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Article

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 \leq 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

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].

increasing distance to land, as also observed in other coral reefs [62].

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 m²) of adult coral colonies recorded at each station during the three years of the study.

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References

- Reaka-Kudla, M.L. The global biodiversity of coral reefs: A comparison with rain forests. In *Biodiversity II:* Understanding and Protecting Our Biological Resources; Reaka-Kudla, M.L., Wilson, D.E., Wilson, E.O., Eds.; The National Academy of Science, Joseph Henry Press: Washington, DC, USA, 1997; pp. 83–108.
- Fisher, R.; O'Leary, R.A.; Low-Choy, S.; Mengersen, K.; Knowlton, N.; Brainard, R.E.; Caley, M.J. Species richness on coral reefs and the pursuit of convergent global estimates. *Curr. Biol.* 2015, 25, 500–505. [CrossRef] [PubMed]
- 3. Moberg, F.; Folke, C. Ecological goods and services of coral reef ecosystems. *Ecol. Econ.* **1999**, *29*, 215–233. [CrossRef]
- 4. Kittinger, J.N.; Finkbeiner, E.M.; Glazier, E.W.; Crowder, L.B. Human dimensions of coral reef social-ecological systems. *Ecol. Soc.* 2012, *17*, 17. [CrossRef]
- 5. Connell, J.H. Diversity in a tropical rain forests and coral reefs. *Science* **1978**, *199*, 1302–1310. [CrossRef] [PubMed]
- 6. Done, T.J. Coral zonation: Its nature and significance. In *Perspectives on Coral Reefs*; Barnes, D.J., Ed.; Australian Institute of Marine Science: Townsville, Australia, 1983; pp. 107–147.
- 7. Huston, M.A. Patterns of species diversity on coral reefs. Annu. Rev. Ecol. Syst. 1985, 16, 149–177. [CrossRef]
- 8. Cornell, H.V.; Karlson, R.H. Species richness of reef-building corals determined by local and regional processes. *J. Anim. Ecol.* **1996**, *65*, 233–241. [CrossRef]
- 9. Connell, J.H.; Hughes, T.P.; Wallace, C.C. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol. Monogr.* **1997**, *67*, 461–488. [CrossRef]
- 10. Karlson, R.H.; Cornell, H.V. Species richness of coral assemblages: Detecting regional influences at local spatial scales. *Ecology* **2002**, *83*, 452–463. [CrossRef]
- 11. Goreau, T.F. The ecology of Jamaican coral reefs. I. Species composition and zonation. *Ecology* **1959**, *40*, 67–90. [CrossRef]
- 12. Ninio, R.; Meekan, M.G. Spatial patterns in benthic communities and the dynamics of a mosaic ecosystem on the Great Barrier Reef, Australia. *Coral Reefs* **2002**, *21*, 95–103. [CrossRef]
- Karlson, R.H.; Cornell, H.V.; Hughes, T.P. Coral communities are regionnally enriched along an oceanic biodiversity gradient. *Nature* 2004, 429, 867–870. [CrossRef] [PubMed]
- Cleary, D.F.R.; Polonia, A.R.M.; Renema, W.; Hoeksema, B.W.; Rachello-Dolmen, P.G.; Moolenbeek, R.G.; Budiyanto, A.; Tufi, Y.; Draisma, S.G.A.; Rud'homme van Reine, W.F.; et al. Variation in the composition of corals, fishes, sponges, echinoderms, ascidians, molluscs, foraminifera and macroalgae across a pronounced in-to-offshore environmental gradient in the Jakarta Bay-Thousand Islands coral reef complex. *Mar. Pollut. Bull.* 2016, *110*, 701–717. [CrossRef] [PubMed]
- Teichberg, M.; Wild, C.; Bednarz, V.N.; Kegler, H.F.; Lukman, M.; Gärdes, A.A.; Heiden, J.P.; Weiand, L.; Abu, N.; Nasir, A.; et al. Spatio-temporal patterns in coral reef communities of the Spermonde Archipelago, 2012–2014, I: Comprehensive reef monitoring of water and benthic indicators reflect changes in reef health. *Front. Mar. Sci.* 2018, *5*, 33. [CrossRef]
- 16. Adjeroud, M. Factors influencing spatial patterns on coral reefs around Moorea, French Polynesia. *Mar. Ecol. Prog. Ser.* **1997**, *159*, 105–119. [CrossRef]
- 17. Koop, K.; Booth, D.; Broadbent, A.; Brodie, J.; Bucher, D.; Capone, D.; Coll, J.; Dennison, W.; Erdmann, M.; Harrison, P.; et al. ENCORE: The effects of nutrient enrichment on coral reefs. Synthesis of results and conclusions. *Mar. Pollut. Bull.* **2001**, *42*, 91–120. [CrossRef]
- 18. McCook, L.; Jompa, J.; Diaz-Pullido, G. Competition between corals and algae on coral reefs: A review of evidence and mechanisms. *Coral Reefs* **2001**, *19*, 400–417. [CrossRef]
- Fabricius, K.; De'ath, G.; McCook, L.; Turak, E.; Williams, D.Mc.B. Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Mar. Pollut. Bull.* 2005, 51, 384–398. [CrossRef]
- 20. Caley, M.J.; Carr, M.H.; Hixon, M.A.; Hughes, T.P.; Jones, G.P.; Menge, B.A. Recruitment and the local dynamics of open marine populations. *Annu. Rev. Ecol. Syst.* **1996**, *27*, 477–500. [CrossRef]
- 21. Hughes, T.P.; Baird, A.H.; Dinsdale, E.A.; Moltschaniwskyj, N.A.; Pratchett, M.S.; Tanner, J.E.; Willis, B.L. Supply-side ecology works both ways: The link between benthic adults, fecundity, and larval recruits. *Ecology* **2000**, *81*, 2241–2249. [CrossRef]

