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Spatial patterns and recruitment processes of coral assemblages among contrasting environmental conditions in the southwestern lagoon of New Caledonia

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ABSTRACT

We investigated the spatial distribution of adult and juvenile coral assemblages in the southwestern lagoon of New Caledonia, from disturbed fringing reefs within bays, to oceanic barrier reefs. Generic richness, abundance, and percent cover were highly variable at this scale, but no clear cross-shelf gradient was found. Rather, community composition was more related to reef biotopes. Correlations and canonical correspondence analyses revealed that composition and abundance of coral assemblages were related to substrate types (cover of turf algae and cover of encrusting coralline algae), but not to water quality or metal concentrations in sediments. We found a strong relationship between juvenile and adult distribution for all dominant genera, which suggests that recruitment processes are also a major factor structuring these populations. The densities of juveniles and their proportion in the coral assemblages were relatively low, which implies that replenishment capacities and potential for recovery are probably limited for these reefs.

1. Introduction

In most marine ecosystems including coral reefs, physical conditions and biological processes show strong spatio-temporal variation at multiple scales (Huston, 1985; Brown, 1997; Connell et al., 1997; Cooper et al., 2007; among others), and recent studies acknowledge the importance of environmental stochasticity as a major driver of diversity patterns on coral reefs (Dornelas et al., 2006). Consequently, community structure of long-lived sessile organisms such as scleractinian corals often exhibit marked spatial heterogeneity at local scales with cross-shelf (i.e., land–ocean), bayhead-bay entrance, or depth gradients in diversity and abundance (Huston, 1985; Adjeroud, 2000, 2006; Cleary et al., 2005). Since the 1960s, several studies have documented spatial patterns of coral assemblages around the world, and have identified some of the major controlling extrinsic factors, such as the availability of adequate substrate, sediment characteristics, light, water quality, hydrodynamic forces, and biotic interactions (Done, 1983; Adjeroud, 1997; Koop et al., 2001; McCook et al., 2001; Fabricius, 2005). In the context of increasing frequency, scale and intensity of various chronic or episodic natural and anthropogenic disturbances, a new challenge for coral reef ecology is to understand their impacts on the structure and dynamics of coral assemblages (Wilkinson, 1999; Hughes et al., 2003; Harrison and Booth, 2007).

Recent studies have also recognized the major role of recruitment processes in structuring adult assemblages, although both pre- and post-settlement events may also influence the local abundance and spatial distribution of corals (Bak and Engel, 1979; Harrison and Wallace, 1990; Caley et al., 1996; Hughes and Tanner, 2000; Hughes et al., 2000). Juvenile corals are immature colonies from several successive cohorts, providing a short-term history of settlement patterns combined with early post-settlement growth and mortality (Edmunds, 2000; Penin et al., 2007). These juvenile colonies, coupled with asexual propagation of adult colonies, represent the major source for the replenishment and maintenance of local populations, and for successful recovery and resilience following disturbances (Hughes, 1990; Hughes et al., 2000; West and Salm, 2003; Harrison and Booth, 2007). Juvenile colonies appear to be more sensitive to changes in substrate and water quality than adult corals (Brown, 1988;

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Ward and Harrison, 1997; Reichelt-Brushett and Harrison, 2000; Fabricius et al., 2003; Fabricius, 2005). Thus, recruitment patterns represent an interesting indicator of the effect of disturbances and ecological changes on long-term coral reef maintenance (Brown and Howard, 1985; Ben-Tzvi et al., 2004). Currently, very few studies have integrated both juvenile and adult corals to better understand the spatial structure and dynamics of coral communities exposed to various environmental perturbations (Brown, 1988; West and Salm, 2003).

Accordingly, the aim of the present study was to examine the spatial distribution of adult and juvenile corals among various reef types in the southwestern lagoon of New Caledonia, from highly degraded fringing reefs within bays, to oceanic barrier reefs. Our first objective was to assess the effect of contrasting environmental conditions, in terms of water and sediment quality and substrate type, on the structure of juvenile and adult assemblages. The second objective was to determine the degree to which spatial heterogeneity in the abundance of adult corals is influenced by recruitment processes, and thus, to estimate the replenishment capacities of local populations.

The New Caledonian barrier reef is the second longest continuous coral reef in the world after Australia's Great Barrier Reef, and comprises a highly diversified coral fauna estimated at 306 zooxanthellate scleractinian species (Pichon, 2006). This high diversity is partly explained by the proximity of New Caledonia to the coral centre of biodiversity, but also by the morphological diversity of its reefs, which includes most reef types (Chevalier, 1973; Andréfouët and Torres-Pulliza, 2004). The southwestern part of the main island is exposed to specific types of anthropogenic inputs, primarily associated with extensive nickel mining for more than a century (New Caledonia is currently the world's third largest producer), which has no counterparts in other reef systems (Wantiez, 2008). Despite these unique characteristics, the coral communities of New Caledonia remain poorly known (Pichon, 2006), and their assessment is therefore timely for a number of reasons. Investigation of corals living in these reefs will provide important insights into the spatial structure and dynamics of coral assemblages, and examination of coral reef replenishment capacities may also assist conservation and management efforts, particularly in the context of New Caledonia's recent inscription on the UNESCO World Heritage List.

2. Materials and methods

2.1. Study area

The study area was located in the southwestern part of the main island ('Grande Terre') of New Caledonia (Fig. 1), and comprised reefs around Nouméa (the most populated and industrialized city of New Caledonia). The southwestern lagoon is mainly composed of three distinct reef biotopes (or 'reef types'): coastal fringing reefs, mid-shelf reefs, and barrier reefs (see Andréfouët and Torres-Pulliza, 2004). The southwestern lagoon is primarily exposed to southeasterly trade winds that govern the general direction of surface currents (Jouon et al., 2006). Oligotrophic oceanic waters enter the lagoon via the open southern shelf, flow through the lagoon, and then exit via the passes on the western shelf (Jouon et al., 2006). As hydrodynamic circulation in the study area is generally very active, the terrigenous influence on water quality and sediment composition is mainly restricted to fringing reefs, particularly those within bays with high water residence time. Conversely, most mid-shelf and barrier reefs are under oceanic influences (Jacquet et al., 2006; Mari et al., 2007; Migon et al., 2007).

Ten study stations distributed in the three lagoonal reef biotopes were selected. Six stations were established on fringing reefs within three different bays (SM1 and SM2 in Sainte Marie Bay, RA1 and RA2 in Grande Rade Bay, and MA1 and MA2 in Maa Bay), two stations were located on mid-shelf reefs (MS1 in Prony reef, and MS2 in Larégnère reef), and two stations were situated on inner barrier reefs (BA1 and BA2, Fig. 1). The three bays selected as fringing reef sites are located in the vicinity of Nouméa, but differ greatly in terms of human activities and types of pollution (Dalto et al., 2006; Fernandez et al., 2006; Jacquet et al., 2006; Dumas et al., 2007). Sainte-Marie and Grande Rade are significantly polluted by heavy metals, notably Ni, Cr, Zn, and Co. Sainte-Marie receives significant terrigenous inputs from the Coulée River, as well as urban wastewaters from the Sainte-Marie area. Grande Rade is also influenced by urban effluents, but in addition, receives industrial effluents originating mainly from the nickel industry and commercial harbour (Breau, 2003). In contrast, Maa Bay receives low terrigenous and anthropogenic inputs, and is often considered as a reference site for fringing reefs within bays (Breau, 2003). Prony (MS1) and Larégnère (MS2), the two mid-shelf stations, are small patch reefs located in the lagoon 10.8 and 15.1 km from Nouméa, respectively. Finally, the two inner barrier reef stations are located north of Dumbéa Pass, approximately 500 m from the reef front, and 22.2 km (BA1) and 21.0 km (BA2) from Nouméa, respectively.

