

**FRINGING REEFS OF REUNION ISLAND
AND EUTROPHICATION EFFECTS**

No. 596

PART 1: Long-Term Monitoring of Two Shallow Coral Reef Communities

*Catherine Tourrand, Odile Naim, Lionel Bigot, Christophe Cadet, Bruce Cauvin,
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PART 2: Long-Term Monitoring of Primary Producers

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PART 3: Long-Term Monitoring of Living Corals

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FRINGING REEFS OF REUNION ISLAND AND EUTROPHICATION EFFECTS. PART 3: LONG-TERM MONITORING OF LIVING CORALS

BY

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ABSTRACT

Spatio-temporal variations of living coral coverage, species richness and diversity were studied on two fringing reef sites at *Saint-Gilles La Saline* on Reunion Island from 1987 to 2009. The Site-Toboggan (T) was characterized by oligotrophy, *Acropora* corals, abundant sea urchins and few primary producers. The Site-Planch'Alizés (P), was characterized by heterotrophy, massive corals, abundant primary producers and rare sea urchins. From the shore to the outer reef slope, both reef flats comprise the back reef at around 1.5m deep ('B'), coral zone 'L' with large shore-normal strips of coral 0.8m deep, coral zone 'N' with narrow shore-normal strips of corals at around 0.4m deep, and an outer reef flat (<0.4m deep, with breaking surf - not studied).

Results are reported in three parts: (1) for 1993, 1996, and 2002, when the survey takes into account the reef flat as a whole on both sites ; (2) for 1987, 1993, 1996 and from 1998 to 2009, when the survey follows changes in two permanent transects on each site ; (3) for 1970 to 2009, in which species richness of Reunion in 2009 is compared to records of species richness over the last 40 years.

In the period 1993 to 2002, a total of 36 coral species was recorded (31 species at T, 19 at P). In 1993, after a 1992-bleaching event, *Acropora* coverage was low and only 3 species were recorded (*A. muricata*, *A. cytherea*, *A. abrotanoides*). By contrast, in 2002, when *Acropora* cover was much higher, there were 11 species, but only two at P in the 1993-2002 interval. The highest coral diversity (Shannon index, H') occurred on the N coral zone at T in 1996, following an increase from 1993, and after which it declined, as the staghorn coral *A. muricata* strongly increased its cover. By comparison, non-*Acropora* coverage remained relatively stable at T. At P, coral coverage increased from 1993 to 2002 in both coral zones but only the increase of *Porites* (*Synaraea*) *rus* was statistically significant. Overall, trends in coral cover and diversity indicate both sites were in better health in 2002. Between 1987 and 2009, changes in the smaller fixed LITs were not typical of the overall trends. Among the

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three dominant species, *Acropora muricata*, *Montipora circumvallata* and *Porites (Synaraea) rus* there was no significant temporal variation at either site (reflecting the small sample size and high variance), although the *P. rus* coverage increased regularly.

The number of coral species on the reef flats may have slightly decreased in the last 40 years. Faure (1982, 2009) recorded 74 species in the 1970s and 71 species in 2009, of which 36 species were recorded on inner reef flats and 62 species on outer reef flats. The number of species recorded by Faure on inner reef flats is the same as we recorded in survey 1. On *Saint-Gilles La Saline*, the genus *Stylophora* was totally absent from 2009 surveys (*Stylophora pistillata* was always rare on Reunion reefs but *S. mordax* was previously very common on the reef flats and outer slopes). At time of writing, the genus has only been recently observed on wave-exposed reef platforms (reef flats and outer reef slopes). In 2009, the third species, missing from Faure's records, is *Favia rotumana*. *F. rotumana* was very common in 1970s on the outer reef flats, but has not been sighted there.

This study suggests that *Acropora* abundance and diversity are reliable indicators of autotrophic functioning. *Acropora muricata* (formerly *A. formosa*) and *A. digitifera* are considered as the most eurytopic *Acropora* species present in Reunion, while *Acropora austra* is considered as environmentally sensitive and perhaps, one of the sentinel species on the reef flat. Many observations suggest that eurytopic *Montipora circumvallata* and *Porites (Synaraea) rus* may both be favored by nutrients and able to tolerate pollutants and large variation of abiotic factors such as temperature and salinity. *Acropora*, though becoming a rare genus in many areas, has been able to recover rapidly in Reunion, and are resilient in the period covered by the present study.

Key words: Coral reefs, benthic community, living corals, *Acropora*, *Acropora muricata*, *Acropora austra*, *Montipora circumvallata*, *Porites (Synaraea) rus*, *Stylophora mordax*, *Favia rotumana*, Faviidae, sea urchins, coverage, diversity, species richness, subtidal, stability, bioindicator.

INTRODUCTION

Health and biodiversity of coral reefs are declining world wide (Gardner *et al.*, 2003; Bellwood *et al.*, 2004; Carpenter *et al.*, 2008; Obura *et al.*, eds, 2008). In the Indian Ocean, human use of coral reefs has increased dramatically in the last few decades (Sheppard, 2000). The coral reefs of the Mascarene Islands (e.g. Reunion, Mauritius and Rodrigues), although far away from major pollution hotspots, are no longer pristine: over-nutrition, hypersedimentation and overfishing are major causes of stress (Naim *et al.*, 2000; Turner & Klaus, 2005). Coral bleaching has had a medium impact to date, although anomalies in subsurface water temperatures have increased (McClanahan *et al.*, 2007; Tessier *et al.*, 2008; Tourrand *et al.*, 2013).

Stony corals are responsible for the very existence of the reef ecosystems. While alive, coral assemblages form a living veneer and provide shelter for many other reef-dwelling organisms. In the 1970's, the reefs surrounding Reunion were renowned for the high abundance and diversity of corals (Faure, 1982; Bouchon, 1996). Reunion reef flat corals shelter many young fish (Letourneur, 1992; Chabanet, 1994; Letourneur *et al.*, 1998), and associated fauna (Ribes, 1978). Blatant

degradation was observed from 1983 (Guillaume *et al.*, 1983) but better water management as well as the creation of a marine reserve in 2007 tend to alleviate these impacts. Coral coverage can be an useful indicator of responses to large-scale disturbances (Bruno & Selig, 2007; Ateweberhan *et al.*, 2011), but the specific composition of the coral assemblages can also be a clear reflection of reef health (Loya *et al.*, 2001). The present paper aims to investigate the evolution of the main coral species present at two selected sites (“Toboggan”, Site-T, and “Planch'Alizés”, Site-P) from the fringing reef-flat of La Saline-Saint Gilles (western coast of Reunion Island) between the 1970s and 2009.

MATERIAL AND METHODS

Generalities

The environmental setting of the *Saint-Gilles La Saline* reef-flat was described and details of methods are given in part 1 (Tourrand *et al.*, 2013). The reef flat was subdivided into 3 zones or subzones, from beach to front: the back-reef zone (B-zone), the coral zone with Large coral strips (L-coral subzone, at mean depths of 0.80m), and the coral zone with Narrow coral strips (N-coral subzone, at shallower depths of 0.40m). According to the considered site, the different subzones were labelled as follows: the back-reef zone: TB-subzone, and PB-subzone, respectively; the inner coral zone with large coral strips: TL and PL subzones; the outer coral zone with Narrow coral strips: TN and PN subzones; the whole coral zone: T_{L+N} and P_{L+N}.

As previously emphasized (Tourrand *et al.*, 2013, Naim *et al.*, 2013), Site-T was characterized by oligotrophic conditions, and a community predominantly composed of *Acropora* corals, abundant sea urchins, together with primary producers (so-called ACR community), while Site-P was typified by heterotrophic conditions, and a community predominantly composed of massive corals, abundant primary producers, together with rare sea urchins (so-called MAS community). Two quantitative surveys were conducted at both sites, during the hot season when algae are most developed (Naim, 1993; Semple, 1997). Survey 1: percent coverage and species composition of corals were estimated at a 1 centimeter resolution, using the Line Intercept Transect (LIT) method (Lucas & Seber, 1977; Loya, 1978) at Sites T and P in 1993, 1996 and 2002. The living coral coverage is noted LCcv. LITs, 50 m in length, are parallel to the reef front, at fixed intervals of 30 m. At 360 m out from the back-reef zone, LIT measurements became too hazardous owing to strong waves breaking at depths not exceeding 0.30 m. Accordingly, the outer reef-flat zone was not investigated. In addition, all the coral species observed while swimming in the two test areas were recorded.

Mean coral coverage is 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 over 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 over the 165 “10m-samples” taken - 55 in each of 1993, 1996 and 2002.

Survey 2 has focused on the monitoring of two permanent transects, one at each site, respectively at 180m and 270m from the beach, in 1987, 1993, 1996 and from 1998 to 2009 (**Table 1**).

Table 1. Summary of the 2 surveys. "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	Estimation 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 and qualitative assessment of coral species located on the 330 * 50 m studied area	1993, 1996, 2002 hot season
Survey 2	Estimation 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 each year from 1998 to 2009, hot season

To assess patterns in benthic data from all stations in all years, we used non-metric multidimensional scaling (MDS) and principal component analysis (PCA), and 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.

Stony corals were identified using Faure's (1982), Wallace's (1999) and Veron's (2000) nomenclatures, and the Iterative Knowledge Base System (IKBS) developed by Faure *et al.* (2008a). The IKBS is based on the collection of the Mascarene corals harvested and studied by G. Faure in the 1970's. Note that the dominant species, so-called *Acropora muricata* according to Wallace (1999) and the Reunion Iterative Knowledge Base System (<http://coraux.univ-reunion.fr/>), was described as *A. formosa* in Veron (2000, vol.1, p.176, see discussion) and in previous papers dealing with Reunion reefs.

RESULTS

Survey 1 (1993-1996-2002, LITs)

Species richness and diversity. From 1993 to 2002, 35 species of living corals, belonging to 12 genera and 8 families, were recorded using LITs at the two sites (**Table 2**), of which 33 species are Scleractinians and 3 Hydrozoans (*Millepora*). Two species were not recorded by the LIT method: *Pavona cactus*, represented by one single colony observed in 1993 in the TL subzone, and *Millepora exaesa*, although relatively abundant in the PB subzone, but missed by LITs.

Table 2. Survey 1: Number of families, genera and species *observed* at both sites (The two species *Pavona cactus* and *Millepora exaesa*, not recorded by LITs, are included in the table).

Living corals	T	P	T + P
Families	8	6	8
Genera	9	9	12
Species	31	20	36

The species richness is higher at Site-T than at Site-P (**Table 2**). At both sites, *Acropora muricata*, *Montipora circumvallata* and *Porites (Synaraea) rus* are dominant (**Fig. 1**). Among *Acropora*, at Site-T, 11 species form 68.3% of the living coral coverage (LCcv), of which 76% were *Acropora muricata* (**Fig. 1, Table 3**). At Site-P, *Acropora* only accounted for 12.6% LCcv (of which 99% were *A. muricata*). Among non-*Acropora* species (NAcr), *Montipora circumvallata* (Mc) and *Porites (Synaraea) rus* (P(S)r) represented 61% of NAcr at Site-T and 89% of NAcr at Site-P, and *M. circumvallata* was roughly twice to three times more abundant than *P. (S.) rus* (Mc/P(S)r ratio: T: 2.1; P: 3.0).

Table 3. Number of species, relative percentage (in coverage) of *Acropora* and of the three dominant species at both sites, *A. muricata*, *Montipora circumvallata*, *Porites (Synaraea) rus* (study 1). (*) *Pavona cactus* at Site-T, *Millepora exaesa* at Site-P.

