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Spatial Patterns and Short-term Changes of Coral Assemblages Along a Cross-shelf Gradient in the Southwestern Lagoon of New Caledonia

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Abstract: Coral reef assemblages generally form gradients of spatial structures which are governed by a variety of interacting physical and biological processes that vary in intensity, frequency, and spatial scale. Assessing the structure of contemporary reef assemblages may help to understand future changes and to identify appropriate conservation actions. The spatial distribution and interannual variability (from 2006 to 2008) of coral assemblages were investigated at 10 stations in the southwestern lagoon of New Caledonia, and the strength of the cross-shelf gradient was evaluated. Coral cover, generic richness, and abundance of adult and juvenile assemblages were highly variable within and among the three major reef habitats (fringing, mid-shelf, and barrier reefs). Abundance increased with distance from shore, whereas generic richness and cover were not correlated with shelf position. Assemblage composition was generally related to habitat, even though some mid-shelf and fringing reef assemblages resembled those observed on other habitats. A significant correlation between juvenile and adult distributions was recorded, suggesting that adult assemblages are partly controlled by the short-term history of recruitment patterns. The interannual variation of coral assemblages was far less pronounced, with significant changes only detected at some mid-shelf and barrier reefs, for a few genera characterised by high turn-over.

Keywords: coral reefs; scleractinian corals; spatial heterogeneity; interannual variability; recruitment; environmental factors; land-ocean gradient; New Caledonia

1. Introduction

Coral reefs are characterised by exceptional biodiversity and complexity, and are among the most productive ecosystems on earth [1,2]. They protect coastlands and provide economical, cultural, social and aesthetical goods and services that are crucial to ~850 million people from more than 100 countries [3,4]. Coral reefs are also recognised for the marked spatio-temporal variability in their biological communities (a 'mosaic of patches' ecosystem) [5], notably of vulnerable and long-lived sessile marine organisms as scleractinian reef-building corals [6–10]. Since the pioneering work of Goreau [11], spatial and temporal patterns within coral communities at multiple scales have been extensively documented worldwide [12–15]. This previous work shows that the distribution and dynamics of coral assemblages are governed by a variety of interacting extrinsic physical and biological drivers, such as the availability of adequate substrate, sediment characteristics, light, water quality, hydrodynamic forces, and biotic interactions [14,16–19]. Among the intrinsic processes, recruitment is widely recognised as being a major driver in the dynamics and recovery of local populations following disturbances, though both pre- and post-settlement events may influence the local abundance and spatial distribution of adult assemblages [20–24].

Like many marine ecosystems, coral reefs are increasingly exposed to various chronic and/or episodic threats, and their resilience capacities are challenged by environmental changes [25–29]. In this context, understanding the spatio-temporal structure of contemporary reef communities will help to construct a valuable baseline to understand future changes, which is crucial in order to identify appropriate management actions [30–32]. Large-scale disturbances such as thermally induced coral bleaching events, cyclones and outbreaks of keystone species, such as the coral-killing sea star *Acanthaster* spp. in the Indo-Pacific, have the potential to substantially alter the structure and dynamics of reef communities, with widespread mortalities of foundation organisms and phase shifts in community structure and habitat degradation [9,26,31,33]. In response to all these physical and biological drivers, reef assemblages are generally organised along gradients or other kinds of spatial structures. Three major types of spatial gradients can be distinguished: (1) cross-shelf gradient (i.e., land to ocean or in- to offshore gradient; [14,16,34–38]); (2) bay-head to bay-entrance gradient [39,40]; and (3) cross-depth gradient [7,16].

Here, we examine the spatial distribution and short-term changes of coral assemblages among various reef habitats in the southwestern lagoon of New Caledonia, from fringing reefs situated within bays to oceanic barrier reefs. We assessed the interannual variability (2006 to 2008) in generic composition and richness, as well as percent cover and abundance of adult but also juvenile corals, to provide a short-term history of recruitment patterns and their links with adult distributions. The overall goal of the study was to evaluate the strength of the cross-shelf gradient in coral assemblage structure in this area. Our work complements a previous study that was restricted to spatial variation in coral assemblages [41]. The spatio-temporal data set examined here constitutes a reference baseline for evaluating future changes in coral communities, a critical step for an effective conservation of these coral reefs, which are recognised by UNESCO as World Heritage since 2008.

New Caledonia represents a unique system to address cross-shelf variation in coral community structure. The barrier reef circling the main island is the second longest in the world, after Australia's Great Barrier Reef, and is composed of a highly diversified fauna (including > 310 scleractinian species; [42]). The morphological diversity of New Caledonian reefs, and their proximity to the coral centre, partly explains this high biodiversity [43,44]. The southwest lagoon of the main island is very large (~10–30 km separates the coast and the outer reef slope) and contains most major reef habitats (fringing reefs, mid-shelf reefs, barrier reefs and outer reef slopes) that represent contrasting environmental conditions [41]. New Caledonia is exposed to some localised anthropogenic impacts, which are primarily associated with extensive nickel mining for more than a century. However, compared to other Pacific reefs, such the Great Barrier Reef or the French Polynesian Islands, large-scale natural disturbances are relatively rare in New Caledonia, and no widespread mass mortality of corals has been recently recorded [45]. Instead, natural disturbances are restricted in time and space, such as the cyclone Erica in 2003 [46,47], the ephemeral and localised outbreaks of the coral-killing *Acanthaster* spp. recorded in 2012–2013 [48], and the bleaching event in 2016 that has affected some fringing reefs of the main island but with low coral mortality (<10%; [49]). However, these perturbations have occurred before or after our survey, and none directly impacted coral assemblages at our sites during the course of this study.