2.2. Coral sampling

Sampling of corals was conducted in October to November 2007. At each station, adult and juvenile corals (scleractinians and the calcareous hydrocoral *Millepora*) were sampled along three replicate 10×1 m belt-transects, laid parallel to depth contours and separated by $\sim$1 m (Penin et al., 2007). All transects were located on the constructed reef framework, and were all between 2–3 m depth, as important variation in benthic assemblages may occur over depth gradients (Faure et al., 1981). As in most previous studies (see Penin et al., 2007), juveniles were defined as all visible coral colonies $\leqslant$5 cm in maximum diameter (which correspond to non-reproductive size classes for the majority of Pacific reef corals, see Harrison and Wallace, 1990), whereas colonies >5 cm maximum diameter were considered as adults. Identification of juvenile colonies at the species level is often impossible; hence coral assemblages at each station were characterized by their generic richness and abundance of colonies.

2.3. Environmental factors

Several environmental factors relating to algal and substrate types, and water and sediment quality were examined to determine their potential effects on the structure of juvenile and adult coral assemblages. Percent cover of four different categories of algae and substrate type that are hypothesized to have important roles in the variation of composition and abundance of corals were quantified: algal turf (mixed species, low structure, and filamentous algae), macroalgae, encrusting coralline algae (ECA), and unconsolidated substrate (including sand and rubble). At each station, three linear 10 m transects were used to estimate substrate cover (Line Intercept Transect Method; Loya, 1978). We also recorded living coral cover, but these data, rather than being used as an explanatory variable, were used to describe the structure of the coral assemblage at each station.

Water and sediment characteristics in the southwest lagoon have been monitored since 1997 (see http://www.ird.nc/PNEC/). In this study, we used sediment and water quality data taken at the 3 reef biotopes, and at close proximity to eight of our coral stations (no data were available for stations MA2 and BA2). Temperature, salinity, and turbidity were measured *in situ* with a CTD SBE19, between 1997 and 2005. Nutrients (NH_4, NO_3, PO_4, Si) and chlorophyll *a* concentrations were measured from water

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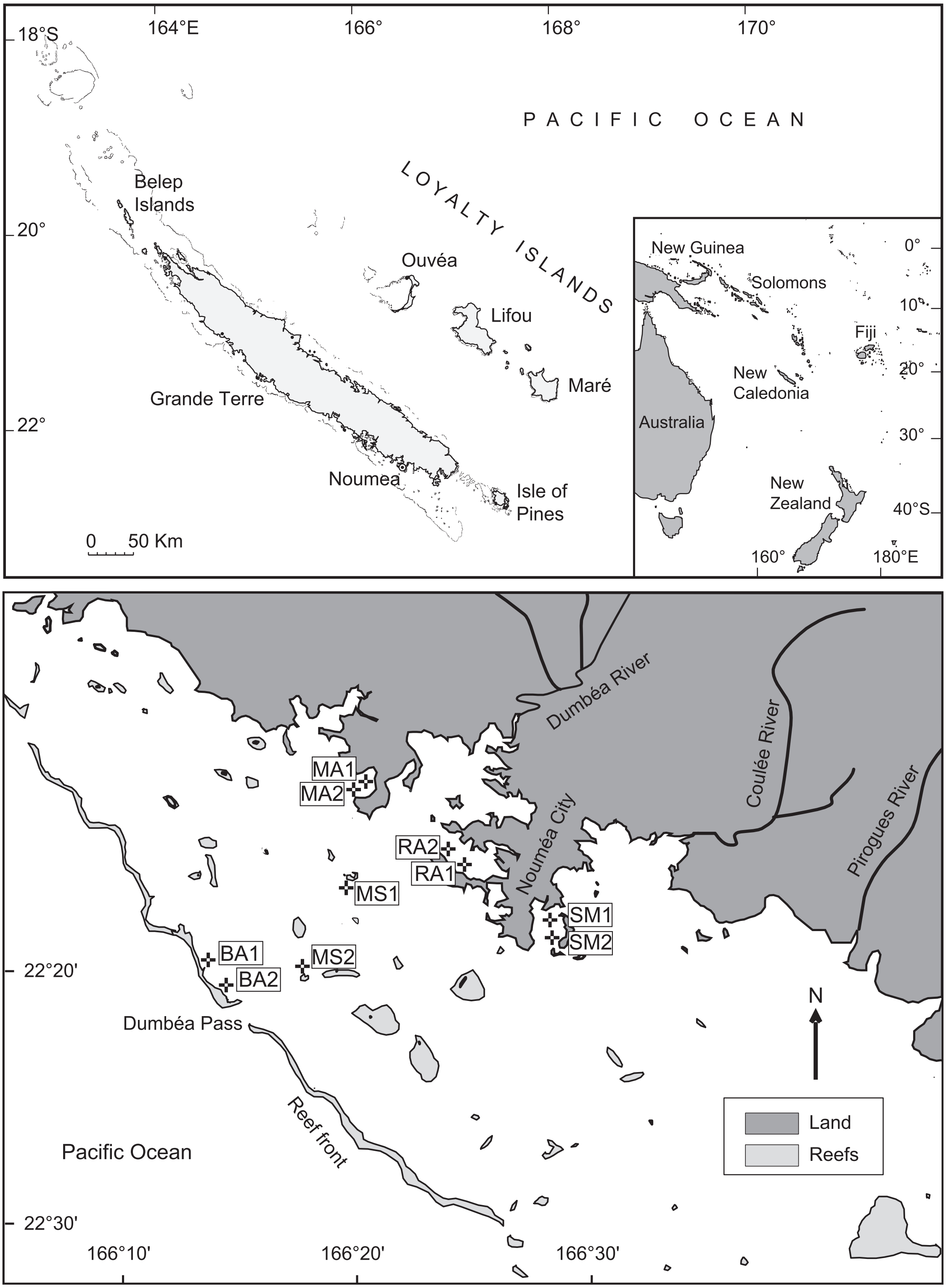

Fig. 1. Map of New Caledonia showing the location of the ten sampling stations in the southwestern lagoon of the main island ('Grande Terre').

samples collected between 1997 and 2003 (see Dalto et al. 2006). In total, between 12 and 26 monitoring campaigns were completed at each station. Sediment was sampled with a lightweight stainless steel (316L) Van-Veen grab (capacity 1.8 litre) to ensure minor disturbance of the top layer of sediment. Concentrations of heavy metals (Fe, Cr, Mn, Co, Ni, Zn) in the surface sediment were analysed by ICP-OES (Optima 3300 FD, Perkin Elmer) following Fernandez et al. (2006).

