food by swallowing large volumes of sediment requiring both microbial and non-living organic matter (Lopez & Levinton, 1987). Numerous holothurid species remain hidden during the day, and their density is also underestimated but less markedly than that of sea urchins. At Site-P, densities of holothurids are far higher than at Site-T, but, from 1993 to 2002, they decreased, in conjunction with the demise in primary producer coverage. Their abundance at Site-P appeared then to be linked to the abundance of primary producers as the bulk of detritus derives mainly from algae (Lewis, 1977). Similarly, Frouin (2000) found a significant difference in ACR and MAS soft-bottom communities.

Conand & De Ridder (1990) and Mangion *et al.* (2004) explained the high density of sea cucumbers in the P-back reef by a high amount of organic matter but also by the reproductive strategy of one of the dominant species, *Holothuria atra*. Conand (1996) reported that 20 percent of the *H. atra* population reproduce asexually in the P-back reef, by transverse fission followed by regeneration of both parts, whilst in the P-coral zone, *H. atra* is much larger and reproduces sexually. In the Western Central Pacific, *H. atra* apparently shows the same two reproductive strategies (Conand, 1998).

Stegastes. These opportunistic damselfish settle on dead corals (Letourneur *et al.*, 1993; Naim *et al.*, 1997; Letourneur, 2000), and are rare or absent from back reef areas. Among the *Stegastes* species recorded here, *Stegastes nigricans* was the dominant species, as demonstrated by Letourneur (1992) on Reunion reef flats. Its dominance among the *Stegastes* community can vary in time (Naim & Tourrand, unpublished).

From 1993 to 2002, the *Stegastes* density was not significantly different between Sites T and P. Very low in 1993 at both sites, the density showed a significant increase in 2002, but to a lesser extent at Site-P. Later, from 1998 to 2009, the *Stegastes* density significantly increased at Site-T and decreased at Site-P. Done *et al.* (1991) emphasized the importance of *Stegastes nigricans* and their turf territories in the dynamics of the benthic community structure. In Reunion, further investigations are needed to better understand the ecological role of this key species of the reef flats.

Primary producers and living corals: do the two sites, T and P, behave oppositely?

Despite the lack of a quantitative approach, the earlier observations are of some interest. As far as we know, in the 1970s, coral populations were luxuriant on the Reunion reef flats (Montaggioni, 1978; Faure, 1982; Bouchon, 1996). In 1983, Guillaume *et al.* reported that 80% of corals were dying: *Acropora* corals from the reef flats and *Porites* on the outer slope down to 20 m deep were particularly affected. This coral demise was at that time partly attributed to a decrease in water quality.

Year 1983 is since known to have been typified by strong positive Sea Surface Temperature (SST) anomaly in the southwest Indian Ocean (**Table 6**). Observations on Sites T and P have begun from 1985.

Site-T. From 1985 to 1992, the inner TL and the outer TN coral zones were characterized by a high coverage in branching corals (Naim, 1989). Data available indicate a very high coverage with a very low standard deviation: TL: $70.0 \pm 5.2\%$ in April 1987 (Naim, 2006), TN: $65.1 \pm 1.6\%$ in January 1992 (Chabanet, 1994).

In September 1992, the *Acropora* assemblages suffered a sharp deterioration due to an important bleaching event, explaining the very low living *Acropora* coverage recorded in 1993. The bleaching occurred mostly on the oceanic side of the reef flat and the associated mortality of *Echinometra mathaei* suggested that corals were not affected by a bleaching event induced by high sea-surface temperature nor by extreme low tides. Hypotheses of a potential contaminant supplied by the ocean waters rather than by terrigenous inputs, or of inimical environmental conditions, were advanced. The sewage treatment plant, established close to the Ermitage ravine at the end of the 1980s, was suspected to release toxins to the ocean and then to the reef. Later, *Acropora* colonies resettled, but without achieving their highest recorded coverage.

From 1985 to 1998, the primary producers remained inconspicuous and living corals dominated. Since 1999, the coverage of primary producers increased and in the 2004-2007 period, it overtook the living coral coverage suggesting that the abiotic conditions became more favorable to algae and/or unfavourable to living *Acropora* (part 2 of the paper). In the same period, the increase in *Stegastes* densities corroborates this assertion.