2. Materials and Methods

2.1. Study Area

The survey presented in this work was conducted in the southwestern part of the main island ('Grande Terre') of New Caledonia, including reefs around Nouméa, the most populated and industrialised city of New Caledonia (Figure 1). The southwestern lagoon is primarily exposed to southeasterly trade winds that govern the general direction of surface currents [50]. Oligotrophic oceanic waters enter the lagoon via the open southern shelf, flow through the lagoon, and then exit via passes along the western shelf [50]. As hydrodynamic circulation in the study area is generally active, the terrigenous influence on water quality and sediment composition is mainly restricted to fringing reefs, particularly those within bays with fresh water inputs and long water residence times. Conversely, most mid-shelf and barrier reefs are under oceanic influences [51–53].

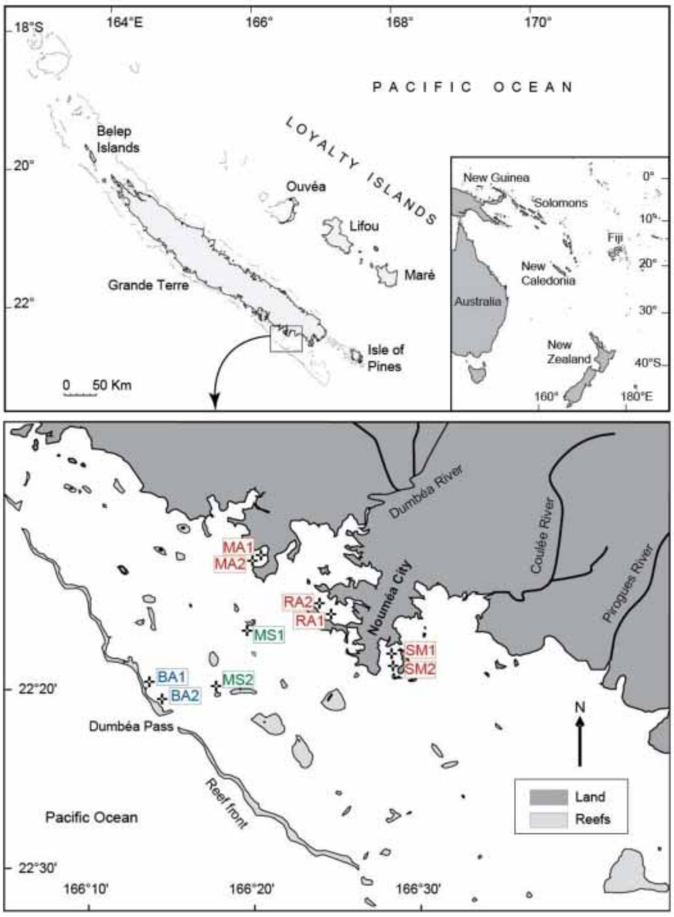

Figure 1. Location of the 10 sampling stations in the southwestern lagoon of the main island ('Grande Terre') of New Caledonia. Stations were located on the three major reef habitats: fringing reefs (in red), mid-shelf reefs (in green), and inner barrier reefs (in blue).

To study the spatio-temporal variability of coral assemblages, 10 stations were selected haphazardly on the three major reef habitats that compose the cross-shelf gradient in the southwestern lagoon (Figure 1, Supplementary Table S1). For fringing reefs, we established six stations within three different bays (SM1 and SM2 in Sainte Marie, RA1 and RA2 in Grande Rade, and MA1 and MA2 in Maa), whereas two stations were located on mid-shelf (MS1 and MS2, at 10.8 and 15.1 km from Nouméa, respectively) and barrier reefs (BA1 and BA2, at 22.2 km and 21.0 km from Nouméa, respectively). The three bays represent different types and levels of pollution [54–56]. Sainte-Marie and Grande Rade are both impacted by heavy metals (notably Ni, Cr, Zn, and Co) emanating from neighbouring mining activities. Sainte-Marie is also characterised by high terrigenous inputs and urban wastewaters, whereas Grande Rade receives industrial effluents primarily originating from the nickel industry and the commercial harbour [57]. In contrast, Maa is often considered to be an unaltered reference site for fringing reefs within bays, with lower terrigenous and anthropogenic inputs [57]. See Adjeroud et al. [41] for detailed data on parameters within the water (temperature, salinity, turbidity, nutrients, and chlorophyll *a*) and the sediments (concentrations of heavy metals) in the surveyed area.