2.4. Data analysis

Spatial variation in mean generic richness (GR), abundance of colonies, living coral cover, algae and substrate cover were analysed using one-way ANOVA tests, with stations as fixed factors. Data were appropriately transformed (log $(x + 1)$ for GR and abundance, and arcsin for cover) to meet the assumptions of normality and homogeneity of variance. Student-Neuman-Keuls tests (SNK)

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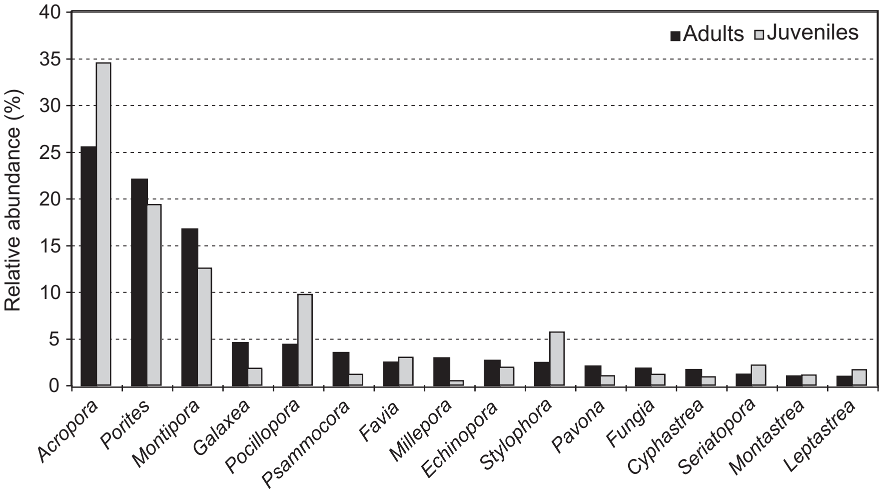

Fig. 2. Relative abundance (in%) of the 16 most abundant coral genera in the overall assemblages of adults and juveniles (all stations pooled).

were performed to determine which pairs of stations showed significant differences. To explore relationships between juvenile and adult spatial distribution, correlations were calculated between the mean abundance of adults and juveniles at each stations ($n = 10$). Parametric Pearson (r) correlations analyses were conducted for each of the seven major coral genera, which were sufficiently abundant as both juveniles and adults to undertake meaningful analyses. The overall variation in composition and abundance of coral assemblages among the ten stations was analysed using correspondence analysis (CA), which is appropriate for examining gradients of stations (Legendre and Legendre, 1998).

Finally, Canonical Correspondence Analysis (CCA; ter Braak, 1986, 1987) was used to determine which environmental factors (i.e., algae and substrate types, and water and sediment quality descriptors) were influencing the distribution and abundance of corals. CCA constrains the axes in classical Correspondence Analysis (CA) to be linear functions of measured variables associated with species records (‘direct gradient analysis’; Legendre et al., 2005). Significant factors used in the final analysis were selected by a permutation test, a stepwise procedure analogous to backward elimination in multiple regression analysis. Moreover, the robustness of the final analysis was determined using a Monte-Carlo permutation test (ter Braak, 1988). In the present study, CCA were undertaken at the eight stations where environmental factors were measured. Parametric Pearson (r) correlation analyses were calculated between each environmental factor and mean generic richness and abundance data recorded at each station.

3. Results

3.1. Coral assemblages

In total, 4367 adult coral colonies from 37 genera, and 1693 juvenile colonies from 25 genera were recorded at the 10 sampling stations, corresponding to a mean density of 14.5 and 5.6 colonies.m^{-2}, respectively. *Acropora*, *Porites* and *Montipora*, were the

Table 1
Mean percent cover of different categories of algae and substrate types recorded at the ten stations sampled during this study. Standard deviations are given in parentheses. ECA: encrusting coralline algae. One-way ANOVA tests for significance of the spatial variation of cover values among the ten stations are given.

Station	Corals	ECA	Turf	Macroalgae	Sand/ rubble
SM1	21.7 (1.6)	3.3 (1.5)	11.8 (5.2)	1.8 (0.8)	60.0 (3.1)
SM2	22.0 (6.8)	3.0 (2.0)	41.0 (14.1)	4.0 (2.6)	23.7 (16.5)
RA1	20.2 (11.1)	3.5 (1.3)	64.0 (15.1)	5.0 (1.0)	5.0 (4.4)
RA2	21.2 (3.3)	5.2 (1.8)	48.8 (10.8)	1.2 (0.8)	4.0 (1.7)
MA1	38.0 (5.6)	1.5 (0.5)	41.0 (3.6)	3.3 (1.5)	3.7 (1.5)
MA2	43.7 (12.2)	0.8 (0.3)	28.3 (6.0)	3.8 (2.8)	23.3 (12.7)
MS1	39.3 (11.8)	2.0 (1.0)	19.3 (5.9)	28.3 (10.6)	11.0 (1.0)
MS2	20.8 (10.1)	26.3 (4.0)	42.7 (2.3)	5.3 (4.5)	4.8 (8.4)
BA1	27.0 (6.9)	47.8 (6.8)	2.0 (2.6)	1.5 (1.3)	7.7 (5.9)
BA2	24.2 (6.5)	61.7 (5.8)	3.8 (4.3)	0.3 (0.6)	6.3 (3.5)
ANOVA F	3.474	116.644	16.401	12.844	16.968
p	0.0098	<0.0001	<0.0001	<0.0001	<0.0001

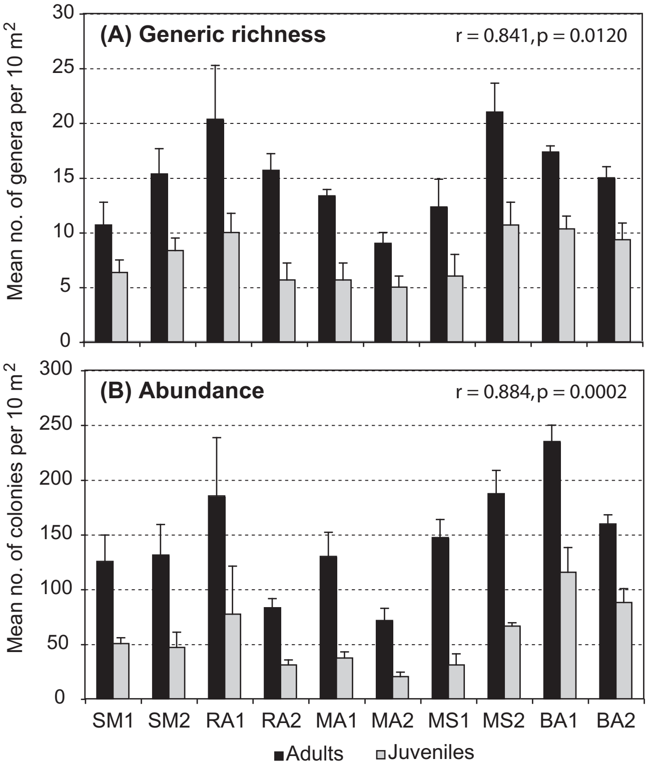

Fig. 3. Variation in (A) mean generic richness, and (B) mean abundance of juvenile and adult corals among the ten stations. Pearson correlation coefficients (r) between variation in juvenile and adult generic richness and abundance, and their associated statistics (P value) are given. Errors bars are standard deviations.