	T		P	
	Nb species	Relative % (in coverage)	Nb species	Relative % (in coverage)
<i>Acropora muricata</i>	1	52.2	1	12.5
Other <i>Acropora</i> species	10	16.1	1	0.1
<i>Montipora circumvallata</i>	1	13.0	1	58.4
<i>Porites (Synaraea) rus</i>	1	6.3	1	19.4
Other non- <i>Acropora</i> species	17	12.4	15	9.6
Species only observed (*)	1	0.0	1	0.0
TOTAL	31	100%	20	100%

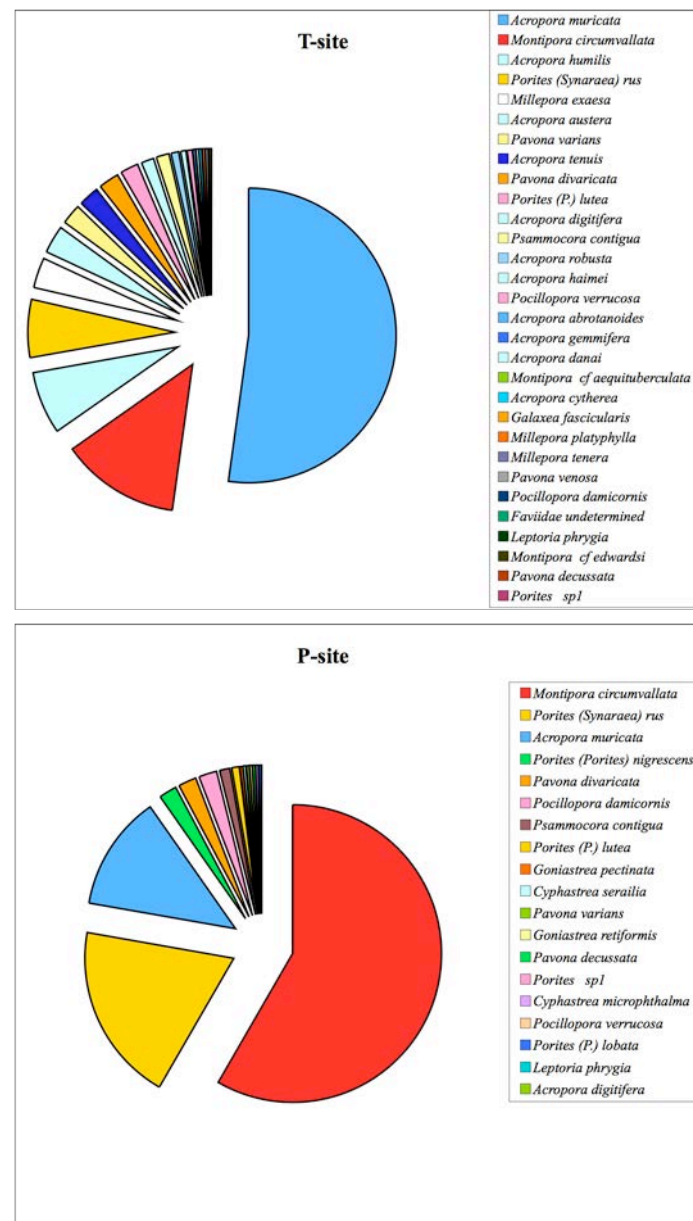


Figure 1: Relative percentage of all the coral species recorded at Site-T and Site-P by LITs (study 1). *Porites sp1* is a branching one. *Pavona cactus* at Site-T, and *Millepora exaesa* at Site-P are not represented here (only observed).

Concerning diversity, the shape of the rank species curve indicates that the two sites present a low diversity and are subjected to significant environmental variations (Fig. 2). Considering the first three dominant coral species on the left, *Acropora muricata*, *Montipora circumvallata*, *Porites (Synaraea) rus*, the curve for Site-T lies below the curve for Site-P, expressing the dominance of one single species (*Acropora muricata*). Then the T-curve goes over the P-one and is far longer, tending to a plateau, thus indicating a higher diversity and a lower ecological disturbance than at Site-P (Frontier, 1985).

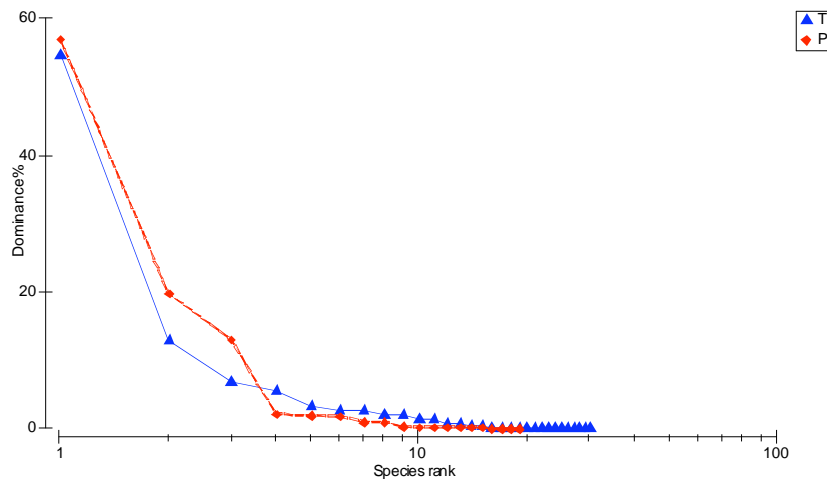


Figure 2: Average ranked abundance curves of living coral species (x-axis: rank, logged), with relative percentage (dominance) on the y-axis at Sites T and P.

Spatio-temporal variations in abundance and diversity. At both sites, the living coral coverage was similar ($T: 17.4 \pm 20.7\%$; $P: 16.2 \pm 16.9\%$), but was higher in the PB than in the TB subzone, and higher in the TN than in the PN subzone. According to the standard deviation, living corals appear to occur randomly at Site-P and mostly in aggregated patches at Site-T.

At Site-T, H' increased from 1993 to 1996 and decreased from 1996 to 2002 while at Site-P, it was increasing from 1993 to 2002 (**Fig. 3a**). Similar variations occurred on the different subzones (**Fig. 3b**), except in TB where H' did not vary very much and in PN where diversity dropped in 2002. In the L-coral subzone, H' was approximately the same at both sites in 1993 and 1996, but became markedly higher in the PL subzone than in the TL one in 2002. From 1993 to 2002, the highest diversity (Shannon index, H') occurred in the TN subzone, and in 1996 (**Fig. 3a,b**).

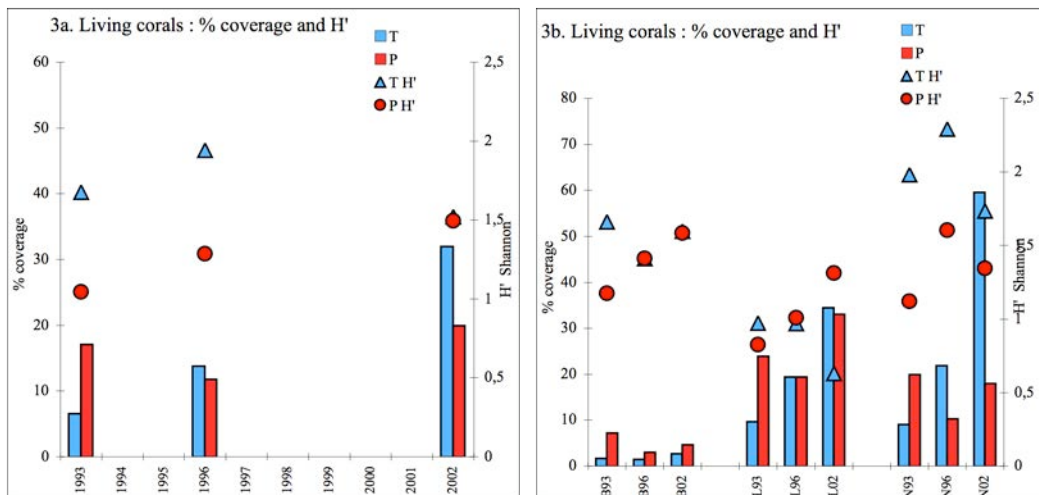


Figure 3a & 3b: Spatio-temporal variation from 1993 to 2002 of the coverage of living corals (in %) and biodiversity (H' Shannon index). Left : across the total site, right: in the three geomorphological zones, B= back reef, L= inner zone of Large coral strips, N= outer zone of Narrow coral strips.

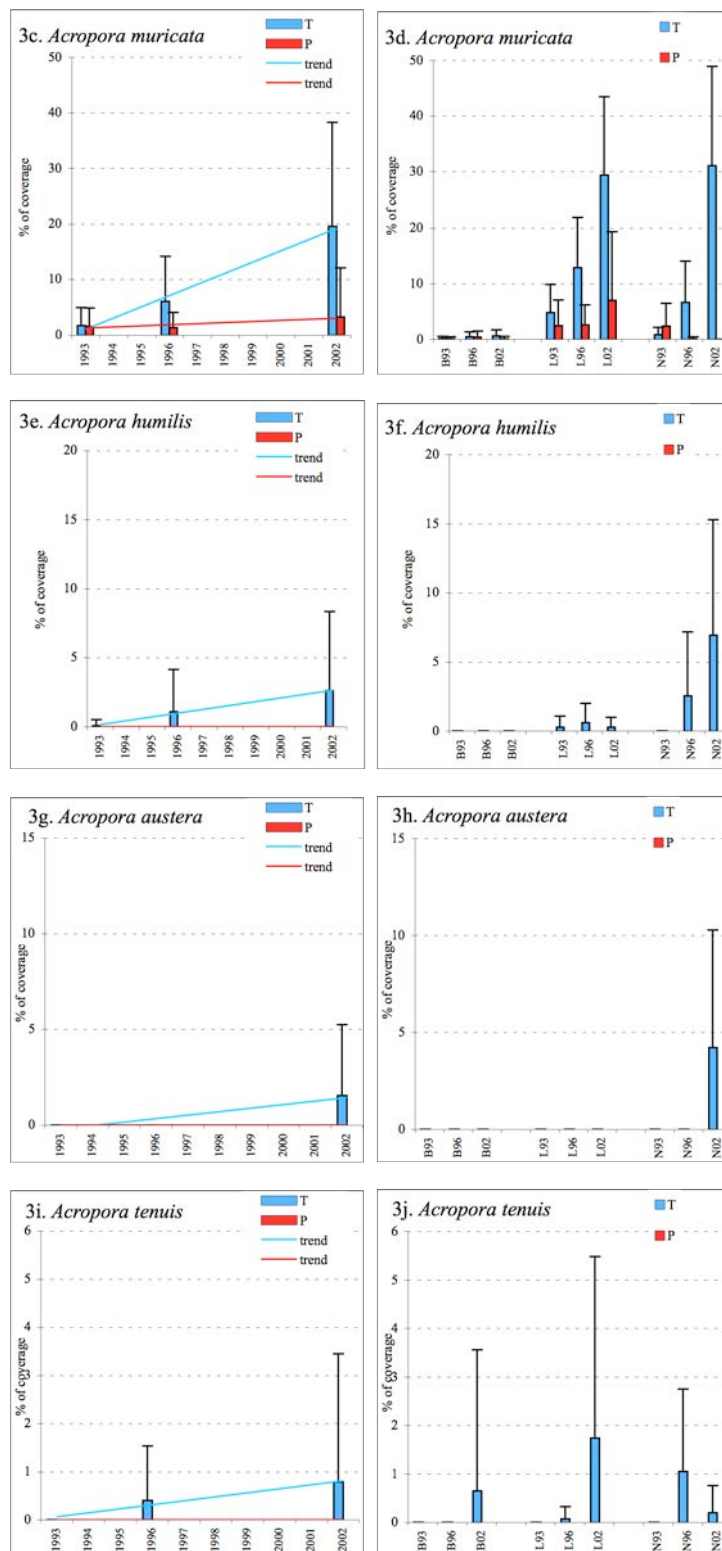


Figure 3c to 3j : Spatio-temporal variation from 1993 to 2002 of the coverage of the dominant *Acropora* species (in %). Left : across the total site, right: in the three geomorphological zones.

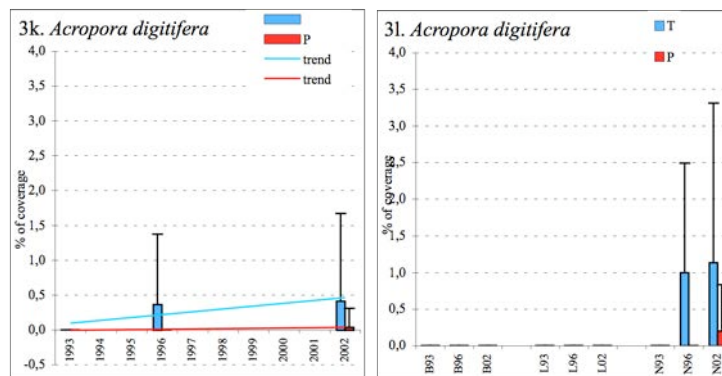


Figure 3k & 3l : Spatio-temporal variation from 1993 to 2002 of the coverage of the dominant *Acropora* species (in %). Left : across the total site, right: in the three geomorphological zones.