Site-P. At Site-P, in 1985-1988, corals could be overgrown by macroalgae within one month (Naim, 1993). In 1995, algal amounts dropped; although still dominant in coverage, their thickness significantly decreased and coral overgrowth by macroalgae was no longer observed (part 2, Naim *et al.*, 2013a). From 1999, the primary producer coverage began also to decline and massive corals appear to do better. Similarly, in the Caribbean (Gardner *et al.*, 2003) and Pacific Southeast Asia (Bruno & Selig, 2007), the greatest decline in coral coverage occurred in the 1980's, due to multi-stress factors such as diseases, hurricane activity and pollution.

Sites T and P. In summary, in the 1980s, corals at Site-T were flourishing while at Site-P, they were overgrown by macroalgae. Then, from 1999, the Site-T health was getting worse, while Site-P health was improving. In 2009, a sharp deterioration at Site-P occurred while a slight health improvement occurred at Site-T.

The two sites seem to behave oppositely. According to Join (1991), at Site-P, the sand aquifer seeps onto the reef flat at low tide and at Site-T, seeps through the reef framework to trickle down on the outer slope. This freshwater affects coral communities (Cuet *et al.*, 1988, Chabanet, 1994; Chabanet *et al.*, 1995).

At the end of the 1990s, nutrient-pollution through groundwater discharge greatly decreased at Site-P, suggesting that the connection of coastal homes to the sewage plant increased (Cuet, 2007). However, the increase in incoming sewage waters is correlated to an increase in discharge of the sewage plant into the Ermitage ravine (36%), and by infiltration in the ravine sub-flow (64%) (www.tco.re). The ravine water flows then southwards and northwards to the ocean and then flows back

onto the reef (Biais & Kopp, 1981) and may bring contaminated water to the inflow Site-T.

Moreover, from 1994, a major project was intended to transfer water available in two rivers in northern and eastern shores of the island, which were well watered, to the west coast, which is naturally arid. It included two major projects: Gallery Mafate and transfer of Salazie. Mafate work started in 1989 and ended in 1999 with the commissioning of « antennas 0 and 4 » (Borca & Margaloff, 2004). In a normal year, the contribution will transfer to the West in low water 60,000 m³ from Mafate and 200,000 m³ from Salazie. The project will ultimately irrigate 7,300 hectares of sugar cane on the West watershed (including new 5.150 ha) (**Fig.7**); this represents a peak demand in a normal year of 260,000 m³.day⁻¹ (SAGE ouest, état des lieux 2006).

While the sewage treatment resulted in improvement in health at Site-P, the increasing freshwater flux, contaminated or not, to the Ermitage watershed may possibly account for the alteration of *Acropora assemblages* at Site-T.