2.2. Coral Sampling

Sampling of corals was conducted from mid-October to mid-November, in 2006, 2007 and 2008. At each station, adult and juvenile corals (scleractinians and the calcareous hydrocoral *Millepora*) were sampled along three randomly replicated 10 × 1 m belt-transects, laid parallel to depth contours and separated by ~1 m [41]. Stainless steel stakes were used as reference markers at each survey station and the GPS locations of each station were recorded in 2006 to allow for a similar survey in following years. However, several stakes were removed during the three-year survey, and some transects were replaced at approximately the same position. All transects were located on the constructed reef framework, at a depth of 3 ± 0.5 m, where coral assemblages are most developed on these shallow subtidal habitats [43,44]. As in most previous studies [23], juveniles were defined as all visible coral colonies ≤ 5 cm in maximum diameter (which correspond to non-reproductive size classes for the majority of Pacific reef corals; [58]), whereas colonies with maximum diameters larger than 5 cm were considered as adults. Coral assemblages were characterised by their generic richness and colony abundance, as the identification of juvenile colonies at the species level is often impossible. In addition, the percent cover of living substrate (corals, algal turf, encrusting coralline algae, and macroalgae) was recorded at each station using three linear 10 m transects (Line Intercept Transect Method; [59]), placed at the centre of the belt-transects.

2.3. Data Analysis

The spatio-temporal variation was assessed through the analysis of the percent cover of living substrate, generic richness (GR), and abundance of coral colonies. A two-way analysis of variance (ANOVA) was performed, with stations and years when samples were collected as fixed factors. GR and abundance data were log (x + 1) transformed, and arcsin transformation was applied to percent cover data to satisfy the assumptions of parametric tests. When ANOVA results indicated significant differences, post-hoc Student-Neuman-Keuls (SNK) tests were performed to compare values between pairs of stations and years. We used the Bonferroni correction for multiple tests to avoid Type 1 error.

To examine the influence of shelf position on the structure of coral assemblages, Pearson correlation coefficients (r) were calculated between percent cover, GR and abundance of corals at each station ($n = 10$), and its distance to the shore (for stations of fringing reefs within bays, we used the distance to the bay-head). Correlation analyses were also used to assess relationships between juvenile and adult spatial distribution. Pearson (r) coefficients were calculated between the mean abundance of adults and juveniles at each station, for the overall assemblages (all genera pooled) and for the seven major coral genera.

Finally, we used non-metric multidimensional scaling (MDS) to examine interannual variation in the composition of the coral assemblage based on the Bray–Curtis dissimilarity index of the abundance of coral genera recorded annually. Analyses were conducted in R version 3.1.0.

3. Results

For each year, the percent cover of corals, turf and encrusting coralline algae (ECA) were spatially variable among the 10 stations (Figure 2; ANOVA, all $p < 0.0001$, see Supplementary Table S2). Macroalgal percent cover was variable between stations in 2007 and 2008, but not in 2006. The highest coral cover values (> 30%) were recorded at the Maa stations (MA) and one mid-shelf station

(MS1; Figure 2A). Coral percent cover was highly similar among the fringing reefs of Sainte-Marie (SM) and Grande Rade (GR), and one barrier reef station (BA2). A decreasing trend was observed at mid-shelf stations (MS), whereas values increased at barrier reef station BA1. However, these variations were not statistically significant (ANOVA, $p > 0.05$). Turf percent cover was low at barrier reef stations, high at most fringing reef stations (except at SM1), and increased at mid-shelf reef stations (Figure 2B). An opposite pattern was observed for ECA, with the highest values exhibited at barrier reef stations and the mid-shelf station MS2, whereas values were much lower at other stations (Figure 2C). Macroalgal percent cover was generally low (<10%), except at the mid-shelf station MS1 in 2007 (Figure 2D).