From 1993 to 2002, considering *Acropora* at Site-T, the cover rate of the five dominant species, *A. muricata*, *A. humilis*, *A. austera*, *A. tenuis*, *A. digitifera*, was increasing, but only *A. muricata* and *A. humilis* coverages increased significantly (**Fig. 3c to Fig. 3l, Table 4**). In 1993 (year when the lowest *Acropora* coverage occurred in the survey time), only 3 species were recorded (*A. muricata*, *A. cytherea*, *A. abrotanoides*), while in 2002 (highest coverage), 11 *Acropora* were found (see list of species in Fig. 1). Coverage of massive species remained stable.

At Site-P, numerous species, including *Acropora formosa*, moderately increased in abundance from 1993 to 2002, especially in the PL and/or PN subzones, while a significant increase in *Porites (Synaraea) rus* was restricted to the PN subzone (**Fig. 3, Table 4**). *Pocillopora damicornis* was the only species that decreased in the PN subzone, but once more moderately. These trends, although not significant, indicated better health conditions at Sites T and P in 2002.

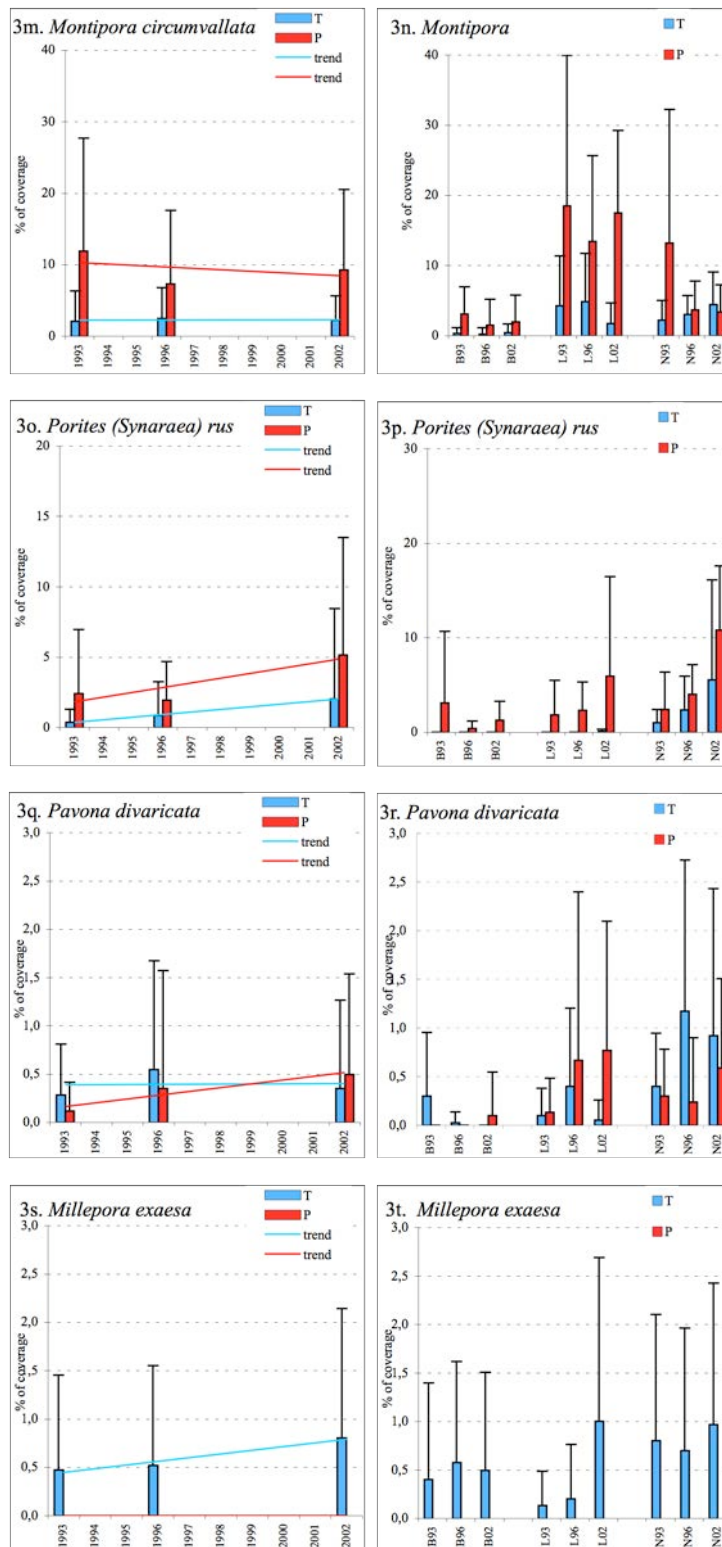


Figure 3m to 3t : Spatio-temporal variation from 1993 to 2002 of the coverage of the dominant *Acropora* species (in %). Left : across the total site, right: in the three geomorphological zones.

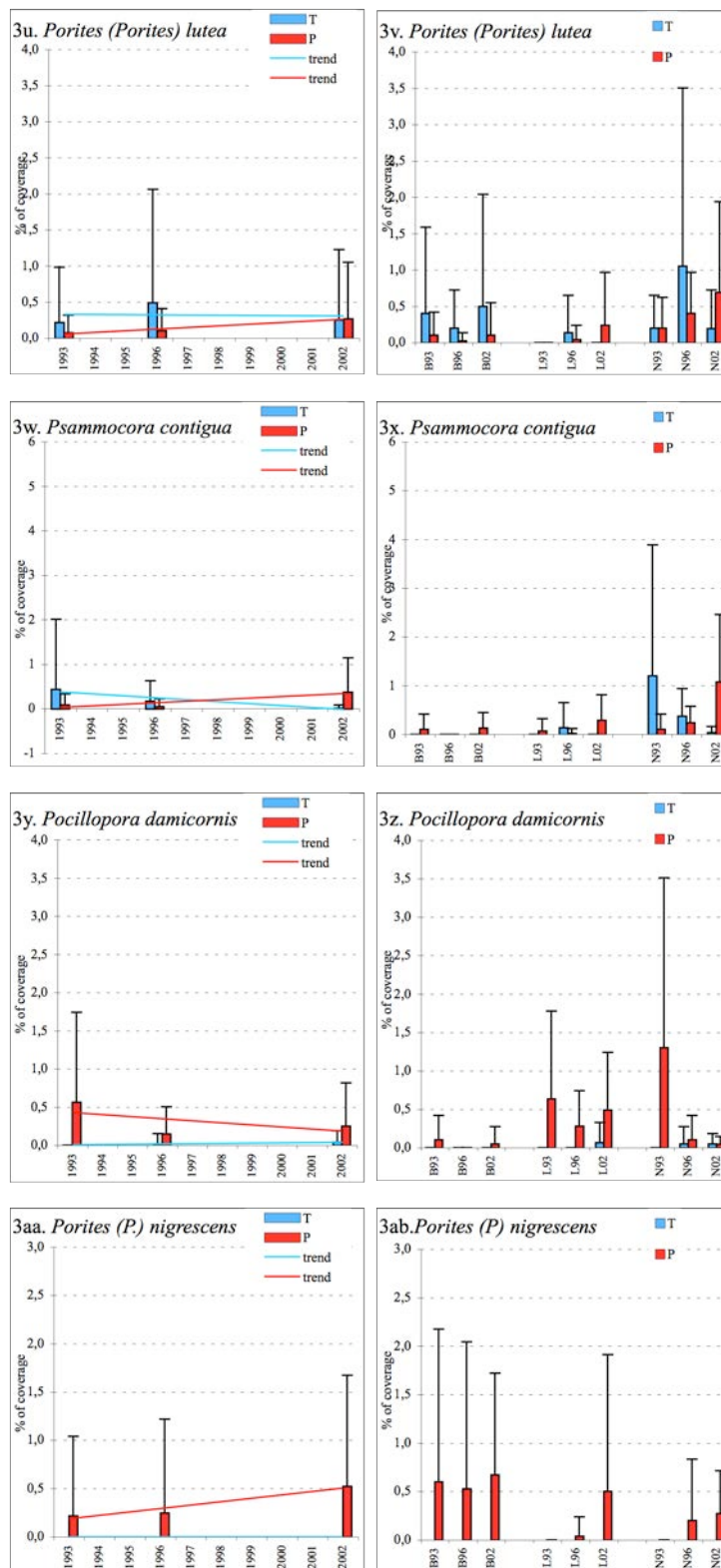


Figure 3u to 3ab : Spatio-temporal variation from 1993 to 2002 of the coverage of the dominant *Acropora* species (in %). Left : across the total site, right: in the three geomorphological zones.

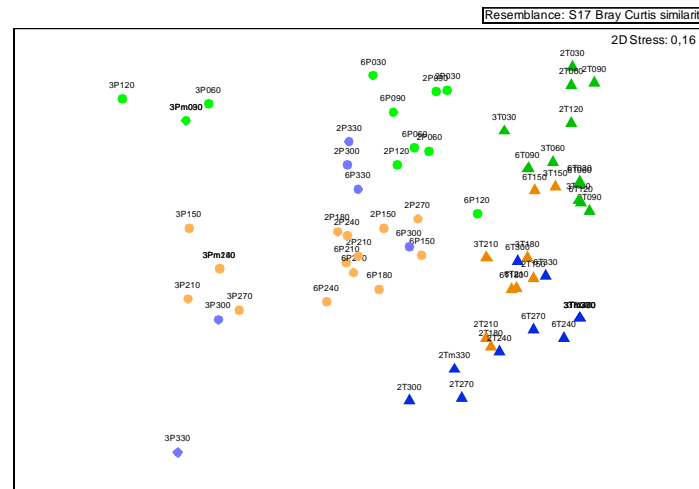
Table 4. Survey 1 (whole site, 1993, 1996, 2002): Kruskal-Wallis test between means (μ) of the variables in the 3 different years, at the two sites (T= Toboggan, P= Planch'Alizés) (>: significant increase, <: significant decrease, Ns: non significant).

		μ 1993- μ 1996	μ 1993- μ 2002	μ 1996- μ 2002		μ 1993- μ 1996	μ 1993- μ 2002	μ 1996- μ 2002
<i>Acropora muricata</i>	T	> p= 0.0247	>>>> p=0.0000	> p= 0.0134	P	Ns	Ns	Ns
	TB	Ns	Ns	Ns	PB	Ns	Ns	Ns
	TL	>> p=0.0093	Ns	Ns	PL	Ns	Ns	Ns
	TN	Ns	>>>> p=0.0000	>>> p= 0.0001	PN	Ns	Ns	Ns
<i>Acropora humilis</i>	T	Ns	> p= 0.0174	Ns	P	absent	absent	absent
	TB	Ns	Ns	Ns	PB	absent	absent	absent
	TL	Ns	Ns	Ns	PL	absent	absent	absent
	TN	Ns	Ns	> p= 0.0188	PN	absent	absent	absent
<i>Porites (Synaraea) rus</i>	T	Ns	Ns	Ns	P	Ns	> p= 0.0220	Ns
	TB	Ns	Ns	Ns	PB	Ns	Ns	Ns
	TL	Ns	Ns	Ns	PL	Ns	Ns	Ns
	TN	Ns	Ns	Ns	PN	Ns	>> p=0.0093	Ns

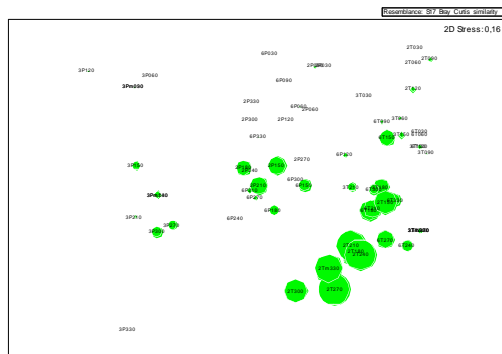
The eight dominant species on both sites. Among the eight dominant species during the survey, three are *Acropora* and five are massive corals. Multidimensional scaling (MDS) shows the exact location on the reef flat of the three dominant *Acropora*. *Acropora muricata* and *A. humilis* were mostly located in the TL and TN subzones, and *A. austera* only in the TN subzone (**Fig. 4b, 4c, 4d**).