- Doropoulos, C.; Ward, S.; Roff, G.; Gonzales-Rivero, M.; Mumby, P.J. Linking demographic processes of juvenile corals to benthic recovery trajectories in two common reef habitats. *PLoS ONE* 2015, *10*, e0128535. [CrossRef]
- 23. Adjeroud, M.; Kayal, M.; Penin, L. The importance of recruitment processes in the dynamics and resilience of reef coral assemblages. In *Marine Animal Forests*; Rossi, S., Bramanti, L., Gori, A., Orejas, C., Eds.; Springer: Cham, Switzerland, 2017; pp. 549–569.
- 24. Kayal, M.; Lenihan, H.S.; Brooks, A.J.; Holbrook, S.J.; Schmitt, R.J.; Kendall, B.E. Predicting coral community recovery using multi-species population dynamics models. *Ecol. Lett.* **2018**, *21*, 1790–1799. [CrossRef]
- 25. Hughes, T.P.; Connell, J.H. Multiple stressors on coral reefs: A long-term perspective. *Limnol. Oceanogr.* **1999**, 44, 932–940. [CrossRef]
- 26. Bellwood, D.R.; Hughes, T.P.; Folke, C.; Nyström, M. Confronting the coral reef crisis. *Nature* **2004**, 429, 827–833. [CrossRef]
- 27. Hoegh-Guldberg, O.; Mumby, P.J.; Hooten, A.J.; Steneck, R.S.; Greenfield, P.; Gomez, E.; Harvell, C.D.; Sale, P.F.; Edwards, A.J.; Caldeira, K.; et al. Coral reefs under rapid climate change and ocean acidification. *Science* **2007**, *318*, 1737–1742. [CrossRef]
- 28. Edmunds, P.J.; Adjeroud, M.; Baskett, M.L.; Baums, I.B.; Budd, A.F.; Carpenter, R.C.; Fabina, N.S.; Fan, T.Y.; Franklin, E.C.; Gross, K.; et al. Persistence and change in community composition of reef corals through present, past, and future climates. *PLoS ONE* **2014**, *9*, e107525. [CrossRef] [PubMed]
- 29. Hughes, T.P.; Barnes, M.L.; Bellwood, D.R.; Cinner, J.E.; Cumming, G.S.; Jackson, J.B.C.; Kleypas, J.; van de Leemput, I.A.; Lough, J.M.; Morrison, T.H.; et al. Coral reefs in the Anthropocene. *Nature* **2017**, *546*, 82–90. [CrossRef] [PubMed]
- 30. Hughes, T.P.; Baird, A.H.; Bellwood, D.R.; Card, M.; Connolly, S.R.; Folke, C.; Grosberg, R.; Hoegh-Guldberg, O.; Jackson, J.B.C.; Kleypas, J.; et al. Climate change, human impacts, and the resilience of coral reefs. *Science* **2003**, *301*, 929–933. [CrossRef] [PubMed]
- 31. Hughes, T.P.; Kerry, J.T.; Baird, A.H.; Connolly, S.R.; Dietzel, A.; Eakin, C.M.; Heron, S.F.; Hoey, A.S.; Hoogenboom, M.; Lui, G.; et al. Global warming transforms coral reef assemblages. *Nature* **2018**, *556*, 492–496. [CrossRef] [PubMed]