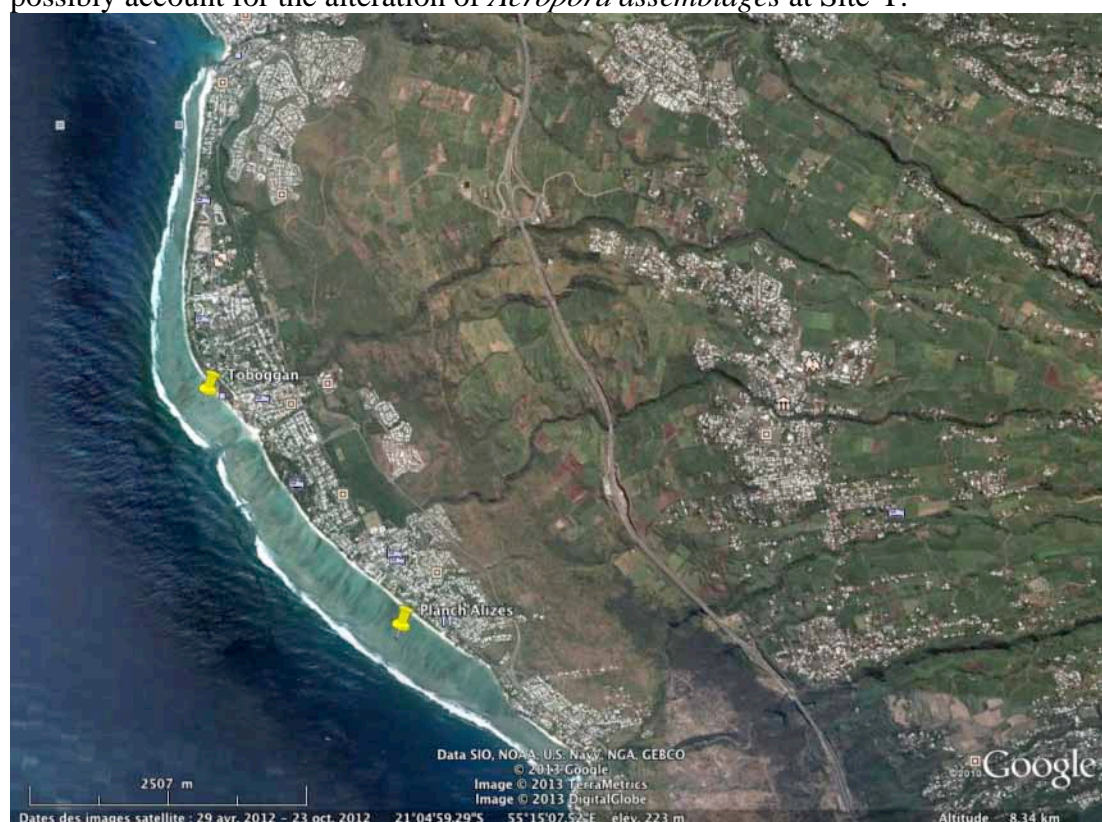


Figure 7: The Saint-Gilles la Saline watershed

Although Tessier *et al.* (2008) showed that increase in sea surface temperature weakly influences the structure of coral populations at Reunion, the 1998 temperature anomaly can be regarded as one of the most prominent factors that are controlling regional change in coral coverage in the Indian Ocean (CORDIO, 1999). Thus, it can be hypothesized that Reunion stands of *Acropora* may have been undermined by this event.

Causes of coral degradation (other than nutrient-enrichment)

Climatic causes of degradation, including cyclone impacts, high SST, extreme low tides, together with crown-of-thorns outbreaks, may have also important impacts

on r-strategist *Acropora*. Nutrient-enrichment is treated in detail in part 2 of the paper (Naim *et al.*, 2013a).

Crown-of-thorns outbreaks. In Reunion Island, research on *Acanthaster planci* outbreaks has been sporadic. On the outer slope, aggregations of tens of individuals have been observed (Faure, Conand, non published), but on the reef flats, only a few isolated individuals have been observed. Degradation of *Acropora* cannot then be attributed to starfish predation.

Runoff, cyclonic impacts. The west coast of the island is generally protected from the impact of hurricanes. However, some cyclones, such as Firinga (1989), Dina (2002) and Gamède (2007) have seriously affected the west and south coasts. In 1989, Saint-Leu and Saint-Pierre coral colonies were destroyed by 99% (Letourneur *et al.*, 1993; Naim *et al.*, 2002) but the *Saint-Gilles La Saline reef* corals remained relatively unaffected.

At the beginning of the 1990s, a runoff outlet was set up at the T-shore, in order to clear out the flooding of the urbanized coastal plain. The runoff has certainly contributed to coral degradation because turbid water plumes occur in the T-coral area after heavy rains. Nevertheless, the coral area is probably relatively protected from runoff by the incoming oceanic waters and by a strong coastal current that flows southwards, to the pass.

For the Site-P, the impact of hurricanes is not really apparent. At both sites, coral breakage due to cyclonic events is negligible, compared to the anthropogenic effect.

Sedimentation processes. Given the strong impact of human activities on the coastal beaches, depositional processes have changed qualitatively and quantitatively on both sites. Beach erosion is intense at Toboggan and contributes to fill the back reef area.

Global change: regional implications. Considering regional-wide changes in composition of coral assemblages, coral reefs throughout South Asia and the central and the western Indian Ocean seem to be undergoing significant changes in coral community composition. This is a result of differential mortality among adult colonies of different genera. *Acropora*, which was easily the most abundant and diverse genus in the Indian Ocean, is now conspicuously absent or has become rare due to severe bleaching events (Obura *et al.*, eds, 2008; McClanahan *et al.*, 2007).

At *Saint-Gilles La Saline*, a number of bleaching events were recorded (**Table 6**), and *Acropora* was recognized as the most sensitive genus by Conand *et al.* (2002b). Nevertheless, after all these events, although the coverage declined since the 1980s at Site-T, and in 2009 at Site-P, both living *Acropora* at Site-T, and living massive corals at Site-P, show a coverage of 40 to 50% in 2011, which can be considered a high coverage.