Among massive corals, MDS results indicate that the two dominant species, *Montipora circumvallata* and *Porites (Synaraea) rus*, mostly occur in the PB and PL subzones, while *Pavona divaricata* grew in both inner sites (back reefs and L-zones). *Porites (Porites) lutea* were ubiquitous at both sites, but the coverage of *P. lutea* is higher at Site-T than at Site-P because of the occurrence of larger colonies (**Fig. 4e, 4f, 4g, 4h, 4i**). *Millepora exaesa* is abundant on both back reefs but was not recorded by LITs in the PB subzone.

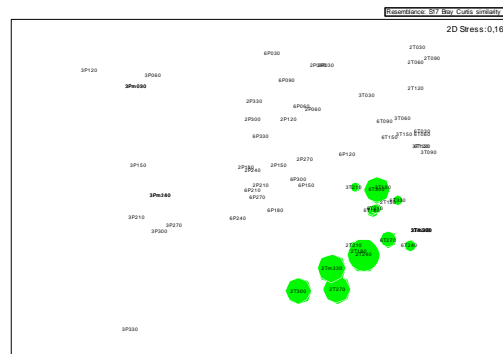
4a. Two dimensional-MDS configuration, all benthic data (see details in Tourrand *et al.*, 2013)
Site-T (triangles) and Site-P (circles). Back reef= green, L-zone= orange, N-zone: blue



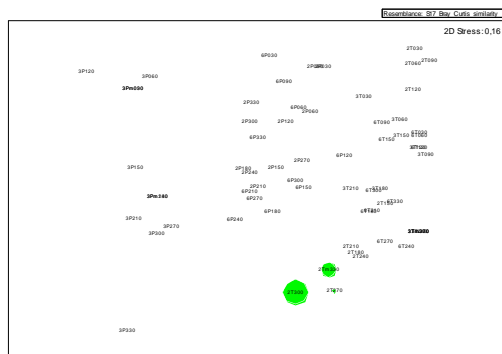
4b. *Acropora muricata*



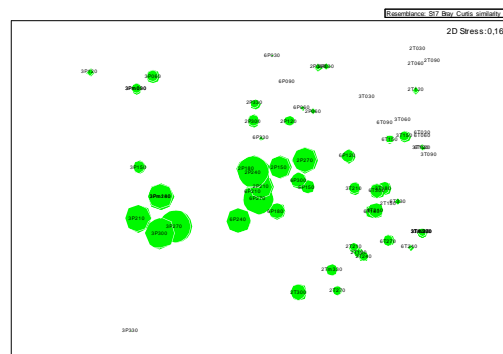
4c. *Acropora humilis*



4d. *Acropora austera*



4e. *Montipora circumvallata*



Figures 4a to 4e: Two dimensional-MDS configuration with surimposed bubbles obtained with a hierarchical clustering of the 58 * 50m-LIT (all benthic data: corals, algae, etc., echinoderms and territorial fish included).

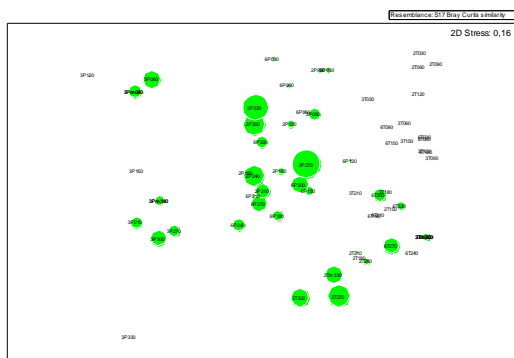
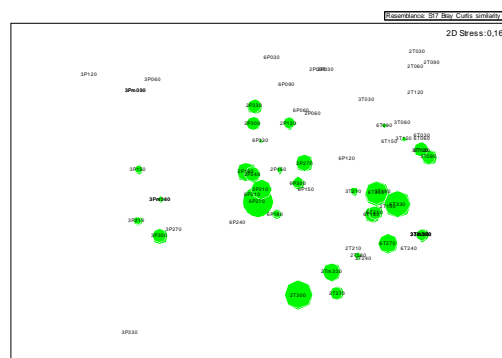
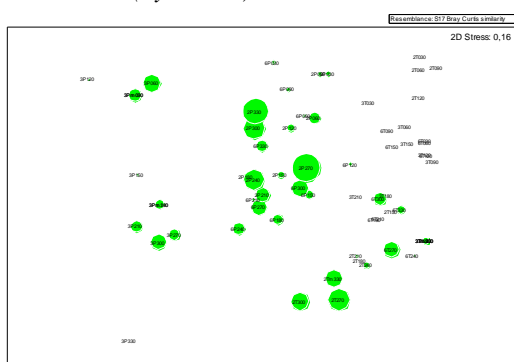
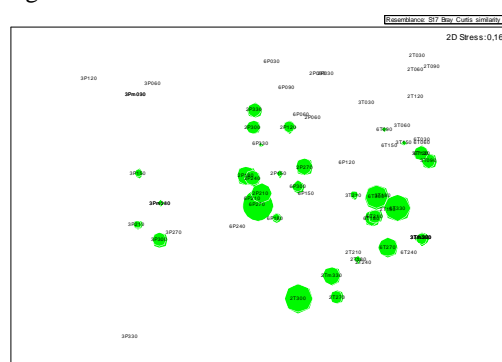
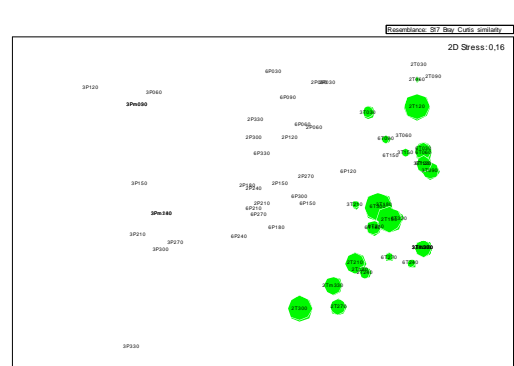
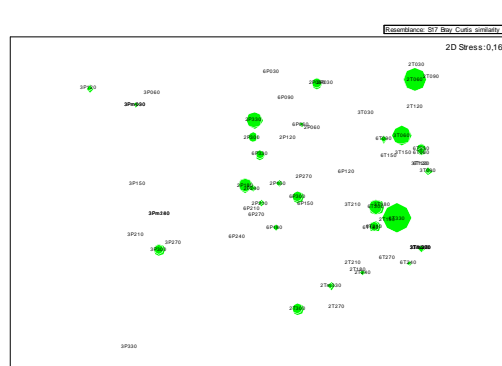
4f. *Porites (Synaraea) rus*4g. *Pavona divaricata*4f. *Porites (Synaraea) rus*4g. *Pavona divaricata*4h. *Millepora exaesa*4i. *Porites (Porites) lutea*

Figure 4f to 4i: Two dimensional-MDS configuration with surimposed bubbles obtained with a hierarchical clustering (all benthic data: corals, algae, etc., echinoderms and territorial fish included).

Principal Component Analysis (PCA) (survey 1, 1993-1996-2002 data together). Using PCA, Factor1 that explains 39.5% of the variance, opposes the back reefs and coral zones (including both Large and Narrow coral strip subzones), owing to the opposition between the dominance of *Porites (Porites) nigrescens* in the PB subzone and that of *Acropora muricata* and *A. humilis* in the T-coral zone (**Fig. 5**).

Factor 2 (24% of the variance) clearly separates the Sites T from P. Discriminating species are given in **table 6** (discussion section).

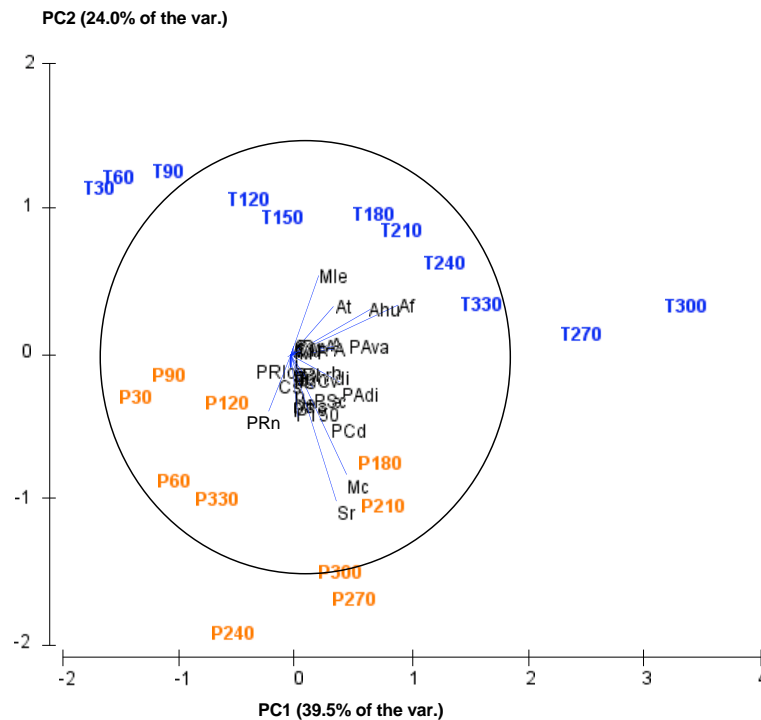


Figure 5: PCA on living corals data, all years (1993, 1996, 2002) together. T= Site-Toboggan, P= Site-Planch'Alizés, T30= Site-Toboggan, 30 meters from the beach. Af= *Acropora muricata*, Ah= *Acropora humilis*, At= *Acropora tenuis*, Mle= *Millepora exaesa*, Mc= *Montipora circumvallata*, PAdi= *Pavona divaricata*, PAVA= *Pavona varians*, PRlo= *Porites (Porites) lobata*, PRn= *Porites (Porites) nigrescens*, Sr= *Porites (Synaraea) rus*.

Coverage and richness according to the distance to shore (survey 1, 1993, 1996, 2002 together). The variation in the living coral coverage, from the beach seawards, is relatively similar at both sites (**Fig. 6a**).

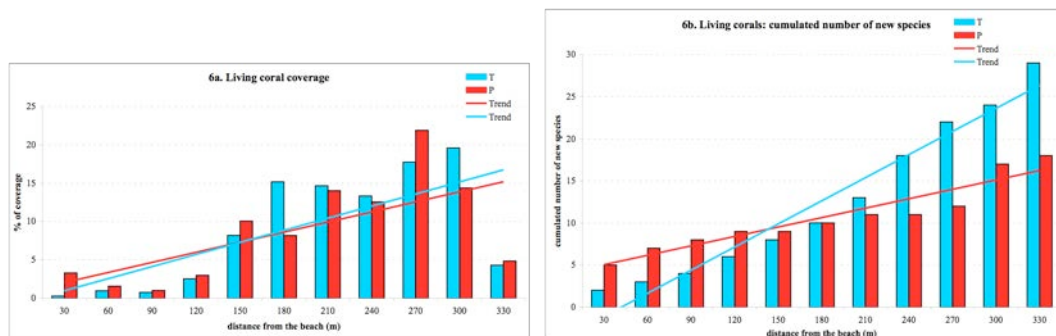


Figure 6a & 6b: living coral coverage and cumulative number of new species of living corals as a function of the distance from the beach.

However, at Site-T, the occurrence of new species increased rapidly from the station at 210 m to the reef front (**Fig. 6b**). *A. muricata*, *A. tenuis*, *A. cytherea* and *A. humilis* were the only *Acropora* species occurring from 30-210 m interval, whereas two-third of *Acropora* species occurred within the 240-330 m interval. Faviidae (1 species) only occurred at the 330 m-station.

By contrast, at Site-P, the number of coral species was high near the shore and increased weakly towards the reef front. Faviidae (5 species) occurred within the 210-330m interval.

Survey 2: from 1987 to 2009

This study, based on the permanent transects T180m and P270m, uses in part the data gained from the Global Coral Reef Monitoring Network (GCRMN). As stated in Tourrand *et al.*, 2013 (Survey 3, section “results”), the monitoring period was divided into 3 periods: 1987-1998, 1999-2003 and 2004-2009. However, the high variance in the results did not allow any detection of significant variations in coral coverage, although *Porites* (*Synaraea*) *rus* coverage steadily increased at P270 from 1987 to 2009 (Fig. 7, Table 5).