- 32. Anthony, K.R.; Marshall, P.A.; Abdulla, A.; Beeden, R.; Bergh, C.; Black, R.; Eakin, C.M.; Game, E.T.; Gooch, M.; Graham, N.A.; et al. Operationalizing resilience for adaptive coral reef management under global environmental change. *Glob. Chang. Biol.* **2015**, *21*, 48–61. [CrossRef] [PubMed]
- Adjeroud, M.; Kayal, M.; Iborra-Cantonnet, C.; Vercelloni, J.; Bosserelle, P.; Liao, V.; Chancerelle, Y.; Claudet, J.; Penin, L. Recovery of coral assemblages despite acute and recurrent disturbances on a South Central Pacific reef. *Sci. Rep.* 2018, *8*, 9680. [CrossRef] [PubMed]
- 34. Done, T.J. Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* **1982**, *1*, 95–107. [CrossRef]
- Adjeroud, M. Zonation of coral assemblages in the Ryukyu islands (southern Japan): The importance of land-ocean gradients in reef habitats. Proceedings of 10th International Coral Reef Symposium, Okinawa, Japan, 28 June–2 July 2004; pp. 310–318.
- 36. Cleary, D.F.R.; Becking, L.E.; de Voogd, N.J.; Renema, W.; de Beer, M.; van Soest, R.W.M.; Hoeksema, B.W. Variation in the diversity and composition of benthic taxa as a function of distance offshore, depth and exposure in the Spermonde Archipelago, Indonesia. *Estuar. Coast. Shelf Sci.* **2005**, *65*, 557–570. [CrossRef]
- Smith, T.B.; Nemeth, R.S.; Blondeau, J.; Calnan, J.M.; Kadison, E.; Herzlieb, S. Assessing coral reef health across onshore to offshore stress gradients in the US Virgin Islands. *Mar. Pollut. Bull.* 2008, 56, 1983–1991. [CrossRef] [PubMed]
- 38. Ellis, J.; Anlauf, H.; Kürten, S.; Lozano-Cortés, D.; Alsaffar, Z.; Curdia, J.; Jones, B.; Carvalho, S. Cross shelf benthic biodiversity patterns in the Southern Red Sea. *Sci. Rep.* **2017**, *7*, 437. [CrossRef] [PubMed]
- 39. Adjeroud, M.; Salvat, B. Spatial patterns in biodiversity of a fringing reef community along Opunohu Bay, Moorea, French Polynesia. *Bull. Mar. Sci.* **1996**, *59*, 175–187.
- Adjeroud, M. Zonation des communautés macrobenthiques le long de deux baies d'un écosystème corallien insulaire (Moorea, Polynésie française). *Comptes Rendus Acad. Sci. Ser. III-Sci. Vie-Life Sci.* 2000, 323, 305–313. [CrossRef]