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most dominant genera, representing 64.0% and 66.3% of the total colonies recorded in the adult and juvenile assemblages, respectively (Fig. 2). However, the overall adult and juvenile assemblages also contained many 'rare' genera. Each of these 'rare' genera individually represented less than 1% of the total colonies recorded (23 and 11 'rare' genera for adults and juveniles, respectively), but collectively they made a substantial contribution to total coral cover. Mean coral cover varied significantly among the ten stations (Table 1; ANOVA, $F = 3.474$, $P = 0.0098$), ranging from 20.2 ± 11.1% (mean ±SD) at station RA1 to 43.7 ± 12.2% at station MA2. Highest mean coral cover values were recorded at the two stations at Maa Bay (MA1, MA2), and at Prony (MS1). At all other stations mean coral cover ranged between 20.1 and 27.0%, and were not significantly different (SNK, all $P > 0.05$).

Mean generic richness (GR) varied significantly among the 10 stations, for both the adult (ANOVA, $F = 10.799$, $P < 0.0001$) and

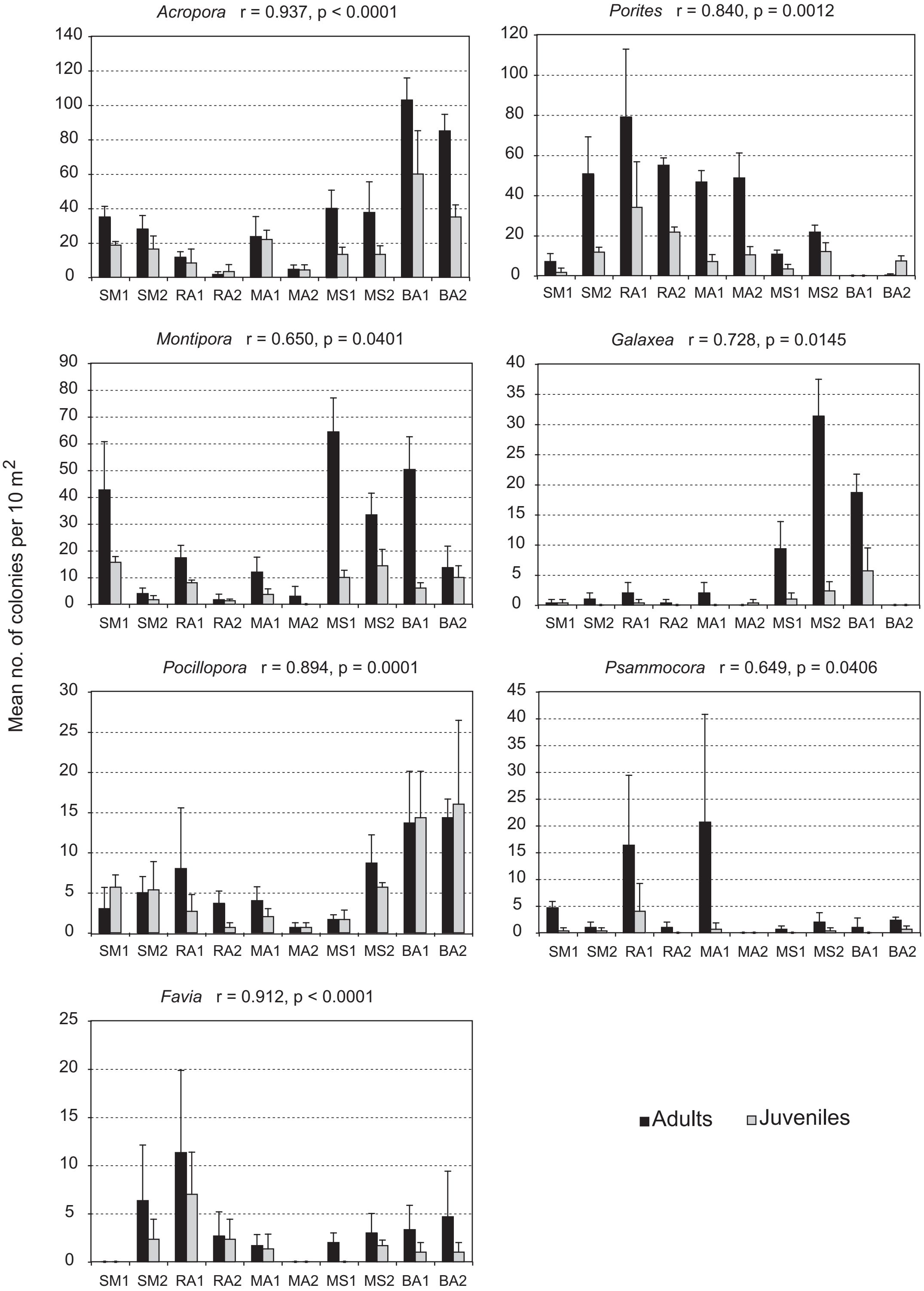

Fig. 4. Variation of adult and juvenile abundances for the seven major coral genera. Pearson correlation coefficients (r) between variation in juvenile and adult abundances and associated statistics (P value) are given for each genus. Errors bars are standard deviations.

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juvenile (ANOVA, $F = 5.605$, $P = 0.0007$) assemblages. Spatial variation in GR of adults was strongly and positively correlated with that of juveniles ($r = 0.841$, $P = 0.0012$; Fig. 3A). Adult GR varied from 9.0 ± 1.0 (MA2) to 21.0 ± 2.6 genera.10 m^{-2} (MS2). Adult GR was not significantly different between the two stations sampled within Grande Rade (RA1, RA2), or between the two barrier reef stations (BA1, BA2; SNK, $P > 0.05$). In contrast, adult GR was different between the two mid-shelf reef stations (MS1, MS2), and between the two stations of Sainte-Marie (SM1, SM2) and Maa bays (MA1, MA2; SNK, all $P < 0.05$). Juvenile GR varied between 5.0 ± 1.0 (MA2) and 10.6 ± 2.0 genera.10 m^{-2} (MS2). No significant differences in juvenile GR were found between the two barrier reef stations, or between the two stations at Sainte-Marie, Grande Rade and Maa bays (SNK, all $P > 0.05$). In contrast, juvenile GR was significantly different between the two mid-shelf reef stations (SNK, $P < 0.05$). No clear gradients (i.e., regular increasing or decreasing trends) in GR between stations from the bays, mid-shelf and barrier reefs were evident for adult or juvenile assemblages.