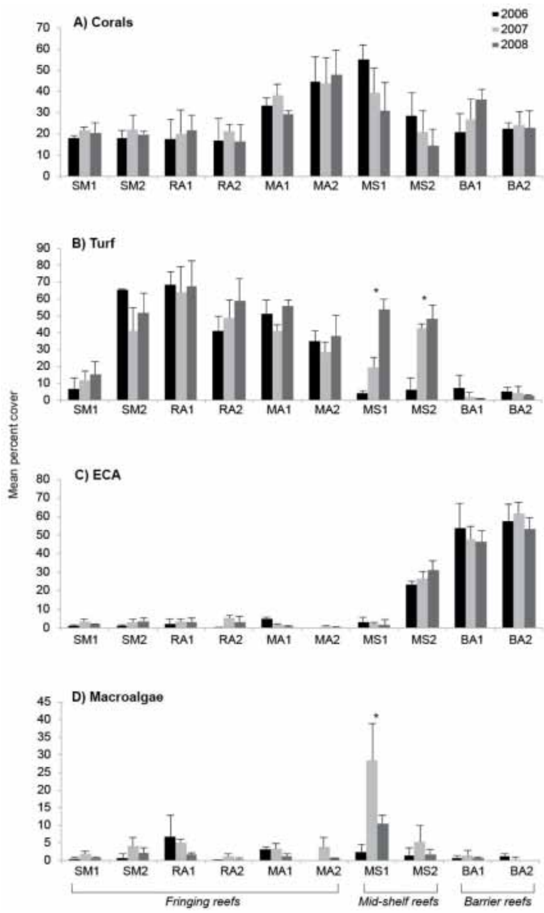

Figure 2. Spatial and interannual variation in mean percent cover of (**A**) corals, (**B**) algal turf (mixed species, low structure, and filamentous algae), (**C**) encrusting coralline algae (ECA) and (**D**) macroalgae at the 10 stations. Error bars represent standard deviation. Asterisks refer to significant interannual variation at the station scale (SNK tests).

A total of 38 coral genera were recorded in 2006, 37 in 2007 and 36 in 2008. For each year, the mean generic richness (GR) varied significantly among the 10 stations, for both adult and juvenile assemblages (Figure 3; ANOVA, all $p < 0.001$, see Supplementary Table S3). The highest GR values for adult corals were recorded at one mid-shelf station (MS2) and one fringing station (RA1; Figure 3A). There were relatively high GR values of juveniles at MS2 and RA1, and at barrier reef stations (BA1 and BA2; Figure 3B). For both adults and juveniles, the GR at each station was highly similar each year; there was no significant temporal variability (ANOVA, $p > 0.05$). However, the spatial variation in GR of adults was strongly and positively correlated with that of juveniles for each of the three years ($r = 0.728$, 0.840 and 0.798 for 2006, 2007 and 2008, respectively; $p < 0.001$).

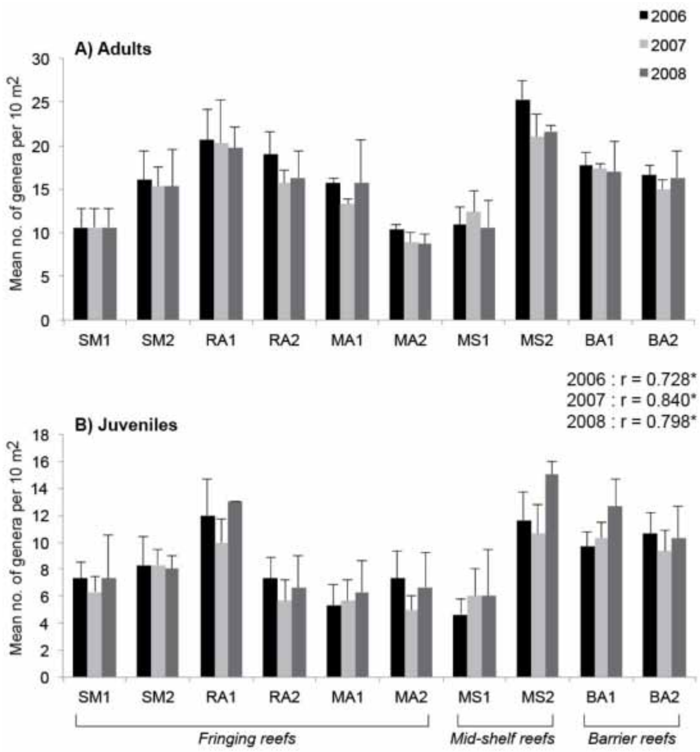

Figure 3. Spatial and interannual variation in mean generic richness of (**A**) adult and (**B**) juvenile corals at the 10 stations. Error bars represent standard deviation. Asterisks refer to significant interannual variation at the station scale (SNK tests). Pearson correlation coefficients (r) between variation in juvenile and adult generic richness, and their associated statistics (*: significant, $p < 0.01$; NS: non-significant) are given.

The mean overall abundance (all genera pooled) was also highly variable among the 10 stations for each of the three years, for both adults and juveniles (Figure 4; ANOVA, all $p < 0.0001$, see Supplementary Table S4). The highest adult abundances were found at barrier reef (BA) stations, one mid-shelf reef (MS2), and one fringing reef stations (RA1), whereas values were significantly lower at stations RA2 and MA1 located at the Grande Rade and Maa bays, respectively (Figure 4A). Adult coral abundances were highly similar among the three years of the survey at most stations. Only one station, MS2, showed significant temporal variability with decreasing abundances between 2006 and 2008. For juveniles, four stations (MA1, MS2, BA1 and BA2) showed significantly higher abundances recorded in 2008 than in prior years (Figure 4B). Spatial variation in the abundance of adults was strongly and positively correlated with that of juveniles in 2007 and 2008 ($r = 0.886$, and 0.854, respectively; $p < 0.001$), but not in 2006 ($r = 0.570$, $p = 0.083$).