- Adjeroud, M.; Fernandez, J.M.; Carroll, A.G.; Harrison, P.L.; Penin, L. Spatial patterns and recruitment processes of coral assemblages among contrasting environmental conditions in the southwestern lagoon of New Caledonia. *Mar. Pollut. Bull.* 2010, *61*, 375–386. [CrossRef]
- 42. Pichon, M. Scleractinia of New Caledonia: Check list of reef dwelling species. In *Compendium of Marine Species from New Caledonia, second edition;* Payri, C., Richer de Forges, B., Eds.; Doc. Sci. Tech. II7; IRD Editions: Nouméa, New Caledonia, 2007; pp. 149–157.
- 43. Chevalier, J.P. Coral reefs of New Caledonia. In *Biology and Geology of Coral Reefs*; Jones, O.A., Endean, R., Eds.; Academic Press: New York, NY, USA; London, UK, 1973; pp. 143–167.
- 44. Andréfouët, S.; Cabioch, G.; Flamand, B.; Pelletier, B. A reappraisal of the diversity of geomorphological and genetic processes of New Caledonian coral reefs: A synthesis from optical remote sensing, coring and acoustic multibeam observations. *Coral Reefs* **2009**, *28*, 691–707. [CrossRef]
- 45. Wantiez, L. Les récifs coralliens de Nouvelle-Calédonie en 2006: États des lieux et réseau de suivi. *Rev. Ecol. Terre Vie* **2008**, *63*, 117–132.
- 46. Wantiez, L.; Château, O.; Le Mouellic, S. Initial and mid-term impacts of cyclone Erica on coral reef fish communities and habitat in the South Lagoon Marine Park of New Caledonia. *J. Mar. Biol. Assoc.* **2006**, *86*, 1229–1236. [CrossRef]
- 47. Guillemot, N.; Chabanet, P.; Le Pape, O. Cyclone effects on coral reef habitats in New Caledonia (South Pacific). *Coral Reefs* **2010**, *29*, 445–453. [CrossRef]
- 48. Adjeroud, M.; Kayal, M.; Peignon, C.; Juncker, M.; Mills, S.C.; Beldade, R.; Dumas, P. Ephemeral and localized outbreaks of the coral predator *Acanthaster* cf. *solaris in the southwestern lagoon of New Caledonia*. *Zool. Stud.* **2018**, *57*, 4.
- 49. Payri, C.; Benzoni, F.; André, L.V.; Houlbrèque, F. Le blanchissement corallien de 2016. In *Nouvelle-Calédonie, Archipel de Corail*; Payri, C.E., Ed.; IRD Editions/Solaris: Marseille, France, 2018; pp. 161–166.
- 50. Jouon, A.; Douillet, P.; Ouillon, S.; Fraunié, P. Calculations of hydrodynamic time parameters in a semi-opened coastal zone using a 3D hydrodynamic model. *Cont. Shelf Res.* **2006**, *26*, 1395–1415. [CrossRef]
- 51. Jacquet, S.; Delesalle, B.; Torréton, J.P.; Blanchot, J. Response of phytoplankton communities to increased anthropogenic influences (southwestern lagoon, New Caledonia). *Mar. Ecol. Prog. Ser.* **2006**, *320*, 65–78. [CrossRef]
- 52. Mari, X.; Rochelle-Newall, E.; Torréton, J.P.; Pringault, O.; Jouon, A.; Migon, C. Water residence time: A regulatory factor of the DOM to TOM transfer efficiency. *Limnol. Oceanogr.* **2007**, *52*, 808–819. [CrossRef]
- 53. Migon, C.; Ouillon, S.; Mari, X.; Nicolas, Z. Geochemical and hydrodynamic constraints on the distribution of trace metal concentrations in the lagoon of Nouméa, New Caledonia. *Estuar. Coast. Shelf Sci.* 2007, 74, 756–765. [CrossRef]
- Dalto, A.G.; Grémare, A.; Dinet, A.; Fichet, D. Muddy-bottom meiofauna responses to metal concentrations and organic enrichment in New Caledonia South-West Lagoon. *Estuar. Coast. Shelf Sci.* 2006, 67, 629–644. [CrossRef]
- 55. Fernandez, J.M.; Ouillon, S.; Chevillon, C.; Douillet, P.; Fichez, R.; Le Gendre, R. A combined modelling and geochemical study of the fate of terrigenous inputs from mixed natural and mining sources in a coral reef lagoon (New Caledonia). *Mar. Pollut. Bull.* **2006**, *52*, 320–331. [CrossRef]
- 56. Dumas, P.; Kulbicki, M.; Chifflet, S.; Fichez, R.; Ferraris, J. Environmental factors influencing urchin spatial distributions on disturbed coral reefs (New Caledonia, South Pacific). *J. Exp. Mar. Biol. Ecol.* **2007**, 344, 88–100. [CrossRef]
- 57. Breau, L. Etude de la Bioaccumulation des Métaux dans Quelques Espèces Marines Tropicales: Recherche de Bioindicateurs de Contamination et Application à la Surveillance de L'environnement Côtier dans le Lagon Sud-Ouest de la Nouvelle-Calédonie. Ph.D. Thesis, Université de La Rochelle, La Rochelle, France, 2003.
- Harrison, P.L.; Wallace, C.C. Reproduction, dispersal and recruitment of scleractinian corals. In *Coral Reef Ecosystems, Ecosystems of the World*; Dubinsky, Z., Ed.; Elsevier Science Publishers: Amsterdam, The Netherlands, 1990; Volume 25, Chapter 7; pp. 133–207.
- 59. Loya, Y. Plotless and transect methods. In *Coral Reefs: Research Methods*; Stoddart, D.R., Johannes, R.E., Eds.; UNESCO: Paris, France, 1978; pp. 197–217.
- 60. Cleary, D.F.R.; Suharsono; Hoeksema, B.W. Coral diversity across a disturbance gradient in the Pulau Seribu reef complex off Jakarta, Indonesia. *Biodivers. Conserv.* **2006**, *15*, 3653–3674. [CrossRef]