Mean abundance was highly variable among the ten stations, both for adult (ANOVA, $F = 14.419$, $P < 0.0001$) and juvenile (ANOVA, $F = 10.067$, $P < 0.0001$) assemblages (Fig. 3B). For adult colonies, mean abundance varied from 83.0 ± 8.5 (RA2) to 235.0 ± 14.7 colonies.10 m^{-2} (BA1). Significant differences in adult abundance were observed between the two stations within each of Grande Rade and Maa bays, and between the two barrier reef stations (SNK, all $P < 0.05$). In contrast, no significant differences were established between the two mid-shelf reef stations, or between the two stations at Sainte-Marie (SNK, all $P > 0.05$). The overall differences in mean abundance among the ten stations were also evident for juvenile assemblages, with values ranging between 20.3 ± 4.0 (MA2) and 115.6 ± 22.4 (BA1). Mean abundance did not significantly differ between SM1 and SM2, MA1 and MA2, or BA1 and BA2 (SNK, all $P > 0.05$), whereas it was significantly different between RA1 and RA2, and between SM1 and SM2 (SNK, all $P < 0.05$). Despite low abundance values within bays, no clear gradients between stations from bays, mid-shelf and barrier reefs emerged for abundance of adult corals. For juvenile corals, the highest abundance was recorded on the barrier reef stations, whereas no consistent difference was found between bays and mid-shelf reefs.

For all genera pooled, the spatial distribution of adult abundance was strongly and positively correlated with variation in juvenile abundance ($r = 0.884$, $P = 0.0002$; Fig. 3B). Such significant and positive correlations between juvenile and adult distribution were also demonstrated for each of the seven dominant genera, with particularly high correlation coefficients for *Acropora*, *Favia*, *Pocillopora* and *Porites* (Fig. 4). The relative abundance of juvenile colonies within the total assemblages (juveniles + adults) varied between 17.2 ± 4.6% (MS1) and 35.4 ± 2.1% (BA2) when considering all genera pooled (Table 2). This proportion was generally high for *Pocillopora*, *Acropora*, and *Favia*, slightly lower for *Porites* and *Montipora*, and reduced for *Galaxea* and *Psammocora* (Table 2). For each of the seven genera examined, no apparent gradients in the relative abundance of juvenile colonies within local assemblages was found between bays, mid-shelf reefs, and barrier reef stations.

Correspondence Analysis (CA) performed on spatial variation in composition and abundance of coral assemblages revealed a discrimination of stations closely related to the three biotopes, for both adults and juveniles (Fig. 5). The two barrier reef stations were clearly distinct, and most stations within bays were also grouped together, whereas station SM1 had similarities with the two mid-shelf reef stations. For adult corals, barrier reef stations showed a high abundance of *Stylophora* (exclusively found at barrier reef stations and at MS2), *Pocillopora*, *Acropora* and *Cyphastrea* (Fig. 5A). Mid-shelf reef stations were distinguished by the high abundance of *Galaxea* and *Merulina*, and by the presence of *Seriatopora*, a genus not found as adult colonies at other stations. Stations from bays (with the exception of SM1) were characterized by several genera not recorded elsewhere: *Echinophyllia* and *Stylocoeniella* in high abundance, and also *Mycedium*, *Oxypora* and *Cynarina*. Some bay stations were also characterized by a higher abundance of *Porites*, and *Psammocora*. Station SM1 had similarities with mid-shelf reef stations, with a lower abundance of *Porites* and a higher abundance of *Montipora* and *Acropora*.

As for adult assemblages, the barrier reef stations were characterized by a high abundance of juvenile colonies of *Acropora*, *Pocillopora*, and to a lesser degree, *Cyphastrea* (Fig. 5B). Barrier reef stations also showed a high abundance of juvenile *Stylophora* and *Montastrea*. Juveniles of *Lobophyllia* were exclusively found at one of the two barrier reef stations. Mid-shelf stations were distinguished by the presence of *Leptoseris*, *Merulina* and *Seriatopora*. Bay stations (with the exception of SM1) were characterized by a high abundance of *Porites* and *Favia*. The juvenile assemblage at station SM1 was more similar to those at mid-shelf reef stations because of a lower abundance of *Porites* and the absence of *Favia*, and also by a relatively high abundance of *Montipora*.

3.2. Environmental conditions

Percent cover of the 4 categories of algae and substrate types was highly heterogeneous among the ten stations (Table 1). Most bay stations, and to a lesser degree, mid-shelf reef stations, were characterized by a high turf cover, whereas barrier reef stations (BA1 and BA2) and SM1 were distinguished by lower values (SNK, all $P < 0.05$). Variability in macroalgal cover among stations was mainly due to the particularly high values found at MS1, whereas percent cover among the nine other stations was low (<5.3%) and not significantly different (SNK, all $P > 0.05$). High cover values of Encrusting Coralline Algae (ECA) were found at the two barrier reef stations, and to a lesser degree at MS2. At all other station, ECA cover was low (<5.1%) and was not significantly different among stations (SNK, all $P > 0.05$). Sand and rubble cover was high at station SM1, moderate at stations SM2 and MA2 (∼23%), and low (<11%) at all other stations.

Variation of water quality descriptors among stations is presented in Table 3. Temperature and salinity did not show any

Table 2
Variation in the mean relative contribution of juvenile colonies within coral assemblages. Values (in%) represent the number of juvenile colonies relative to the total (adults + juveniles) colony abundance at each of the 10 stations. Standard deviations are given in parentheses.

Genera	SM1	SM2	RA1	RA2	MA1	MA2	MS1	MS2	BA1	BA2	All stations
Pocillopora	69.6	48.7	49.1	17.7	34.7	50.0	47.2	41.3	51.6	47.6	45.8 (4.9)
Acropora	34.9	36.8	35.2	52.7	49.4	45.9	24.9	26.9	36.0	29.1	34.5 (5.3)
Favia	–	25.3	42.2	45.8	41.6	–	–	40.0	16.6	22.2	32.2 (1.9)
Porites	17.2	19.8	28.5	28.2	13.1	17.1	23.0	35.0	–	96.9	25.2 (2.8)
Montipora	28.7	28.3	32.1	61.1	23.9	-	13.6	29.9	11.2	43.5	22.6 (3.5)
Galaxea	33.3	–	16.6	–	–	33.3	11.6	6.4	22.3	–	12.8 (3.8)
Psammocora	4.7	16.6	15.4	–	1.4	–	–	6.6	–	19.4	10.1 (2.6)
All genera	29.0	26.3	27.6	27.3	22.6	22.4	17.2	26.2	32.8	35.4	27.9 (1.7)