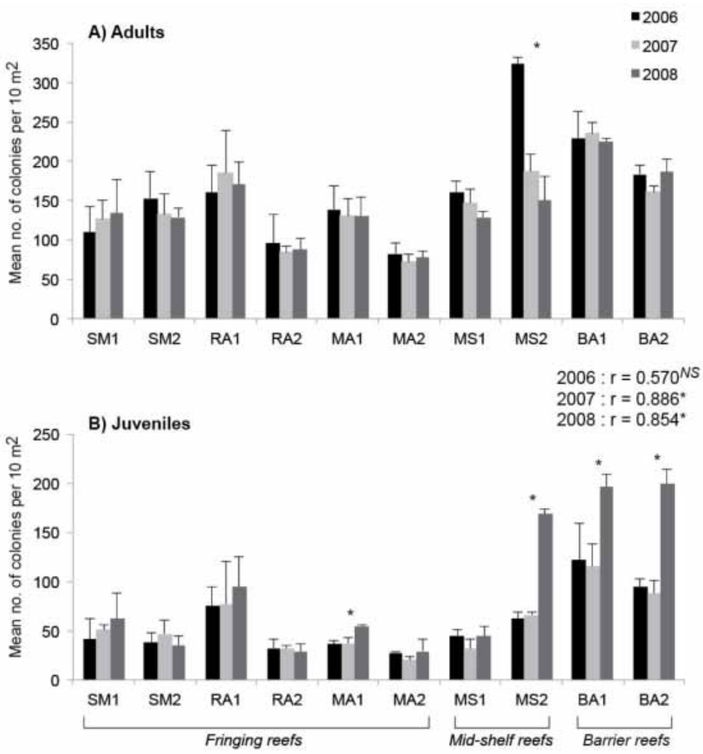

Figure 4. Spatial and interannual variation in mean abundance of (**A**) adult and (**B**) juvenile coral colonies at the 10 stations. Error bars represent standard deviation. Asterisks refer to significant interannual variation at the station scale (SNK tests). Pearson correlation coefficients (r) between variation in juvenile and adult abundance, and their associated statistics (*: significant, $p < 0.01$; NS: non-significant) are given.

Coral percent cover, and GR of both adult and juvenile corals were not significantly correlated with the shelf-position (Table 1). In contrast, abundance of adult and juvenile colonies were positively correlated with the distance to the shore. In addition, these significant correlations were recorded for each of the three years of the survey.

Table 1. Influence of shelf position on the structure of coral assemblages. Pearson correlation coefficients (r) between percent cover, generic richness, and abundance of juvenile and adult corals at each station ($n = 10$), and the distance to the shore, and their associated statistics (*: significant, $p < 0.01$; NS: non-significant).

Descriptor	2006	2007	2008
Percent cover	0.043 NS	0.099 NS	0.048 NS
Generic Richness			
Adults	0.289 NS	0.343 NS	0.321 NS
Juveniles	0.387 NS	0.518 NS	0.548 NS
Abundance			
Adults	0.701 *	0.696 *	0.733 *
Juveniles	0.815 *	0.725 *	0.886 *

A significant spatial variation for all the seven major coral genera was recorded for both adults and juveniles (Figure 5; ANOVA, all $p < 0.001$). Juvenile and adult colonies of *Acropora*, *Pocillopora*, *Galaxea*, and *Stylophora* were more abundant at mid-shelf and barrier reef stations, whereas higher abundance of *Porites* and *Dipsastraea* (formerly *Favia, partim)* were recorded at fringing reef stations. Adult and juvenile colonies of *Montipora* showed high abundance values at some fringing reef (SM1) and barrier reef (BA1) stations, together with mid-shelf stations (MS1 and MS2). Interannual variability of adult abundance was restricted to few stations, with a decrease of *Acropora*, *Pocillopora*, and *Stylophora* and an increase of *Porites* at MS2. For juveniles, we detected a significant increase of *Acropora*, *Porites*, *Montipora*, and *Galaxea* abundance in 2008 at MS2 and at one of the barrier reef stations, together with *Stylophora*. A significant increase of *Dipsastraea* juvenile abundance was also recorded in 2008 at one fringing reef station (RA1). The spatial variation in juvenile and adult abundances was highly and positively correlated on all years for all coral genera, except in 2008 for *Montipora* (Figure 5).