ACR coral zones such as “Toboggan” and “Petit Trou d’eau” have been included into a sanctuary area in 2007. This will favour the resilience capacity of *Acropora* communities. In this context, in addition to monitoring the coral populations in the reserve after the initial state (Bruggemann *et al.*, 2007), further monitoring of the T-coral zone is required, especially focusing on benthic communities, coral biodiversity and abiotic conditions, in order to see if, in the

absence of direct human impacts, *Acropora* coverage is able to recover its previous 1980s health state or if it is still delayed by pollution effects and/or bleaching events.

Table 6: Significant bleaching events, extreme low tides recorded in Reunion and/or in the southwest Indian Ocean (due either to climatic conditions or low tides). T180: Site-T, 180m from the beach. General data come from Burke *et al.* (2011).

Year	Events
1983	Guillaume <i>et al.</i> (1983) reported a high coral bleaching and mortality event on Reunion reef flats and along outer slopes. This episode also affected the Mozambique channel (Mayotte Island, Faure <i>et al.</i> , 1983, 1984), Indonesia (PulauPari, Seribu island, Dauget, 1983), and the Pacific coast of Panama (Gulf of Chiriqui) and Galapagos (Glynn, 1983).
1987	In April, 30% of <i>Acropora muricata</i> bleached and died over the whole <i>Saint-Gilles La Saline</i> reef flat (Naim, 2006). In addition, this bleaching event affected Saint-Leu and Saint-Pierre reef flats: other <i>Acropora</i> species including <i>A. digitifera</i> , <i>A. abrotanoides</i> , <i>A. austera-hemprichi</i> , <i>A. cytherea</i> , ... but also <i>Platygyra</i> , <i>Millepora</i> were totally bleached to death.
1992	A large bleaching event was observed at Site-T in September, and around the mouth of the Ermitage ravine. This event may be related to a possible pollution from the Ermitage sewage treatment plant.
1998: the extreme El Niño-La Niña switch	This climatic event resulted in the most extensive coral bleaching and mortality ever recorded with approximately 16% of the world's coral reefs being destroyed (approximately 3/4 of the bleached corals recovered). The warm phase was particularly devastating to the western Indian Ocean (Quod, 1999; Goreau <i>et al.</i> , 2000, Turner <i>et al.</i> , 2002). However, while some locations, such as the Maldives, Comoros, Mayotte and the inner Seychelles suffered 75-99% mortality, in Reunion, in 1998, the coral coverage was the highest for the 1990-2000 period (GCRMN data).
1999	In 1999, Tessier <i>et al.</i> (2008) reported exceptional low tides.
2001	In March 2001, a large bleaching event occurred in the <i>Saint-Gilles La Saline</i> reef. Bleaching affected more than 45% of living corals at Site-T and 70% at Site-Livingstone (mainly <i>Acropora</i> communities) (Turquet <i>et al.</i> , 2002).
2002	Early in the year 2002, large scale bleaching affected the world's largest continuous coral reef. More than 60% of the Great Barrier Reef bleached and up to 5% was severely damaged as a result. Bleaching events have also been recorded in Rodrigues in February (Hardman <i>et al.</i> , 2007). At Site-T, <i>Acropora</i> corals were flourishing, indicating that they recovered from the 2001-bleaching event.
2003	In February 2003, a new local bleaching phenomenon is recorded in Reunion, with variable intensity. The more affected sites were situated on the North of Saint Gilles La Saline, Pointe des Chateaux and Colimaçons (St Leu reef). Since 2001, Site-Livingstone showed a very low recovery (living coral cover < to 8%) (Turquet <i>et al.</i> , 2002). In the T-coral zone, <i>Acropora</i> bleached and a month later, all colonies of <i>A. austera-hemprichi</i> were dead (Naim & Tourrand pers.obs.), explaining in part the decrease in living coral coverage in 2004 (GCRMN). In Mauritius, McClanahan <i>et al.</i> (2005) documented 24% coral death.
2004	In 2004, a bleaching event affecting Site-T caused a decrease in coral coverage from 41 to 27% at Site-T while Site-P was hardly affected (GCRMN, Tessier <i>et al.</i> , 2008).
2005	Coral bleaching reported affected western Madagascar, Mauritius, and Reunion in March-April but did not cause significant mortality.
2009	In March, corals bleached intensely at Saint-Gilles la Saline. A large number of species were affected, including <i>Pavona</i> spp, <i>Pocillopora damicornis</i> , but also the fire coral <i>Millepora</i> , Alcyonarians. The species <i>Porites nigrescens</i> appeared to be the most resistant. Since 2004, it was the most widespread bleaching phenomenon at Reunion. Global sea surface temperature measurements (NOAA) in this period suggested a coral bleaching related to thermal stress. GCRMN: at Site-T, half of <i>Acropora muricata</i> coverage bleached but was not dead at the time of the analysis. At Site-P, Cauvin observed a reduction of 50% living coral coverage whereas this coverage remained relatively stable for 11 years. <i>Montipora circumvallata</i> and <i>Porites (Synaraea) rus</i> and the few <i>Acropora muricata</i> were affected but only <i>P. (S.) rus</i> recovered. Living <i>M. circumvallata</i> coverage dropped from 34% in 2008 to 10% in 2009.
2010	GCRMN: at Site-T, <i>Acropora muricata</i> recovered from the 2009-bleaching event, and the living coral coverage still reached 43%. At Site-P, in 2010, some <i>Montipora circumvallata</i> recovered (2009 : 10% coverage, 2010 : 15%). <i>Porites (S.) rus</i> , which has withstood the 2009-bleaching, became the dominant species (2009 : 14%, 2010 : 20%).