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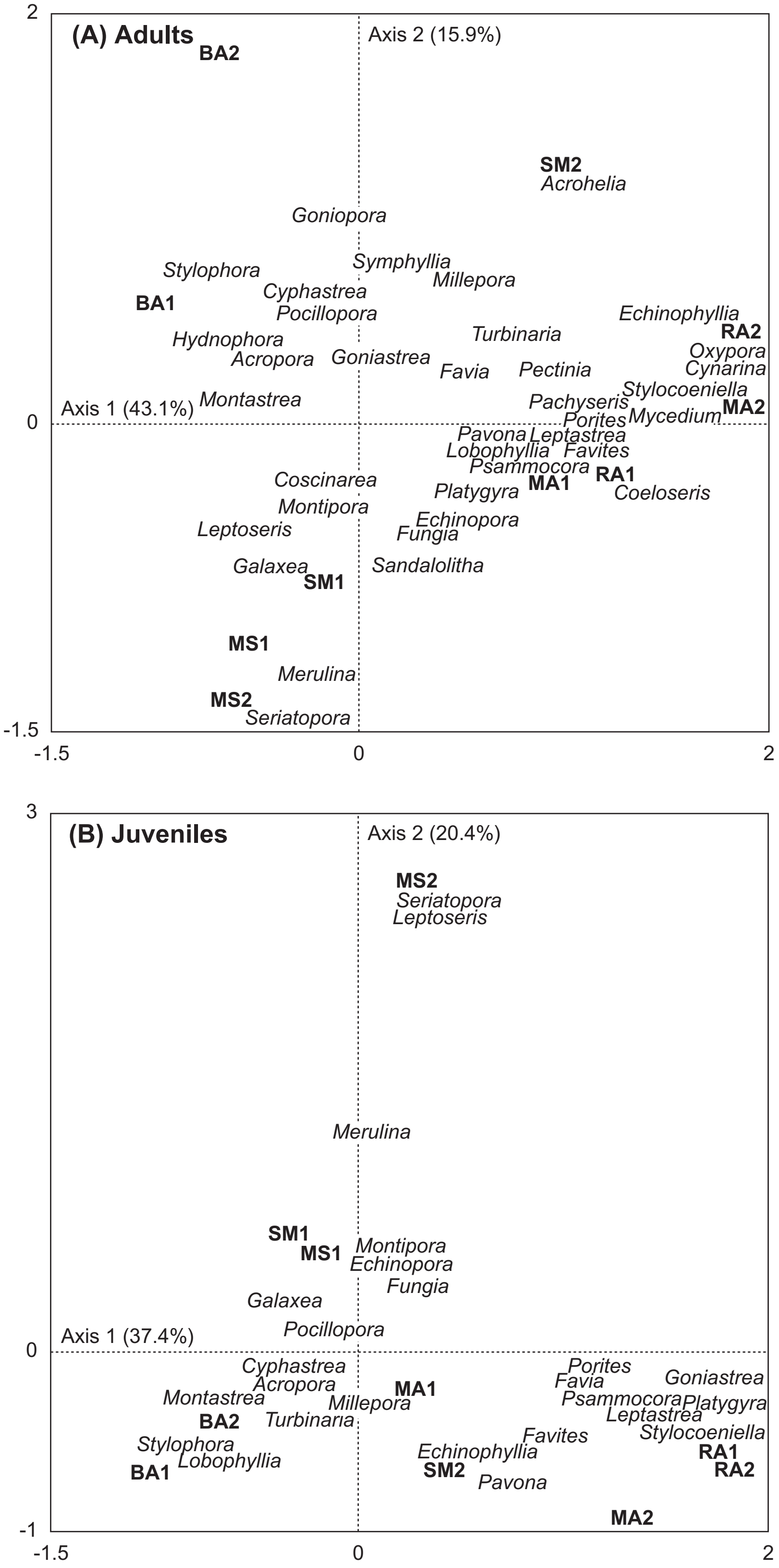

Fig. 5. Plots of the Classification Analysis (CA) showing the overall variation in composition and abundance of (A) adult and (B) juvenile coral assemblages. Analyses were performed on the mean abundance of the 37 (adults) and 25 (juveniles) genera recorded at each of the ten stations. The percentage of variance (inertia) and the position of stations and genera along the first two axes are given.

significant variation among the eight stations. Higher values of turbidity were measured within bays, particularly at stations SM1 and RA1. Chlorophyll *a* concentrations were higher within Grande Rade and Sainte Marie bays, notably at station SM1. This station was also characterized by high concentrations in NH_4, NO_3 and PO_4. Si concentrations were higher within bays than at mid-shelf and barrier

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Table 3
Variation in water quality characteristics among the eight monitoring stations. Data represent mean of measurements made during several monitoring periods organized between 1997 and 2005 for temperature, salinity and turbidity, and between 1997 and 2003 for other variables. Standard deviations are given in parentheses.

Stations	Temperature (°C)	Salinity psu	Turbidity FTU	NH_4 (μM)	NO_3 (μM)	PO_4 (μM)	Si (μM)	Chloro. *a* (μg l^{-1})
SM1	24.74 (2.47)	35.20 (0.70)	1.82 (0.93)	0.331 (0.413)	0.333 (0.549)	0.164 (0.143)	3.506 (1.293)	1.908 (1.358)
SM2	22.76 (1.34)	35.34 (0.04)	0.59 (0.74)	0.144 (0.143)	0.024 (0.007)	0.058 (0.059)	4.360 (3.487)	0.681 (0.276)
RA1	25.47 (1.98)	35.53 (0.40)	1.13 (0.53)	0.233 (0.135)	0.055 (0.090)	0.048 (0.024)	6.272 (2.336)	0.496 (0.321)
RA2	24.69 (2.31)	35.20 (0.43)	0.71 (0.42)	0.141 (0.084)	0.014 (0.010)	0.049 (0.048)	3.910 (1.975)	0.358 (0.096)
MA1	24.41 (3.58)	35.38 (0.43)	0.86 (0.20)	0.188 (0.169)	0.028 (0.031)	0.047 (0.058)	2.352 (0.814)	0.289 (0.074)
MS1	25.15 (1.91)	35.47 (0.35)	0.51 (0.25)	0.229 (0.182)	0.017 (0.018)	0.036 (0.029)	2.035 (0.887)	0.261 (0.140)
MS2	23.87 (2.02)	35.20 (0.28)	0.30 (0.20)	0.241 (0.162)	0.031 (0.035)	0.044 (0.028)	1.380 (0.695)	0.199 (0.073)
BA1	24.38 (2.65)	35.27 (0.56)	0.66 (0.45)	0.143 (0.125)	0.021 (0.013)	0.051 (0.039)	2.786 (1.253)	0.185 (0.023)

Table 4
Variation in mean metal concentrations (in μg g^{-1}) in surface sediment among the monitoring eight stations.

Stations	Chrome (Cr)	Manganese (Mn)	Iron (Fe)	Cobalt (Co)	Nickel (Ni)	Zinc (Zn)
SM1	192.5	213.6	24002	29.9	292.3	52.5
SM2	159.7	202.3	13996	31.6	270.0	51.1
RA1	357.9	382.3	35996	62.7	1308.0	170.9
RA2	267.0	229.6	24816	38.7	797.0	77.9
MA1	135.0	137.8	19008	26.2	216.2	31.0
MS1	121.1	63.1	9303	23.8	219.7	25.1
MS2	83.5	25.2	4661	23.5	92.8	10.7
BA1	47.2	30.6	3335	27.5	94.7	15.8

reef stations. Table 4 presents the variation in metal concentrations in surface sediment among the eight stations. High concentrations of all metals were recorded within bays, particularly at Sainte Marie and Grande Rade. Station RA1 was distinguished by particularly high values of Ni, Zn, Cr, Mn, Fe and Co. In contrast, mid-shelf and barrier reef stations showed significantly lower concentrations of metals, with the exception of a relatively high concentration of Ni at MS1.