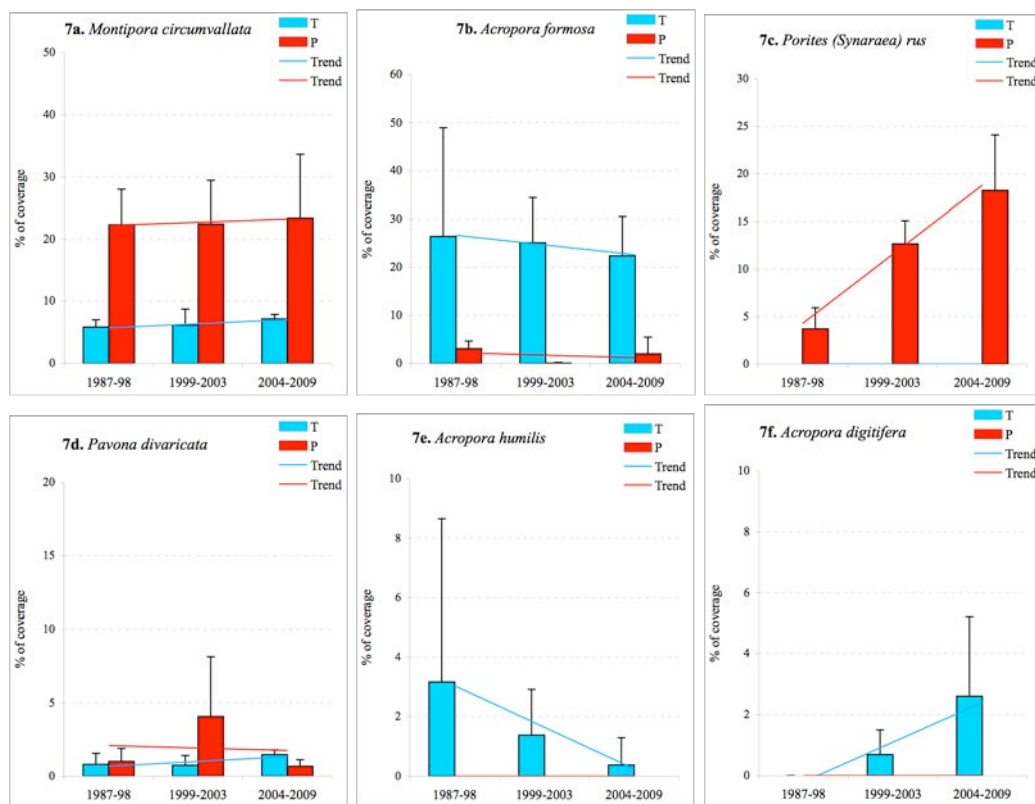


Figure 7a to 7f. Survey 2: temporal variations of the dominant species on the T180 and the P270 transects.

Table 5. Study 2 (GCRMN data): Kruskal-Wallis test between means (μ) of the variables in the 3 "year-blocks", on the two permanent transects (T180= "Toboggan" 180m off shore, P= "Planch'Alizés", 270 m off shore). (Ns: non significant).

		μ (1987-1998)	μ (1999-2003)	μ (1987-1998)	μ (1987-1998)	μ (1999-2003)	μ (1987-1998)
		$-\mu$ (1999-2003)	$-\mu$ (2004-2009)	$-\mu$ (2004-09)	$-\mu$ (1999-2003)	$-\mu$ (2004-2009)	$-\mu$ (2004-2009)
<i>Acropora muricata</i>	T180	Ns	Ns	Ns	P270	Ns	Ns
<i>Montipora circumvallata</i>		Ns	Ns	Ns		Ns	Ns
<i>Porites (Synaraea) rus</i>		Ns	Ns	Ns		Ns	Ns

The apparent inverse variation in the coverage of *A. humilis* and *A. digitifera* (**Fig. 7e, 7f**) may be due to the fact that the two species can be confused.

DISCUSSION

Coral communities at Sites T and P: metabolism and characteristic species

MAS: a phase shift of ACR ? From 1993 to 2002, although the living coral coverage was not significantly different between Sites T and P, the composition of the coral community was totally dissimilar. Site-T was dominated by *Acropora* while Site-P was dominated by non-*Acropora* corals. **Table 6** gives the most characteristic species on the two reef flats (results from PCA, whole site, F2 axis). For Acroporidae, *Acropora* was a distinguishing genus, but *Montipora* was not (see discussion below). The distributional pattern of *Pavona* and *Porites* did not allow the two sites to be differentiated. Faviidae are mostly recorded at Site-P. By contrast, *Galaxea* has never been observed at Site-P.

Table 6. Discriminating coral species in PC2 (24.0% of the variance) in order of importance (Survey 1, PCA on living coral coverage, 1993-1996-2002-data combined).

Site-T	Site-P
1. <i>Acropora muricata</i>	1. <i>Montipora circumvallata</i>
2. <i>Acropora humilis</i>	2. <i>Porites (Synaraea) rus</i>
3. <i>Acropora austera</i>	3. <i>Pocillopora damicornis</i>
4. <i>Acropora cytherea</i>	4. <i>Porites (Porites) nigrescens</i>
5. <i>Galaxea fascicularis</i>	5. <i>Psammocora contigua</i>
6. <i>Pavona varians</i>	6. <i>Pavona divaricata</i>
7. <i>Acropora robusta</i>	7. <i>Cyphastrea serailia</i>
8. <i>Porites (Porites) lutea</i>	8. <i>Goniastrea pectinata</i>
9. <i>Acropora danai</i>	9. <i>Cyphastrea microphthalma</i>
10. <i>Acropora haimeii</i>	10. <i>Goniastrea retiformis</i>
11. <i>Montipora cf aequituberculata</i>	11. <i>Pavona decussata</i>
12. <i>Pavona venosa</i>	
13. <i>Acropora digitifera</i>	
14. <i>Millepora platyphylla</i>	
15. <i>Acropora gemmifera</i>	
16. <i>Montipora cf edwardsi</i>	
17. <i>Acropora abrotanoides</i>	

Despite these differences, the four dominant coral species were the same at both sites: *Acropora muricata*, *Montipora circumvallata*, *Porites (Synaraea) rus* and *Pavona divaricata*. Otherwise, from coast to reef front, the number of newly appearing coral species was slower and remained lower at Site-P (**Fig.6**). This indicates that, at Site-P, ambient conditions were conducive to the growth of some species, but did not permit the hard coral community to reach a high diversity, even in the outer subzone PN, and this despite the fact the reef is very exposed to swells. At Site-T, *A. muricata*, *A. tenuis*, *A. cytherea* and *A. humilis* were the only *Acropora* present in the back-reef zone, whereas two-third of *Acropora* species occurred on the coral zone, within the 240-330 m interval.

Classified as ruderal or r-strategist by Edinger and Risk (2000), *Acropora* genus and, especially *A. muricata/formosa*, have dominated and still are dominating the reef flat overstory space in Reunion (Faure, 1982; Despinoy *et al.*, 2000; Naim, 2002, 2006; Bruggemann *et al.*, 2007; Faure, 2009). When *A. formosa/muricata* is dominant, as at Site-T in 1987 or 2002, very few substrates are suitable for the

settlement of coral larvae. This limits the recruitment by sexual reproduction of any species. *A. formosa/muricata* recruitment is, however, not affected as it reproduces very often by fragmentation of already established colonies on reef flats (Naim, pers. obs., Highsmith, 2002). Numerous sea urchins contribute to help *Acropora muricata* to be dominating by clearing primary reefal producers (McClanahan *et al.*, 1995; Tourrand *et al.*, 2013), and by eroding dead corals (Conand *et al.*, 1997). In this study, the sensitivity of *Acropora* to environmental factors as well as its ability to quickly recolonize space, either in coverage or specific richness, when abiotic conditions are favourable, is demonstrated.

By contrast, massive corals, although possessing stress-tolerant morphologies, become the dominant forms when *Acropora* and other stenotopic corals are mostly excluded by environmental factors (Pastorok & Bilyard, 1985; Rogers 1990; Edinger & Risk, 2000). At Site-P, the two submassive *Montipora circumvallata* and *Porites (Synaraea) rus* are thought to occupy the space vacated by *Acropora*, and particularly by the fast-growing *Acropora muricata* (despite the lack of long-term historical data, it may be assumed that these massive corals have occupied the outflow Site-P for a very long time). Similarly, in Great Comoro, Anasse *et al.* (2003) reported that, after the 1998-dramatic bleaching event, *Acropora* disappeared and was replaced at the beginning of 2000's by a community dominated by Melobesiae (70% of coverage) and by *Pocillopora verrucosa*, *Porites (Synaraea) rus* and the faviids *Platygyra daedalea* and *Favites spp.* In the Caribbean, the coverage of the massive and dominant *Porites astreoides* is increasing on declining reefs suffering a drop in coral cover (Green *et al.*, 2008). Similarly, long-term monitoring in Moorea (French polynesia) showed that the cover rate of *Acropora*, *Montipora* and *Pocillopora* are decreasing over time while *Porites* coverage is unaffected (Adjerouh *et al.*, 2009).

Among environmental factors, nutrient-loading can cause large shifts in coral reef community structure (Smith *et al.*, 1981; Lapointe *et al.*, 1997). In Reunion, the ACR communities are autotrophically functioning at *inflow sites*, e.g. "Toboggan" and "Petit Trou d'eau", while the MAS communities are typified by a heterotrophic regime at *outflow sites*, e.g. "Planch'Alizés" and "Club Med" (Mioche 1998; Mioche *et al.*, 2002; Conand *et al.*, 2002).

Elevated respiration rates (Mioche, 1998) can act negatively on the *Acropora* metabolism at the dystrophic Site-P, as observed in 1985-86 during one year-long monitoring: large natural transplants of *A. muricata* brought by waves and resettling at Site-P, were systematically dying during the hot season (Naim, 1993), while not at Site-T. Then, hypoxia (Herreid, 1980; Diaz & Rosenberg, 1995) may be one of the key factors explaining the MAS coral assemblage, and MAS may be considered as the "phase shift" of ACR, *sensu* Done (1992), triggered by dystrophic conditions. Dystrophy and hypoxia may lead also to undergrazing and to primary producer dominance by feedback (Naim *et al.*, 2013).

In addition, this study suggests that *Acropora* abundance and diversity, as well as the occurrence of *Echinometra mathaei* and Diadematidae can be used as reliable indicators for autotrophic functioning; in addition, the occurrence of *Montipora circumvallata* and *Porites (Synaraea) rus* with scarce *Acropora* and abundant benthic primary producers may reflect heterotrophy and freshwater enrichment (Semple, 1997; Naim *et al.*, 2013, Tourrand *et al.*, 2013).

The ACR characteristic species. Among autotrophic *Acropora* (Mioche, 1998), *Acropora muricata/formosa* and *A. digitifera* are the most abundant, and the

later species to develop at Site-P and thus, can be considered as the most eurytopic *Acropora* species present in Reunion.



Photograph 1. 1970's. ACR community, L-zone. *Acropora muricata* beds at la Saline during a very low tide (Photography: G. Faure).



Photograph 2. 1987. ACR community, N-zone. *Acropora* strips during a very low tide (Photography: O. Naim).

They were and they are also among the most abundant *Acropora* on the *Saint-Gilles La Saline* reef flat (Faure, 2009). On oligotrophic reef flats, *A. muricata* can form large monospecific banks in the L-zone (ten to twenty meters wide at la Saline, Saint-Leu, Saint-Pierre, **photograph 1**), and *Acropora*-dominated narrow strips on the N-subzone (**Photograph 2**). However, in Reunion, monospecific coral stands do

not reach sizes as large as those usually found in the Arabian Sea where corals, such as *Montipora foliosa* or *Pocillopora damicornis* (and other species), can develop banks extending over several hundred meters (Wilson, 2000). After the major 2009-bleaching event recorded at Sites T and P (**Table 5**, Tourrand *et al.*, 2013), 50% of the bleached *A. muricata* recovered without problem at Site-T, but died at Site-P. This observation once more highlights the prominent role played by abiotic factors in the resilience of corals sensitive to global warming.