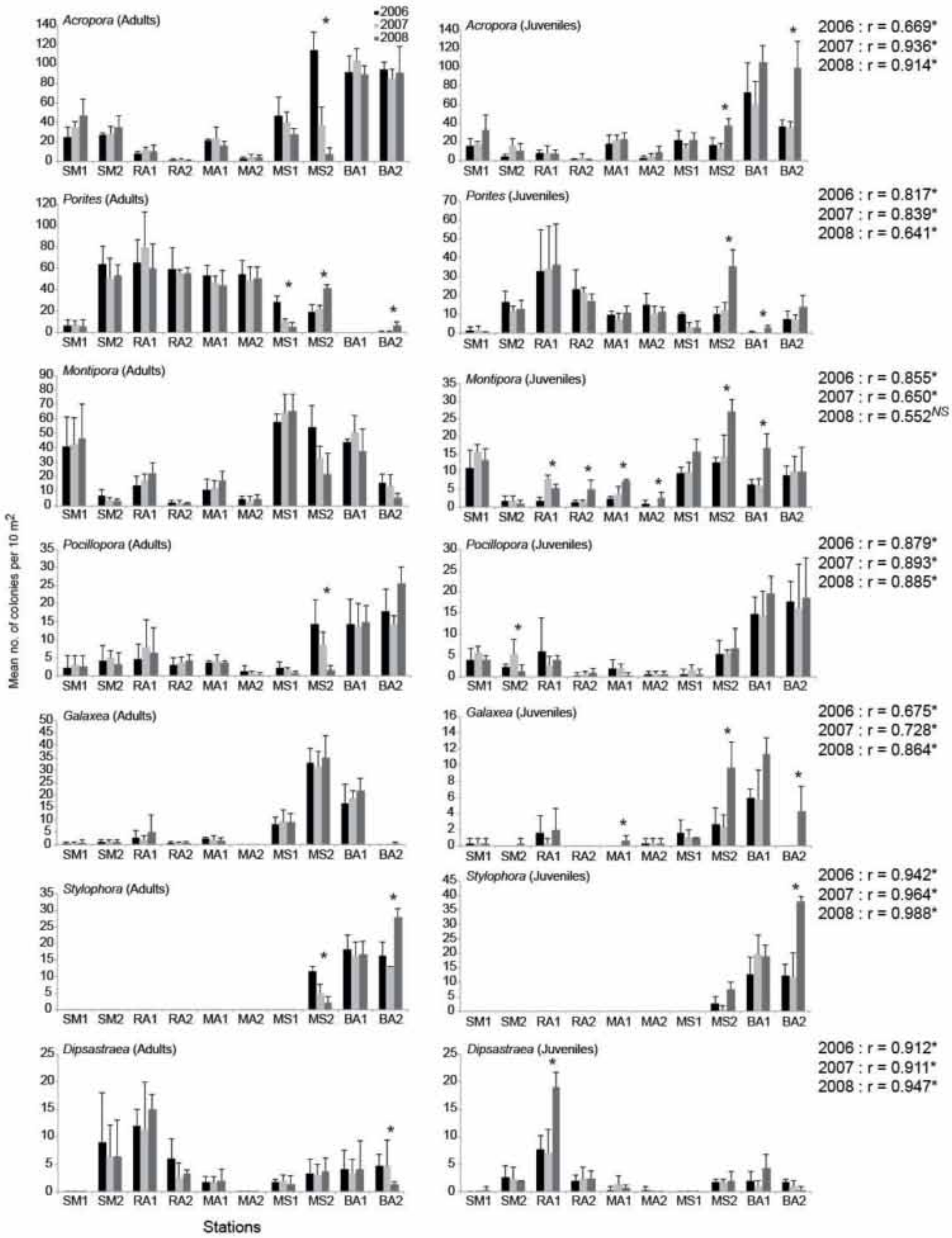

Figure 5. Spatial and interannual variation in mean abundance of adult and juvenile colonies for the seven major coral genera at the 10 stations. Error bars represent standard deviation. Asterisks refer to significant interannual variation at the station scale (SNK tests). Pearson correlation coefficients (r) between variation in juvenile and adult abundance, and their associated statistics (*: significant, $p < 0.01$; NS: non-significant) are given.

A non-metric MDS was performed to determine the spatio-temporal variation in composition and abundance of coral assemblages (Figure 6). For the adult populations, the first two axes discriminated stations from the barrier reef (left lower corner, Figure 6A), characterised by a higher dominance of *Acropora*, *Pocillopora*, *Stylophora*, *Astrea* (formerly *Montastraea*, *partim*) and *Cyphastrea* (see Supplementary Table S5).

Fringing reef stations were also discriminated by the first two axes and characterised by a higher dominance of *Porites*, *Stylocoeniella* and *Psammocora*, apart from SM1, which instead resembled mid-shelf stations. Mid-shelf stations were mainly distinguished by their higher abundance of *Montipora* and *Echinopora*. For each station, the species composition and abundance were similar among the three years, except for MS2, where there was a decline in *Acropora*, *Pocillopora* and *Stylophora* in 2008. For juveniles, the discrimination between stations was less pronounced, although barrier reef stations were grouped together (Figure 6B). As for adults, the species composition and abundance of juvenile assemblages at each station were highly similar among the three years, except at MS2, where there was higher abundance of *Acropora*, *Porites*, *Montipora*, and *Galaxea* in 2008 (Figure 6B; see Supplementary Table S6).