3.3. Factors influencing the spatial distribution of corals

Two factors were significantly correlated with the variation in community composition and abundance of adult coral genera; turf and Encrusting Coralline Algae (ECA) cover (Fig. 6; Table 5). Percent cover of algal turf was the most significant factor, and was closely associated with the distribution and abundance of genera such as *Leptastrea*, *Stylocoeniella*, *Favia*, and *Favites* (Fig. 6A). These genera were more abundant and predominately found at bay stations RA1, RA2 and SM2. Percent cover of ECA was associated with the distribution and abundance of *Stylophora*, *Montastrea*, *Leptoseris*, *Hydnophora*, and *Galaxea*, which characterized stations MS1 and BA1. Percent cover of turf algae was also significantly correlated with the variation in composition and abundance of the juvenile coral assemblage (Table 5). The distribution and abundance of *Leptastrea*, *Goniastrea*, *Psammocora*, *Porites*, *Platygyra*, *Stylocoeniella*, and *Echinophyllia* was closely associated with the high turf cover found at bay stations RA1, RA2 and SM2 (Fig. 6B).

Correlation analyses revealed that cover of ECA was the only factor positively and significantly correlated with the variation of mean adult and juvenile abundance (all genera pooled; $r = 0.786$, $P = 0.0177$, and $r = 0.0842$, $P = 0.0060$, respectively), whereas no correlation was found with any of the other 17 selected environmental factors.

4. Discussion

4.1. Structure of coral assemblages and controlling environmental factors

As for the majority of coral reefs throughout the world (Chiappone and Sullivan, 1996; Edmunds, 2000; Ruiz-Zarate and Arias-Gonzales, 2004; Penin et al., 2007), coral assemblages in the southwest lagoon of New Caledonia were characterized by significant spatial heterogeneity, both for adults and juveniles. Generic richness, abundance of colonies, percent cover and community composition were highly variable among the ten stations surveyed during this study. However, there was no clear cross-shelf gradient in coral diversity, abundance or cover between the fringing reefs, mid-shelf reefs, and the inner barrier reefs. Fringing reefs exhibited high variability in coral generic richness and abundance, and had the highest pollution levels. The relatively high diversity, abundance and cover of coral assemblages observed within some bays seems to be a characteristic of some Western Pacific reefs (but see Golbuu et al., 2008), as has been documented in the Ryukyus (Horikoshi, 1981, 1988), the Solomon Islands (Morton, 1974), the GBR (Fabricius and De'ath, 2004), the Philippines (Licuanan and Gomez, 1988), and Palau (Horikoshi, 1988). In Central Pacific reefs, bays are characterized by low diversity, abundance and cover of corals, and generally by a marked increasing trend from the bayhead to the bay entrance, as described in French Polynesia (Adjeroud and Salvat, 1996; Adjeroud, 2000) and Hawaii (Maragos JE and Holthus P, 1985).

In contrast to other descriptors of coral assemblages, community composition was closely related to reef biotopes, with distinct assemblages between coastal fringing reefs and oceanic barrier reefs. These outcomes highlight the importance of the descriptor used to assess the effects of perturbations on coral assemblages, and suggest that synthetic descriptors such as cover or diversity are not always adequate indicators for detecting terrigenous impacts (Golbuu et al., 2008; Smith et al. 2008).

Spatial variation in the relative contribution of coral genera within local assemblages was closely related to substrate types. Percent cover of turf algae was correlated with composition of both adult and juvenile assemblages, and percent cover of encrusting coralline algae (ECA) was linked to the composition of adult assemblages. Moreover, variation in total abundance of juveniles and adults was correlated with percent cover of ECA. Even if correlations revealed by statistical analyses do not necessarily indicate a direct causal relationship that is explained by physiological or biological mechanisms, our results suggest that the type of algal community present and its spatial extent probably influence a large part of the coral community composition. This relationship may

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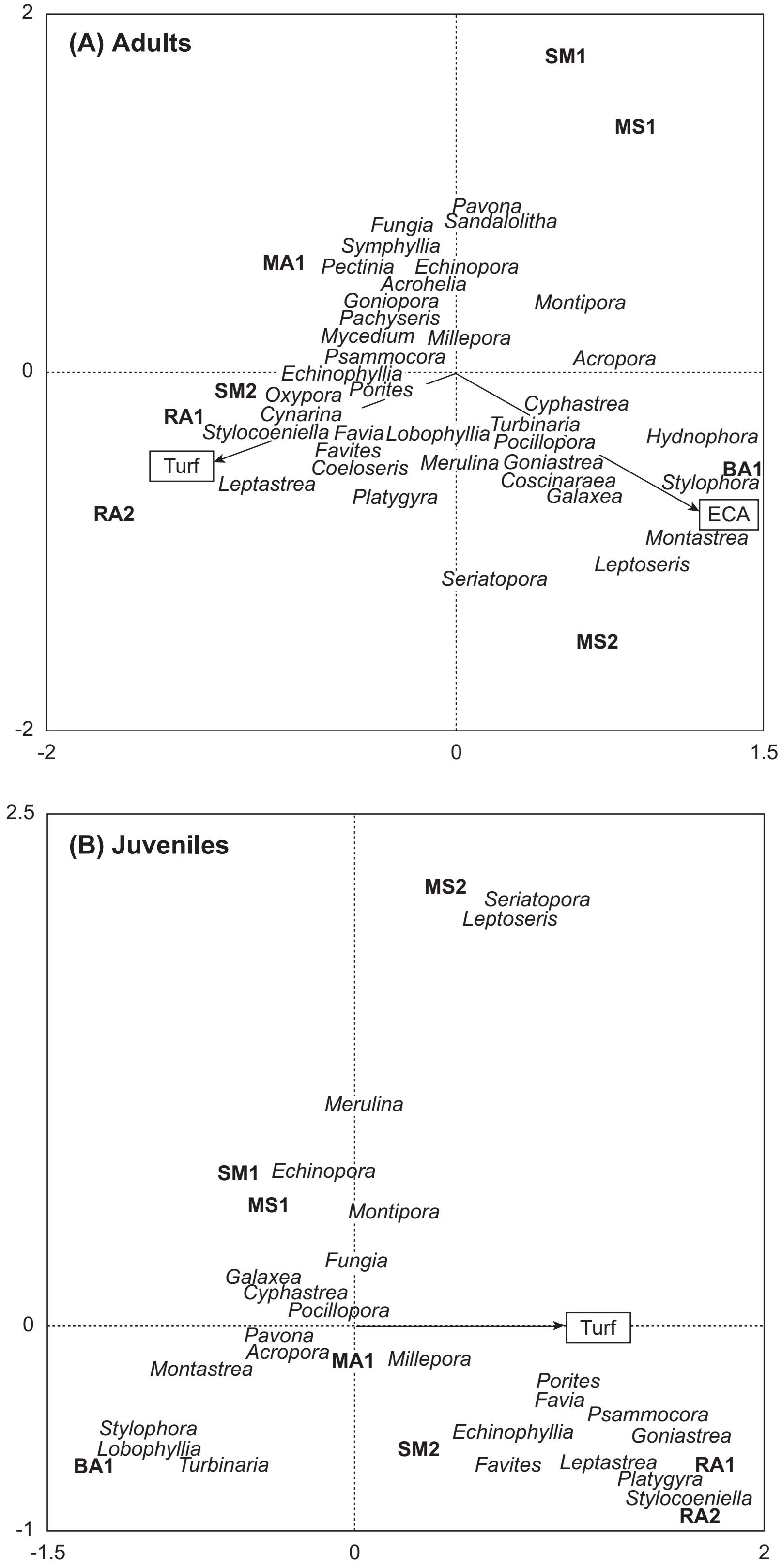