In contrast to *Acropora muricata*, *Acropora austra* may be considered in Reunion to be very sensitive and perhaps, one of the sentinel species on the reef flat zone. After the 2002-bleaching event affecting *Acropora* at Site-T, 99% of *A. austra* bleached to death at Site-T whereas all the ten other *Acropora* species mainly recovered (Naim & Tourrand, unpublished).

The MAS characteristic species. In the literature, there is little information on *Montipora circumvallata*, the dominant species encountered at Site-P. This species is regarded as rare by Veron (2000), but is, and has been, recorded as common to locally abundant in shallow inner reef flats at Reunion and Mauritius (Faure, 1982, 2009). Its successful development in nutrient-enriched areas, both in



Photograph 3. 1987. Planch'Alizés (Site-P), L-zone. *Montipora circumvallata* buried into macroalgae (*Gracilaria canaliculata*, *Dictyosphaeria verluysii*).

Reunion and Mauritius lagoons (Cuet & Naim, non published), suggests that the species is favoured, or at least not disturbed, by nutrient input. Given freshwater fluxes are often accompanied by high nutrient amounts (Cuet, 1989), the development of *M. circumvallata* can be also promoted, or not disturbed, by low salinity. It may be considered to be an opportunistic form which takes advantage of not competing with *Acropora*. From 1985 to 2002, this species was the only *Montipora* recorded at Site-P, whereas *M. aequituberculata* and *M. edwardsi* were present at Site-T.

Similarly, in the famous eutrophic Kaneohe Bay (Oahu, Hawaii), *Montipora verrucosa* was observed to be a resistant species to the *Dictyosphaeria cavernosa* invasion (Banner, 1974) while *Montipora dilatata* declined dramatically over the past few decades (Hunter, 2009). It is interesting to note that, in outdoor tanks, Rodrigues and Grottoli (2007) showed that, after a period of eight post-bleaching months, the arborescent *Montipora capitata* was twice as likely to recover and had a lower mortality than *Porites lutea* and the branching *Porites compressa*, both known to be very tolerant species. While bleached, *Montipora capitata* increased heterotrophic feeding rates to meet more than 100% of daily needs. This indicates that the *resistance* of *Montipora* varies among species: *M. circumvallata*, *M. capitata* can be considered to be stress-tolerant species, and perhaps favoured by heterotrophy (**Photograph 3**), while *M. aequituberculata*, *M. edwardsi*, *M. dilatata* can be regarded as sensitive species. Nevertheless, after a large bleaching event observed in Reunion in 2009, *Montipora circumvallata* was more widely affected than *Porites (Synarea) rus* and *Porites (P.) nigrescens* at Site-P, and also than *Acropora formosa* at Site-T (**Table 5**, in Tourrand *et al.*, 2013). As *Acropora* is generally the most sensitive to global warming, this recent *M. circumvallata* demise raises the question of a possible recent change in abiotic and/or biotic (disease?) conditions at Site-P.

Porites (Synarea) rus is a ubiquitous species, abundant in Mascarene lagoons (Faure, 1982, 2009). It can be locally dominant in the outer channels cutting the Reunion reef flats (Naim, pers. obs.).

Prevalent at Site-P (**Photograph 4**), *P. (S.) rus* has also been observed to significantly develop close to a sewage pipe in Hawaii (Dollar, 1994). This suggests that the species may be favoured by nutrient-enrichment, explaining partly its success in the MAS community. Nevertheless, in Jakarta bay (Indonesia), where human-induced disturbance is intense, the reefs are typified by the virtual absence of otherwise abundant coral species, such as *Acropora hyacinthus* and *Porites (S.) rus*, and the prevalence of some species, such as *Oulastrea crispata* and *Favia maxima* (Cleary *et al.*, 2006). Thus, although it appears to be euryecious and/or nutrient-favoured, *P. (S.) rus* may be nevertheless sensitive to high levels of pollution. *Porites (P.) nigrescens* appears also to be much more abundant at Site-P. By contrast, *Porites (P.) lutea* is not a species liable to distinguish between Sites based on its coverage, but the relevant colonies are much larger at Site-T than at Site-P.



Photograph 4. 2009. Planch' Alizés (Site-P), L-zone. *Porites* (*Synaraea*) *rus* (photography: B. Cauvin).

At *Saint-Gilles La Saline*, Faviidae were and are generally absent from back reefs, rather rare in L and N-zones (about 150 to 330m from the beach), but colonize the outer reef flats (about 350 to 550m from the beach) and some of them are reef front builders (Faure, 1982, 2009). Their abundance on the Reunion incipient fringing reefs, north and south Saint-Gilles (Boucan Canot, Cap Champagne, Saint-Leu platforms) indicates that their occurrence may be correlated positively with wave agitation. The presence and richness of Faviidae at Site-P (inner L-subzone) can be linked to dystrophy, especially the presence of *Goniastrea*, that is often dominant on intertidal mudflats (Veron, 2000). Their occurrence at the PL subzone may also be related to the absence of spatial competition with *Acropora muricata*. Indeed, on the reef flat located in front of Saint-Leu city, five years after the impact of cyclone Firinga (99% coral mortality), Faviids became extremely abundant and diversified but, 10 years after, they were totally overgrown by the fast-growing and overwhelming *A.muricata* (Naim *et al.*, 1998; 2002). Similarly, on the Australian Great Barrier reef, Done & Potts (1992) observed that young *Porites* were likely to die from overgrowth by much faster growing corals.

In the 1980's, in the P-coral zone, numerous *Pocillopora damicornis* colonies were buried by the abundant macroalgae (**Photograph 5**). These colonies displayed the *acuta* form while at Site-T the species was mostly represented by the *bulbosa* form (<http://etic.univ-reunion.fr/ikbs/French/Pdamicornis.html>). Since this time, the abundance of *P.damicornis* has greatly decreased at Site-P, indicating that the species could have been promoted by nutrients in 1980's, and/or young recruits may have been protected from fish grazing owing to the growth of upalatable macroalgae.



Photograph 5. 1987 Planch' Alizés (Site-P), L-zone: Numerous *Pocillopora damicornis* among macroalgae (photography: O. Naim).

In Tahiti, from 22 species of hard corals recorded in the Papeete polluted harbour, *Pocillopora damicornis* and *Porites (Synaraea) rus* are the only ubiquitous species, observed in the whole area (Adjeroth *et al.*, 2000), thus suggesting their high resistance once more.

Pavona divaricata is also a dominant species at Site-P. Ubiquitous on the Reunion reefs (Faure, 1982, 2009), this species was scarce at Site-T from 1993 to 2002, although it may develop in the form of colonies several meters in diameter at Site-Petit Trou d'eau, southern part of la Saline reef flat, an oligotrophic site, but where branching corals are not as dominant as at Site-T (Bouchon, 1996; Mioche, 1998; Naim, non published). This suggests that *P. divaricata* may be limited in part by the overwhelming increase of branching coral coverage. Concerning its resistance, *P. divaricata* was the only species, with *Porites lutea*, remaining alive after the huge hypersedimentation caused by the runoff after cyclone Firinga in 1989 on the Saint-Leu reef flat (Naim *et al.*, 1998; 2002). This observation therefore indicates that *P. divaricata* and *P. lutea* are highly resistant to severe change in abiotic factors.

Temporal variations: the 1999-shift

In 1999, the demise of macroalgae at Site-P reflected an important shift in the nutrient supply to the reef flat (Naim *et al.*, 2013) resulting in an improvement in the health of massive corals. Conversely, the dramatic increase in primary producers (mostly *Stegastes* territory turfs) at Site-T indicated an increasing disturbance of living corals (bleaching, very low tides, etc.). However, although the massive coral coverage was increasing at Site-P from 1987 to 2009 no significant change in coral species coverage has been demonstrated. In 2007-2008, Denis *et al.* (2011) studying the regeneration of lesions in *Porites lutea* in the ACR and MAS communities at Reunion, demonstrated that lesion repair was still the poorest at Site-P. This site is

also the one where degeneration was observed during the hot season. This indicates that, although the macroalgae disappeared and the coral health improved, corals have still not fully recovered.

Species richness and diversity

Diversity at Sites T and P. When the TL and PL-coral subzones are in their most healthy condition (2002), biodiversity was the lowest at Site-T (*A.muricata* dominance) and the highest at Site-P (**Fig.3**). At Site-T, after the high degradation suffered by *Acropora* in 1993, diversity first increased and later, after nine years, decreased when *A.muricata* became dominant in the TL and TN-coral subzones (Fig. 3b). A similar changing trend in diversity was observed on the reef flat close to Saint-Leu city (Naim *et al.*, 2002), when *A.muricata* reconquered space 10 years after the disturbance event.

Diversity measured at Site-T and P was to a great extent lower than that recorded by Bouchon (1996), in the 1970s on Petit Trou d'eau, south of Saline reef flat (**Table 7**).

Table 7. Comparison of 1970s and 1993-2002 diversity (H' , Shannon index) of hard living corals (*Millepora* included). Petit Trou d'eau location on figure 1 (Tourrand *et al.*, 2013).

H' (Shannon index)	Site-T ("Toboggan") mean 1993-1996-2002 (max.) (Survey 1)	Site-P ("Planch'Alizés") mean 1993-1996-2002 (max) (Survey 1)	Site-PTE ("Petit Trou d'eau") 1976 (Bouchon, 1996)
B-subzone	1.75 (max. 1.66 in 1993)	1.49 (max. 1.58 in 2002)	3.25
L-subzone	0.89 (max. 0.97 in 1993 & 1996)	1.15 (max. 1.31 in 2002)	3.00
N-subzone	2.06 (max. 2.29 in 1996)	1.56 (max. 1.60 in 1996)	3.25

These findings can be explained by the fact that both Sites T and P expressed two extreme situations: a very high dominance of *Acropora* at Site-T (*i.e.* a « pure » ACR community) and a scarceness of *Acropora* at Site-P (*i.e.* a « pure » MAS community). Although experiencing autotrophy (Mioche, 1998), the Site-Petit trou d'eau can be considered to be a transitional site where diverse *Acropora* and non-*Acropora* communities occur (Naim, unpublished). This may be also explained by a global loss in coral diversity from the 1970s to the 2000s. Further quantitative investigations at Site-Petit Trou d'eau are needed to define more precisely the evolution of coral diversity from the 1970s.

Species richness at the scale of Reunion reefs. Faure *et al.* (2008b) give a list of corals identified from the Faure's coral collection (1982), referring to 14 families, 53 genera and 190 species of hard corals in the Mascarene Islands. However, marine richness and diversity showed a general decrease in the islands (Bourmaud *et al.*, 2006). According to these authors and the Marine Species Data Base for Eastern Africa (MASDEA, <http://www.vliz.be/vmdcdata/masdea/>), Reunion still harbours 42% of the Cnidarians recorded in the region. This percentage is considered to be high, relative to the age of the island (2.1 million years, Bachèlery, 2000) and the small size of its fringing reefs. Recent discovery of four new species of Octocorallians (Benayahu & van Ofwegen, 2012; Schleyer, non published) highlights

again the possible endemism and thus, the fragility of the marine communities in a remote island such as Reunion.

Between 1993 and 2002, 36 species were recorded at the Sites T and P (16.500 m² explored in each one). In 2007, Bruggemann *et al.*, using the Coral Count Point method, recorded 22 species on 4 stations located in the Saline outer N-zone.

At a much larger scale, two studies yielded a qualitative and semi-quantitative inventory of the Reunion living coral species in each habitat, the first carried out in the 1970s throughout the Mascarene reefs (Faure, 1982) and the second in 2009 restricted to the Reunion reefs (Faure, 2009). In 40 years, the species richness slightly decreased but remains high on reef flats (1970s: 74 species recorded; 2009: 71 species, of which on inner reef flats (B+L+N zones): 36 species and on outer reef flats: 62 species).

The decrease in richness was due to the demise of *Stylophora*. Widely growing in the 1970s, the genus appeared totally absent in 2009. Although *Stylophora pistillata*, preferring calm conditions, usually was rare in the exposed Reunion reef settings, *S. mordax* was a common species on the reef flats and outer slopes in *Saint-Gilles La Saline* and St-Leu (Faure, 1982). This species now seems to be located only on areas of high water energy, like those related to the incipient reefs at Boucan Canot and Grand Fond, and to the outer slopes off Saint-Leu city.