Climate change is now considered to be one of the greatest long-term threats to coral reefs, with some future unavoidable change despite mitigation efforts (Hughes *et al.*, 2003; Bellwood *et al.*, 2004; Wild *et al.*, 2011). Managers must therefore focus on supporting the natural resilience of reefs, requiring identification of resilient reefs and reef regions. Considering the 1998-bleaching event in the southwest Indian Ocean, coral coverage suffered negligible damage in South Africa (Obura, 2005). Similarly, in Mauritius the impact was minimal with less than 10% coral cover affected (Moothien-Pillay *et al.*, 2002; Turner & Klaus 2005) although,

later, in 2004, 24% was affected (McClanahan *et al.*, 2005). After these two events, in Mauritius, coral cover was still dominated by thermally sensitive genera such as *Acropora* and overall cover appeared to have risen since a broad survey in 1992 (McClanahan *et al.*, 2005). Graham *et al.* (2007) recorded the composition and distribution of benthic and fish communities on a reef flat in Mauritius during five surveys between 1994 and 2005. They reported a trend of increasing coral coverage and the dominance of *Acropora*, highlighting Mauritius as a regional refugium for temperature-sensitive corals and specialized species of fish.

In the southwest Indian Ocean, McClanahan *et al.* (2007) showed that, from Kenya to Mauritius, coral communities were less disturbed, with *Acropora* and *Montipora* as dominating forms. Similarly, a survey of coral along Madagascar's northeast coast by researchers from Conservation International (CI), suggests that these island's reefs may have so far escaped the damaging effects of warmer ocean temperatures attributed to global climate change.

These findings suggest that the southern Indian Ocean often escape rising temperatures. In the Mascarenes, 189 reef-building coral species were recorded and *Acropora* was considered as the most diversified genus with 39 species (Faure, 1982; Faure *et al.*, 2008). Reefs from the southern Indian Ocean region can contribute then to the maintenance of *Acropora* biodiversity in the southwest Indian Ocean. These living *Acropora* may ultimately be used to reseed damaged reefs and may also provide valuable information about how to protect corals from future damage.

CONCLUSION

In summary, the ACR-type community, typified both by the abundance of several *Acropora* species and by dense populations of sea urchins, has occurred at Site-Tobbogan for 25 years at least. During the same time interval, Site-Planch'Alizés has been occupied by the MAS-type community as dominating features. This is typified by massive corals, abundant benthic primary producers and lack of sea urchins. There is a greater temporal variability of composition of the ACR assemblages, due to a higher sensitivity of acroporids to ambient disturbances. However, recovery of ACR is quite rapid, resulting in *Acropora* populations recovering at a rate of up to 5% per year. By contrast, the cover rate of massive corals is more stable through time, except for some exceptional bleaching events (2009). Perennial macroalgal stands which invaded the MAS community during the 1980's, declined in abundance from the beginning of the 1990's. Related to this, massive coral colonies increased in coverage. Sea urchins permanently remained absent from the MAS assemblages and, as such, undergrazing lasted until now. In 2011, ACR and MAS communities still remain apparently luxuriant on the reef flats of Reunion.