Fig. 6. Plots of the Canonical Correspondence Analysis (CCA) performed to analyse the relationships between spatial variation in the abundance of coral genera and the selected environmental factors (water and sediment quality, and substrate type). CCA were made separately for adult (A) and juvenile (B) coral assemblages. Position of the eight stations in relation to the significant factors is given along the first two axes. ECA: encrusting coralline algae.

be established through biotic interactions during larval settlement, and/or through spatial competition (Rogers et al., 1984; Gleason, 1996; Carlon, 2001). In particular, competing algae may affect coral recruitment and adult distribution through space pre-emption or overgrowth (Kuffner et al. 2006; Vermeij 2006). Several studies have also demonstrated that encrusting coralline algae may

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Table 5
Summary of the CCA performed on the spatial variation of adult and juvenile coral assemblages and the selected environmental factors. Significant factors are selected by a stepwise procedure analogous to backward elimination in multiple regression analysis. ECA: encrusting coralline algae.

	Adults				Juveniles		
	Axis 1	Axis 2			Axis 1	Axis 2	
Correlation of factors with ordination axes							
(1) % Turf	−0.860	−0.306		(1) % Turf	0.952	0.000	
(2) % ECA	0.559	−0.735					
Summary statistics for ordination axes							
Eigenvalues	0.317	0.140			0.398	0.235	
Species-environment correlations	0.909	0.951			0.952	0.000	
Sum of all unconstrained eigenvalues			0.901				1.050
Sum of all canonical eigenvalues			0.457				0.398
Variation explained by the factors			50.72%				37.90%
Probability of Monte Carlo tests			0.01				0.01

enhance recruitment success of some coral species, through the production of chemical cues that induce larval settlement (Morse et al. 1988; Vermeij 2005).

Hydrological conditions and metal concentrations were not significantly correlated with the variation in the composition, abundance and richness of coral assemblages. It is nevertheless important to note that the environmental factors not selected by the CCA are not necessarily irrelevant to species distribution. In fact, environmental factors can co-vary in such a manner that it is difficult to distinguish their relative contribution. Furthermore, other factors may also have indirect or synergistic effects that are not revealed by the CCA. For example, water and sediment pollution are known to affect coral reproductive success (Heyward, 1988; Richmond, 1993; Reichelt-Brushett and Harrison, 2000, 2005; Harrison and Ward, 2001),); however, such an effect may be masked when examining juvenile or adult density if there is a sufficient supply of coral larvae sourced from less disturbed nearby reefs (Harrison and Wallace, 1990). The lack of significant correlation between the distribution, diversity and density of corals and water and sediment characteristics has also been demonstrated in some previous studies. For example, in Indonesia, environmental factors across a disturbance gradient primarily affected coral species composition, while percent cover and species richness were virtually not affected (Cleary et al., 2006). Similarly, in Hawaii, no negative impacts from the discharge of sewage effluents on coral species richness and abundance were observed, suggesting that species richness is a weak indicator of the effects of sewage discharge and differential fishing pressure at this location (Grigg, 1994). Along the coast of Barbados, no significant relationships between partial mortality and abundance of coral colonies, and eutrophication gradients were recorded (Lewis, 1997). Collectively, these studies demonstrate that the effects of some natural and anthropogenic disturbances remain highly variable among coral reefs, and may range from an apparent lack of serious damage (Sheppard, 1980; Dollar and Grigg, 1981; Brown and Holley, 1982), to severe effects (Loya, 1976; Rogers et al., 1982).

4.2. Mechanisms of population regulation and replenishment capacities

Spatial patterns of juvenile and adult coral assemblages were quantitatively and qualitatively highly concordant. Spatial variability in abundance of adult and juvenile colonies was strongly and positively correlated, for the seven dominant genera as well as the overall coral community (all genera pooled). As shown for other coral reefs worldwide (Chiappone and Sullivan, 1996; van Woesik et al., 1999; Mundy and Babcock, 2000), our results indicate that spatial patterns of adult assemblages are closely linked to the short-term history of recruitment patterns. Such a strong link between juvenile and adult spatial distribution may indicate a strong recruitment-limitation (where juveniles drive the number of adults) or stock-recruitment (where adults drive the number of juveniles) mechanisms of population regulation (Edmunds, 2000; Carlon, 2001; Baird et al., 2003; Penin et al. 2007). This relationship between adult and juvenile corals would be more effective if we consider the size of adult colonies within populations, which is more related to fecundity than adult colony densities. Finally, the strong link between juvenile and adult spatial distribution may also be the result of an aggregative settlement caused by preference for similar substrate types (Harrison and Wallace, 1990). This hypothesis is supported by the relationship observed between spatial distribution of several coral genera and particular algae, such as ECA and turf.

The densities of juvenile colonies recorded during this survey (mean = 5.6 juveniles.m^{-2}, range = 2.0–11.5 juveniles.m^{-2}) were relatively low. They are similar to values found at Moorea, French Polynesia (Penin et al., 2007), but substantially lower when compared to other coral reefs such as Heron Island on the GBR (Connell et al., 1997), or some Atlantic reefs (Ruiz-Zarate and Arias-Gonzales, 2004), where up to 30 juveniles.m^{-2} were recorded. Moreover, the contribution of juveniles within the total assemblages was relatively low (<30% of colonies), with the exception of the two inner barrier reef stations (30–35%). In contrast to the findings of previous studies (Wittenberg and Hunte, 1992; Tomascik, 1991; Hunter and Evans, 1995; Fabricius et al., 2003; Fabricius and De'ath, 2004), our survey demonstrates that recruitment rates and replenishment capacities in areas with high nutrient and metal concentrations are not necessarily reduced when compared to less polluted locations. The fact that adult populations appear dependant on recruitment, and that densities of juveniles are relatively low, implies that replenishment capacities and potential for recovery following major disturbances are probably limited in the three reef biotopes surveyed during this study. In this context, we conclude that major conservation and management effort is required to protect and manage these biotopes, with particular attention given to fringing reefs within bays, where anthropogenic activities are the most intense.

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