Similarly, the abundance/dominance of Faviidae, mainly of *Favia rotumana*, decreased on the outer reef flats from 1970s to 2009. In the 1985-2000 intermediary period, a number of surveys confirmed that *Stylophora* as well as *Favia rotumana* already were almost absent on *Saint-Gilles La Saline* reef flat (Naim, pers. obs.). As for *Stylophora*, Faviids are still numerous and diverse on Reunion incipient reefs, and on the exposed reef flats of Saint-Leu.

Hypotheses to explain the decrease in coral species richness

Decrease in Stylophora. By studying the reproduction of *Stylophora pistillata* at Eilat (Israel), Rinkevitch & Loya (1979) showed that fecundity was four times lower on a chronically polluted reef, compared to a control oligotrophic site. The population affected exhibited fewer breeding colonies, fewer ovaries and planulae per polyp, and a marked decrease in the reproductive index. Similarly, Loya *et al.* (2004) strongly suggested that nutrients released from fish farms have adverse effects on successful production of *S. pistillata* larvae. In *Saint-Gilles La Saline*, as cropland and urbanized areas have developed tremendously on the watershed over the last 40 years, the decrease of *Stylophora* may be due to the supply of more (or new) pollutants to the reef.

Considering bleaching, some species are more susceptible to this disturbance than others, as evidenced by shifts in community composition (Loya *et al.*, 2001, in which *Porites* is the « winner » in Okinawa reefs). Branching and plate-shaped corals, such as *Acropora*, *Montipora*, and *Seriatopora*, may have higher mortality rates after bleaching events (Birkeland, 1977; Adjeroud *et al.*, 2009 ; Fitt *et al.*, 2009 ; McClanahan, 2004 ; McClanahan *et al.*, 2004). Surveys in Kenya and Madagascar during the 1998-bleaching event revealed that *Montipora* and *Favia* displayed a high susceptibility to bleaching (>70%) but had low mortality rates as compared to *Acropora* and *Stylophora*, which had the highest frequencies of mortality (Hsieh *et al.*, 2000). *Stylophora* was considered by Fitts *et al.* (2009) to be « thermally-sensitive ». By using *Stylophora pistillata* as a model, Sampayo *et al.* (2008)

monitored individual *in-situ* colonies over a two-year period and showed that fine level genetic variability in symbionts (within clade C) was positively correlated to differences in bleaching susceptibility.

Furthermore, the impact of reef trampling is well documented (Woodland & Hopper, 1977). Before 2007, Reunion reef flats used to be harvested by people at spring low tide (for *Octopus*, molluscs, etc.), and *Stylophora* was mostly located on the trampling zones. However, although the species has a strong matrix and can resist mechanical human impacts, perhaps this is not the case for young recruits. Further investigations would be therefore required for identifying the controlling factors of the *Stylophora* demise at Saint-Gilles-La Saline over the last two decades.

Decrease in Faviidae. McClanahan (2004) recorded that during a bleaching event, *Favia*, *Favites*, *Goniopora*, and *Leptoria*, did not die. Similarly, in Reunion, observations on recovery after bleaching showed that, although they bleach, few Faviids die after bleaching, especially on the incipient reefs and exposed reef flats where these corals are abundant (Naim, unpublished). The regression of Faviids may be also attributed to pollution/trampling or to a combination of ecological factors. In *Saint-Gilles La Saline*, surveys of the two newly established sanctuaries (2007) and within reef areas opened to human activities, will help to understand the impact of trampling on the recruitment of reef-flat corals.

CONCLUSION

In many cases, it is difficult to pinpoint the exact causes of coral decline that is currently happening around the world. Degradation frequently occurs through the interaction of a combination of human-derived and natural factors, which then leads reef communities to become less resistant to natural disturbances (Done, 1992). If in Reunion and Mauritius, the MAS communities appear to be mainly the result of nutrient inputs and undergrazing (this study ; Cuet & Naim, non published), they reflect also the physiological capacities of the massive and submassive corals to resist large variation in abiotic factors (temperature, salinity, etc.) and pollutants (Edinger & Risk, 2000). They are regarded therefore as highly *resistant* communities.

The reefs rich in *Acropora* (the ACR community) show an aesthetism, a myriad of colors and forms, a diversity not seen in the MAS communities (Chabanet & Faure, 1994; Chabanet *et al.*, 1997). In the Indian Ocean, *Acropora* is becoming a rare genus in many reefs that have been heavily impacted by the 1998-bleaching event (Obura *et al.*, eds, 2008). But these fragile ACR communities, are still dominant on the Reunion reef flats. Even though coral bleaching poses a serious threat to these *Acropora*-dominated communities, they are able to recover rapidly if oceanographic, ecological and physiological factors remain favourable (Tourrand *et al.*, 2013), and can still be considered to be *resilient* in Reunion.

In Reunion, the human pressure has hugely increased. The population of the island is expected to grow at an annual rate of 1.1% in the next ten years. Most inhabitants are living along the coast, and the *Saint-Gilles La Saline* coral reefs are the most attractive for beach activities and tourism. In addition, large amounts of freshwater are at present supplied from the eastern coast, thus promoting urbanization along the western island flanks (Borca & Margoloff, 2004; Cuet, 2007).

Accordingly, the western coastal areas are more and more populous and there is high pressure on the watershed for developing agricultural activities, building tourism infrastructures and new homes. That is why our efforts must focus on better management of these fragile coral communities, particularly through the Marine Reserve action (<http://www.reservemarinereunion.fr/>). The management should focus, among other things, on reducing « hidden » pollution, including chemical and pesticide inputs, coming *via* polluted run-off (ravines, sewage plants) and *via* freshwater seepage onto reef flats and slopes.

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REFERENCES

- Adjerouh, M., S. Planes and B. Delesalle
2000. Coral and fish communities in a disturbed environment: Papeete harbor, Tahiti. *Atoll Research Bulletin* 484: 1-6.
- Adjeroud, M., F. Michonneau, P.J. Edmunds, Y. Chancerelle, T. Lison de Loma, L. Penin, L. Thibaut, J. Vidal-Dupiol, B. Salvat and R. Galzin
2009. Recurrent disturbances, recovery trajectories, and resilience of coral assemblages on a South Central Pacific reef. *Coral Reefs* 28: 775-780.
- Anasse, F., S. Ahamada, J. Jantzen, L. Bigot, J.-P. Quod, O. Tyack, Y. Hamadi, M. Hamidou and S. Ahamed
2003. *Atlas de vulnérabilité des zones coralliennes peu profondes sud et nord de la Grande Comore*. Union des Comores, Projet régional environnement 7, ACP.RPR.068, AIDE, ARVAM, DGE, CNDRS, 51 pp.
- Ateweberhan, M., T.R. McClanahan, N.A.J. Graham and C.R.C. Sheppard
2011. Episodic heterogeneous decline and recovery of coral cover in the Indian Ocean. *Coral Reefs* 30: 739-752.
- Bachèlery, P.
2000. Origin of the Mascarene Islands. In: *Coral reefs of the Indian Ocean: their Ecology and Conservation* (McClanahan, T., Sheppard, C., Obura, D.O. eds), Oxford Univ. Press, Pp. 360-361.
- Banner, A.H.
1974. Kaneohe Bay, Hawaii: urban pollution and a coral reef ecosystem. *Proceedings of the 2nd International Coral Reef Symposium*, Brisbane, Australia 2: 685-702.
- Bellwood, D.R., T.P. Hughes, C. Folke and M. Nystroëm
2004. Confronting the coral reef crisis. *Nature* 429: 827-833.
- Benayahu, Y. and L.P. van Ofwegen
2012. Octocorals (Cnidaria, Anthozoa) from Reunion, with a description of two new species of the genus *Simularia* May, 1898 and notes on the occurrence of other species. *Zoosystema*, 34 (4): 673-699.
- Birkeland, C.
1977. Disturbances to reefs in recent times. In: *Life and death of coral reefs* (Birkeland, C., ed.), Chapman and hall, New York, Pp 365-367.
- Borca, T. and N. Margoloff

2004. Basculement des eaux de la Réunion: Un chantier titanesque. La Reunion Island: shifting waters from East to West, a giant jobsite. *Tunnels et ouvrages souterrains*, ISSN 0399-0834, CODEN TNOSAI 182 : 71-74.
- Bouchon, C.
1996. *Recherche sur les peuplements de Scléractinaires Indo-Pacifiques (Mer Rouge, Océan Indien, Océan Pacifique)*. Doctorat ès Sciences, Univ. Aix-Marseille II, 338 pp.
- Bourmaud, C.A-F., L. Leclere, P. Mangion, F. Michonneau and G. Pennober
2006. Biodiversity of Reunion coral reefs. *Proceedings of the 10th International Coral Reef Symposium*, Okinawa, Japan 2: 207-212.
- Bruggemann, H., M.M.M. Guillaume, V. Denis, L. Bigot, O. Naim, M. Tessier, P. Durville and T. Mulochau
2007. The recent marine reserve at Reunion Island: Initial state of the benthic communities of the coral reefs of Saint-Leu and la Saline. *Proceedings of the 5th Western Indian Ocean Marine Science Association (WIOMSA) Conference*, Durban, South Africa, abstract
- Bruno, J.F. and E.R. Selig
2007. Regional Decline of Coral Cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS ONE* 2 (8): e711.
- Carpenter, K.E., M. Abrar, G. Aeby, R.B. Aronson, S. Banks, A. Bruckner, A. Chiriboga, J. Cortes, J.C. Delbeek and L. De Vantier
2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* 321: 560-563.
- Chabanet, P.
1994. *Étude des relations entre les peuplements coralliens et les peuplements ichtyologiques sur le complexe récifal de Saint-Gilles La Saline*. Doct. spéc. Environnement marin, Univ. Aix-Marseille III, France, 200 pp.
- Chabanet, P. and G.F. Faure
1994. Interrelations entre peuplements benthiques et ichtyologiques en milieu corallien. *Comptes Rendus à l'Académie des Sciences*, Paris 317: 1151-1157.
- Chabanet, P., H. Ralambondrainy, M. Amanieu, G.F. Faure and R. Galzin
1997. Relationships between coral reef substrata and fish. *Coral Reefs* 16: 93-102.
- Cleary, D.F.R., Suharsono and B.W. Hoeksema
2006. Coral diversity across a disturbance gradient in the Pulau Seribu complex off Jakarta, Indonesia. *Biodiversity and Conservation* 15 (11): 3653-3674.
- Conand, C., P. Chabanet, P. Cuet, and Y. Letourneur
1997. The carbonate budget of a fringing reef in la Reunion Island (Indian Ocean): sea urchin and fish bioerosion and net calcification. *Proceedings of the 8th International Coral Reef Symposium*, Smithsonian Tropical Research Institute, Panama 1: 953-958.
- Conand, C., P. Cuet, O. Naim and D. Mioche
2002. Des coraux sous surveillance. *Pour la Science*, 298 : 75-81.
- Cuet, P.
1989. *Influence des résurgences d'eau douce sur les caractéristiques physico-chimiques et métaboliques de l'écosystème récifal à La Réunion*. Doctorat de spécialité en Environnement marin, Univ. Aix-Marseille III, France, 204 pp.
2007. *Influence de l'irrigation du littoral Ouest sur la qualité du milieu naturel. Suivi du réseau qualitatif Antenne 4. Années 2004-2005 et synthèse 1999-2005 (rapport final)*. Rapport Université de la Réunion - Département de la Réunion, 77 pp.
- Denis, V., J. Debreuil, S. De Palmas, J. Richard, M.M.M. Guillaume and H. Bruggemann
2011. Lesion regeneration capacities in population of the massive coral *Porites lutea* at Reunion Island: environmental correlates. *Marine Ecology Progress Series* 428: 105-117.
- Despinoy, M., M. Petit, A. Minghelli-Roman and O. Naim
2000. Hyperspectral remote sensing and high spatial resolution: a relevant tool for a cartography of coral reef systems. *International Coral Reef Initiative (ICRI) meeting*, Communication and poster on la Saline reef communities.
- Diaz, R.J. and R. Rosenberg