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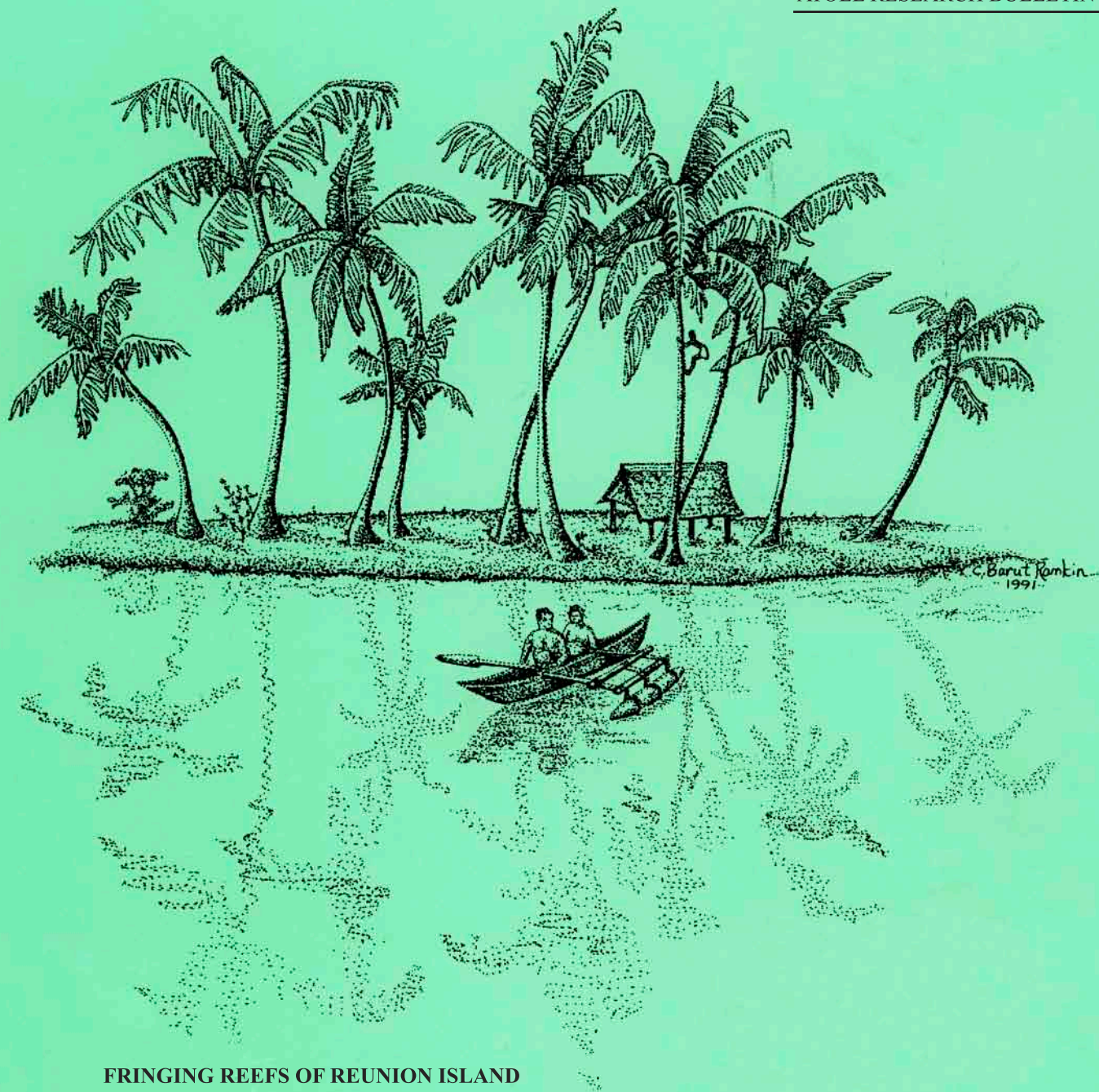
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