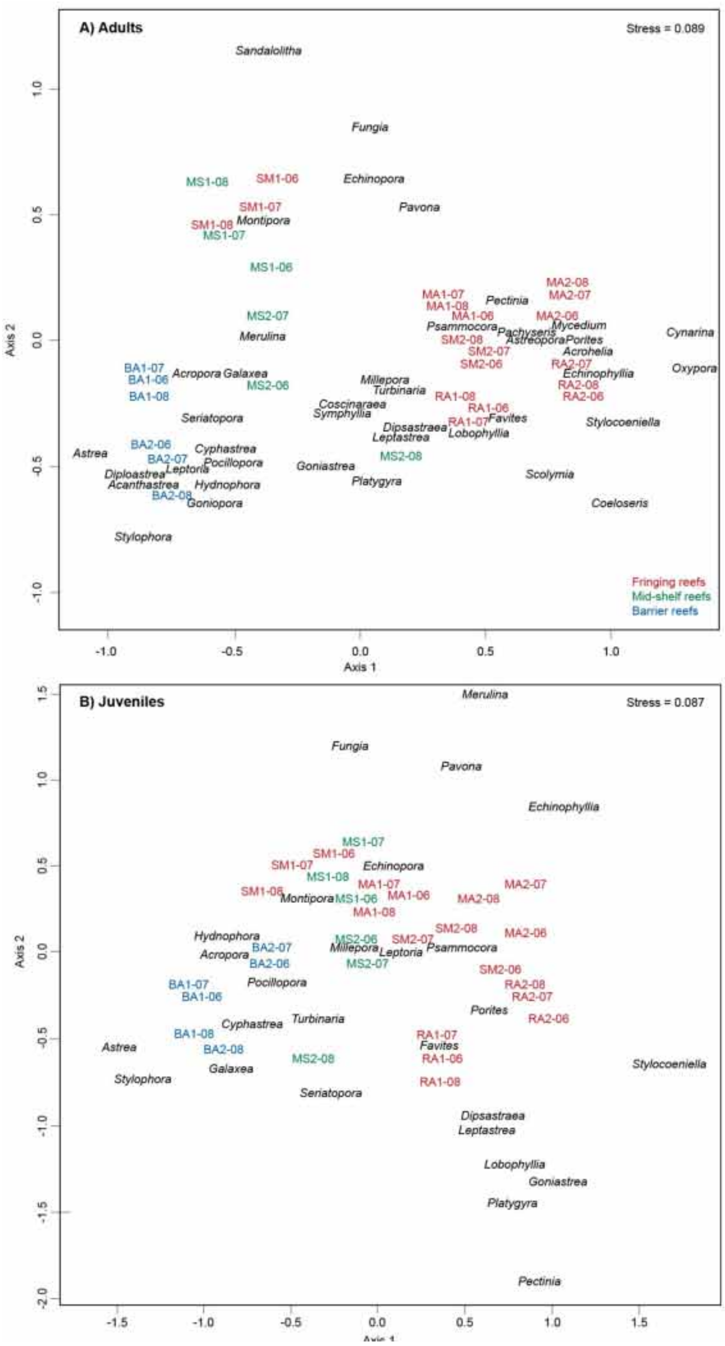

Figure 6. Non-metric multidimensional scaling (MDS), using the Bray–Curtis dissimilarity index, showing the spatial and temporal variation in the composition of (**A**) adult and (**B**) juvenile coral assemblages.

4. Discussion

The results highlight the pronounced spatial heterogeneity in coral assemblages among the 10 stations surveyed in the southwestern lagoon of New Caledonia. Generic richness, abundance and composition of both adult and juvenile assemblages were not only highly variable among the three major reef habitats (fringing, mid-shelf, and barrier reefs), but also among stations within habitats. In fact, generic richness, abundance and percent cover of corals showed higher variation among fringing reef stations, as compared to other habitats. The community composition was more related to habitats, with some genera clearly associated with barrier reefs and other to fringing reefs. In any case, the overall composition of some mid-shelf and fringing reef assemblages were nevertheless similar. Abundance of both adult and juvenile corals were partly linked to shelf position, with higher values with increasing distance from shore. In contrast, there was no clear decreasing or increasing trend in percent cover and generic richness of coral assemblages from fringing reefs to oceanic barrier reefs, contrary to other reefs [14,15,38,60]. As for corals, species richness and biomass of fish assemblages in the southwestern lagoon of New Caledonia were not related to the reef-ocean distance, whereas species composition was more associated with the location of the reef and its distance to the oceanic barrier reef [61]. These results demonstrate that coral and fish communities in New Caledonia do not clearly follow the typical cross-shelf patterns of increasing diversity, biomass and composition with increasing distance to land, as also observed in other coral reefs [62].

Marked spatial heterogeneity of coral assemblages has also been documented at multiple scales in several other studies from the Indo-Pacific [9,16,34,40,63], suggesting that it is a key characteristic of coral assemblages within coral reefs. As described in more detail in Adjeroud et al. [41], the spatial heterogeneity in coral assemblages of the southwestern lagoon of New Caledonia is closely related to the nature and proportion of the available substrate, most notably with algal turf and encrusting coralline algae. However, this heterogeneity is poorly correlated with hydrological conditions and metal concentrations [41]. This link between coral and algal distributions may result from positive interactions during the settlement phases and/or through competition for space during the benthic phases of these species [64–66].