1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology: an annual review* 33: 245-303.
- Dollar, S.
1994. Sewage discharge on coral reefs: not always pollution. *Coral reefs* 13: 224.
- Done, T.J.
1992. Phase shifts in coral communities and their ecological significance. *Hydrobiologia* 247: 121-132.
- Done, T. J. and D.C. Potts
1992. Influences of habitat and natural disturbances on contributions of massive *Porites* corals to reef communities. *Marine Biology* 114 (3): 479-493.
- Edinger, E.N. and M.J. Risk
2000. Reef classification by coral morphology predicts coral reef conservation value. *Biological Conservation* 92: 1-13.
- Faure, G.F.
1982. *Recherche sur les peuplements de Scléractiniaires des récifs coralliens de l'Archipel des Mascareignes (Océan Indien Occidental)*. Doctorat ès Sciences, Univ. Aix-Marseille II, vol.1 & 2.
2009. Biodiversité des Scléractiniaires, la Saline 2009. Rapport non publié Réserve marine Réunion, 10 pp.
- Faure, G.F., M. Pichon, F. Trentin, Y. Geynet, N. Conruyt, P. Gigord and D. Caron
2008a. Base de connaissance sur les coraux des Mascareignes (Iterative Knowledge Base System, IKBS). Univ. Réunion, 50pp. <http://coraux.univ-reunion.fr>
- Faure, G.F., M. Pichon and Y. Geynet
2008b. List of Scleractinian coral species cited from the Mascarene archipelago based on Faure (1982). IUCN
- Fitt, W.K., R.D. Gates, O. Hoegh-Guldberg, J.C. Bythell, A. Jatkar, A.G. Grottoli, M. Gomez, P. Fisher, T.C. Lajuenesse, O. Pantos *et al.*
2009. Response of two species of Indo-Pacific corals, *Porites cylindrica* and *Stylophora pistillata* to short-term thermal stress: the host does matter in determining the tolerance of corals to bleaching. *Journal of Experimental Marine Biology and Ecology* 373: 102-110.
- Frontier, S.
1985. Diversity and structure in aquatic ecosystems. *Oceanography and Marine Biology: An Annual Review* 23: 253-312.
- Gardner, T.A., I.M. Cote, J.A. Gill, A. Grant and A.R. Watkinson
2003. Long-term region-wide declines in Caribbean corals. *Science* 301: 958-960.
- Green, D. H., P.J. Edmunds and R.C. Carpenter
2008. Increasing relative abundance of *Porites astreoides* on Caribbean reefs mediated by an overall decline in coral cover. *Marine Ecology Progress Series* 359 (1-10): 271-283.
- Guillaume, M.M.M., C.E. Payri and G.F. Faure
1983. Blatant degradation of coral reefs at la Reunion Island (West Indian Ocean). *International Society for Reef Studies*, annual meeting, Nice, France 28.
- Herreid, C.F.
1980. Hypoxia in invertebrates. *Comparative Biochemistry and Physiology* 67A: 311-320.
- Highsmith, R.C.
1982. Reproduction by fragmentation in corals. *Marine Ecology Progress Series* 7: 207-226.
- Hsieh, C.-I., R. Ormond and D.O. Obura
2000. Coral bleaching in the Indian Ocean and the El Niño Southern Oscillation. In: *Coral reefs of the Indian Ocean : their Ecology and Conservation* (McClanahan, T., Sheppard, C., Obura, D.O. eds), Oxford Univ. Press, Pp. 72-74.
- Hunter, C.
2009. Distribution and abundance of *Montipora dilatata* in Kaneohe Bay, Oahu, Hawaii. *University Hawaii-Manoa, BIOL 403*, NOAA Contract Number: 133F08SE2838, 14 p.
- Lapointe, B.E., M.M. Littler and D.S. Littler

1997. Macroalgal overgrowth of fringing coral reefs at Discovery Bay, Jamaica: bottom-up *versus* top-down control. *Proceedings of the 8th International Coral Reef Symposium*, Townsville, Australia 1: 927-932.
- Letourneur, Y.
1992. *Dynamique des peuplements ichthyologiques des platiers récifaux de l'île de la Réunion*. Doctorat de spécialité en Océanologie, Universités Perpignan-Réunion, France, 244 pp.
- Letourneur, Y., P. Chabanet, L. Vigliola, and M.L. Harmelin-Vivien
1998. Mass settlement and post-settlement mortality patterns of juvenile *Epinephelus merra* Bloch (Pisces, Serranidae) on Reunion coral reefs. *Journal of the Marine Biological Association of the United Kingdom* 78: 307-319.
- Loya, Y.
1978. Plotless and transect methods. In: *Coral research methods* (Stoddart D.R., Johannes R.E., eds). UNESCO, Paris, Pp. 197-217.
- Loya, Y., K. Sakai, K. Yamazato, Y. Nakano, H. Sambali and R. van Woesik
2001. Coral bleaching: the winners and the losers. *Ecology Letters* 4: 122-131.
- Loya, Y., H. Lubinevsky, M. Rosenfeld and E. Kramarsky-Winter
2004. Nutrient enrichment caused by *in situ* fish farms at Eilat, Red Sea is detrimental to coral reproduction. *Marine Pollution Bulletin* 49: 344-353.
- Lucas, H.A. and G.A.F. Seber
1977. Estimating coverage and particle density using the line intercept method. *Biometrika* 64 (3): 618-622.
- McClanahan, T.R.
2004. The relationship between bleaching and mortality of common corals. *Marine Biology* 144: 1239-1245.
- McClanahan, T.R., A.T. Kamukuru, N.A. Muthiga, M. Gilagabher Yebio and D.O. Obura
1995. Effect of sea urchin reduction on algae, coral and fish populations. *Conservation Biology* 10: 136-154.
- McClanahan, T.R., A.H. Baird, P.A. Marshall and M.A. Toscano
2004. Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. *Marine Pollution Bulletin* 48: 327-335.
- McClanahan, T.R., M. Ateweberhan, C. Ruiz Sebastian, N.A.J. Graham, S.K. Wilson, H. Bruggemann and M.M.M. Guillaume
2007. Predictability of coral bleaching from synoptic satellite and *in situ* temperature observations. *Coral Reefs* 26: 695-701.
- Mioche, D.
1998. *Aspects du cycle de la matière sur les récifs frangeants de l'île de la Réunion (Océan Indien): signature des dégradations et mécanismes de l'eutrophisation*. Doctorat de Spécialité en Écologie Marine, Université Réunion, France, 292 pp.
- Mioche, D., R. Troadec, N. Germain, C. Esbelin, C. Tourrand, M. Psaradellis, O. Naim and J. Coudray
2002. Relations entre l'équilibre sédimentaire des plages, la structure des communautés et le budget des carbonates dans l'écosystème corallien de la Réunion. *The Journal of Nature (Reunion)* 14 (1): 35-43.
- Montaggioni, L. and P. Nativel
1988. *La Réunion-Maurice: géologie et aperçus biologiques. Guides Géologiques Régionaux*. Ed. Masson, Paris, 192 p.
- Naim, O.
1993. Seasonal responses of a fringing reef community to eutrophication (Reunion Island, western Indian Ocean). *Marine Ecology Progress Series* 99: 307-315.
2002. *Acropora formosa* (Dana, 1846) (Anthozoaire, Scléractiniaire), une espèce de corail structurant les biocénoses de platiers récifaux (Ile de la Réunion, S.O. Océan Indien). *The Journal of Nature (Bourbon Sciences)* 14 (3): 27-35.
2006. The coral reef communities at Saint-Gilles La Saline in 1987 (Reunion Isl., S.W. Indian Ocean). *The Journal of Nature (Reunion)* 18(1) : 13-33.
- Naim, O. and P. Cuet

2002. Benthic community structure *versus* nitrate input at Reunion (SW Indian Ocean). *Proceedings of the 9th International Coral Reef Symposium*, Bali, Indonesia, summary.
- Naim, O., G.F. Faure and A. Engelmann
1998. Coral recolonization three years after the impact of a cyclone on a reef flat (Saint-Leu, Reunion, SW Indian Ocean). *International Society for Reef Studies*, annual meeting, Perpignan, France, abstract
- Naim, O., P. Cuët and V. Mangar
2000. The Mascarene Islands. In: *Coral reefs of the Indian Ocean: their Ecology and Conservation* (McClanahan, T., Sheppard, C., Obura, D.O. eds), Oxford Univ. Press, Pp. 353-381.
- Naim, O., P. Chabanet, T. Done, C. Tourrand and Y. Letourneur
2002. Regeneration of a reef flat ten years after the impact of the cyclone Firingia (Reunion, SW Indian Ocean). *Proceedings of the 9th International Coral Reef Symposium*, Bali, Indonesia, 1: 547-552.
- Naim, O., C. Tourrand, E. Ballesteros, S. Semple, L. Bigot, B. Cauvin, P. Cuët and L.F. Montaggioni
2013. Fringing reefs of Reunion Island and eutrophication effects. Part 2: Long-term monitoring of primary producers. *Atoll Research Bulletin* 597, 36 p.
- Obura, D.O, J. Tamelander and O. Lindén, O. eds
2008. *Coral Reef Degradation in the Indian Ocean (CORDIO). Status report*. 2 vol., 494 pp.
- Pastorok, R.A. and G.R. Bilyard
1985. Effects of sewage pollution on coral-reef communities. *Marine Ecology Progress Series* 21: 175-189.
- Ribes, S.
1978. *La macrofaune vagile associée à la partie vivante des Scléractiniaires sur un récif frangeant de l'île de la Réunion (océan Indien)*. Doctorat de spécialité en Océanologie, Université Aix-Marseille II, 150p.
- Rinkevitch, B. and Y. Loya
1979. The reproduction of the Red Sea coral *Stylophora pistillata*. I. Gonads and planulae. *Marine Ecology Progress Series* 1, 133-144.
- Rodrigues, L.J. and A.G. Grottoli
2007. Energy reserves and metabolism as indicators of coral recovery from bleaching. *Limnology and Oceanography* 52, 1874-1882.
- Rogers, C.S.
1990. Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* 62: 185-202.
- Sampayo, E.M., T. Ridgway, P. Bongaerts and O. Hoegh-Guldberg
2008. Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type. *Proceedings of the National Academy of Sciences, U.S.A.* 105 (30): 10444-10449.
- Semple, S.
1997. The use of temporal variations in algal cover and biomass as a tool for the quantification of the degree of eutrophication of a fringing coral reef in Reunion Island, S.W. Indian Ocean. *Oceanologica Acta* 20 (6): 851-861.
- Sheppard, C.R.C.
2000. Coral reefs of the Western Indian Ocean: an overview. In: *Coral reefs of the Indian Ocean : their Ecology and Conservation* (McClanahan, T., Sheppard, C., Obura, D.O. eds), Oxford Univ. Press, Pp. 3-38.
- Smith, S.V., W.J. Kimmerer, E.A. Laws, R.E. Brock and T.W. Walsh
1981. Kaneohe Bay sewage diversion experiment : perspectives on ecosystem responses to nutritional perturbation. *Pacific Science* 35 (4): 279-395.
- Tessier, E., L. Bigot, C. Cadet, B. Cauvin, P. Chabanet, C. Conand, J.-B. Nicet and J.-P. Quod
2008. Les récifs coralliens de la Réunion en 2007: état des lieux et réseau de suivi. *Revue d'Ecologie (Terre & Vie)* 63: 85-102.

- Tourrand, C., O. Naim, L. Bigot, C. Cadet, B. Cauvin, S. Semple, L.F. Montaggioni, P. Chabanet and H. Bruggemann
 2013. Fringing reefs of Reunion Island and eutrophication effects. Part 1: Long-term monitoring of two shallow coral reef communities. *Atoll Research Bulletin* 596, 35 p.
- Turner, J. and R. Klaus
 2005. Coral reefs of the Mascarenes, Western Indian Ocean. *Philosophical Transaction of the Royal Society A* 363: 229-250.
- Veron, J.E.N.
 2000. *Corals of the world* (M. Stafford-Smith ed.). Australian Institute of Marine Science and CRR, Qld Pty Ltd, Townsville, 3 vol., 1381 pp.
- Wallace, C.
 1999. *Staghorn corals of the world. A revision of the genus Acropora*. CSIRO Publication, Melbourne, 422 pp.
- Wilson, S.
 2000. Monospecific reef formations. In: *Coral reefs of the Indian Ocean : their Ecology and Conservation* (McClanahan, T., Sheppard, C., Obura, D.O. eds), Oxford Univ. Press, Pp. 285-286.
- Woodland, R.V. and N.A. Hopper
 1977. The effect of human trampling on coral reefs. *Biological Conservation* 11: 1-14.