Our results highlight that spatial patterns of adult and juvenile coral assemblages were highly correlated, not only in abundance but also composition. Such results have been previously observed in several other studies [23,62,67–69], suggesting that adult assemblages are partly controlled by the short-term history of recruitment patterns. This link between adult and juvenile distribution may indicate a either strong recruitment-limitation of populations, where juveniles drive the number and spatial distribution of adults, or a stock-recruitment process where the density and fecundity of adult colonies drive the number of juveniles [62,65,70,71]. Alternatively, this relationship may result from an aggregative settlement caused by similar substrate preference for adult and juvenile corals [20,23].

Several studies have documented a lower diversity and abundance of nearshore (inshore) coral assemblages from Pacific [14,15,34,36,60,72], Red Sea [38] and Atlantic [37] reefs. These depauperate nearshore coral assemblages are generally the result of adverse environmental conditions, as inshore habitats are often characterised by higher nutrients, heavy metals, sedimentation, temperature, lower salinity and altered trophic structures from overfishing [73]. In contrast, some coral assemblages on fringing reefs situated within bays of the southwestern lagoon of New Caledonia were as diverse and abundant as those from mid-shelf and barrier reefs where environmental conditions are supposedly more favourable. In fact, we recorded relatively high generic richness and abundance of corals in Grande Rade, a bay located close to Nouméa city and impacted by urban and industrial effluents originating from the nearby nickel industry and commercial harbour, notably heavy metals including Ni, Cr, Zn, and Co [57]. Even if pollution from the city or the nickel industry may have impacted the nearby fringing reefs in past decades, our results failed to detect any significant difference among the three bays that may be clearly attributed to their contrasted characteristics in environmental conditions. Although the relatively short time and spatial scales of our study, these results suggest that small-scale variation is probably controlled by other factors than proximal sources of pollution [60,74].

In contrast to the marked spatial heterogeneity, interannual variation in coral assemblages of the southwestern lagoon of New Caledonia was notably less pronounced. Similar conclusions were found in the Spermonde Archipelago, Indonesia, where coral assemblages varied with distance from shore, but this cross-shelf pattern showed little interannual variation [15]. In fact, the present study recorded a significant temporal variability of coral assemblages only at stations from mid-shelf and barrier reefs. At mid-shelf reefs, percent cover and abundance of branching adult of *Acropora*, *Pocillopora* and *Stylophora* decreased. In contrast, barrier reefs were characterised by an increase in the abundance of juvenile *Acropora* and *Stylophora*. Although our sampling was not designed to precisely identify factors controlling the observed spatio-temporal patterns, we hypothesise that such declines may be the result of ephemeral and localised high densities of the coral-killing sea star *Acanthaster* spp., which occurred between our annual surveys. This scenario is supported by the presence at these stations during the 2007 and 2008 surveys (M. Adjeroud, pers. obs.) of recently dead skeletons of branching corals, the favourite prey of *Acanthaster*, and increases in the percent cover of turf algae colonising these newly available substrate [75]. We may also underline that the coral taxa that show a significant interannual variability are characterised by high rates of turn-over, with higher rates of recruitment and growth compared to other taxa, but also higher mortalities (assimilated to *r* type life strategies) [76,77]. Our results are similar to those found in other coral reefs, where higher temporal variation of coral assemblages was recorded at sites exposed to oceanic influences compared to more sheltered environments such as fringing reefs situated within bays [9,78].

The results of this study constitute an empirical baseline for the long-term monitoring of the southwestern lagoon of New Caledonia, facilitating future evaluations of the status and trajectory of the coral communities in this region. The outcomes of this study also have important implications for management and designing marine protected areas through identifying representative habitats that incorporate the majority of the diversity within coral reef communities. The marked spatial heterogeneity that we recorded within and among major habitats underscores the importance of conservation strategies that adequately integrate this multi-scale spatial variation. In fact, the apparent successes (or failures) of reserves can be obscured by marked variations in reef communities prevailing at small spatial scales, while similar adjacent habitats exhibit the opposite behaviour [79]. Considering this variability within a habitat is obviously difficult in the vast and highly connected southwestern lagoon of New Caledonia. However, this challenge must be addressed in order to successfully implement effective management actions, which is imperative for the future of this recent UNESCO World Heritage reef.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/11/2/21/s1, Table S1: Characteristics of the 10 sampling stations, Table S2: Summary of the ANOVA and Student-Neuman-Keuls (SNK) tests to analyse spatial and temporal variation for corals, turf, encrusting coralline algae, and macroalgae percent cover, Table S3: Summary of the ANOVA and Student-Neuman-Keuls (SNK) tests to analyse spatial and temporal variation in the mean generic richness of adult and juvenile corals, Table S4: Summary of the ANOVA and Student-Neuman-Keuls (SNK) tests to analyze spatial and temporal variation in the abundance of adult and juvenile corals, Table S5: Abundance (mean no. of colonies per 10 m^2) of adult coral colonies recorded at each station during the three years of the study, Table S6: Abundance (mean no. of colonies per 10 m^2) of juvenile coral colonies recorded at each station during the three years of the study.

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Conflicts of Interest: The authors declare no conflict of interest.

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