- 61. Grimaud, J.; Kulbicki, M. Influence de la distance à l'océan sur les peuplements ichtyologiques des récifs frangeants de Nouvelle-Calédonie. *Comptes Rendus Acad. Sci. Ser. III-Sci. Vie-Life Sci.* 1998, 321, 923–931. [CrossRef]
- 62. Moustaka, M.; Mohring, M.B.; Holmes, T.; Evans, R.D.; Thomson, D.; Nutt, C.; Stoddart, J.; Wilson, S.K. Cross-shelf heterogeneity of coral assemblages in Northwest Australia. *Diversity* **2019**, *11*, 15. [CrossRef]
- 63. Edmunds, P.J. Patterns in the distribution of juvenile corals and coral reef community structure in St John, US Virgin Islands. *Mar. Ecol. Prog. Ser.* **2000**, *202*, 113–124. [CrossRef]
- 64. Rogers, C.S.; Fitz, H.C.; Gilnack, M.; Beets, J.; Hardin, J. Scleractinian recruitment patterns at Salt River Canyon, St. Croix, U.S. Virgin Islands. *Coral Reefs* **1984**, *3*, 69–76. [CrossRef]
- 65. Gleason, M.G. Coral recruitment in Moorea, French Polynesia: The importance of patch type and temporal variation. *J. Exp. Mar. Biol. Ecol.* **1996**, 207, 79–101. [CrossRef]
- 66. Carlon, D.B. Depth-related patterns of coral recruitment and cryptic suspention-feeding invertebrates on Guana Island, British Virgin Islands. *Bull. Mar. Sci.* **2001**, *68*, 525–541.
- 67. Miller, M.W.; Weil, E.; Szmant, A.M. Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayne National Park, USA. *Coral Reefs* **2000**, *19*, 115–123. [CrossRef]
- Mundy, C.N.; Babcock, R.C. Are vertical distribution patterns of scleractinian corals maintained by pre- or post-settlement processes? A case study of three contrasting species. *Mar. Ecol. Prog. Ser.* 2000, 198, 109–119. [CrossRef]
- 69. Penin, L.; Adjeroud, M. Relative importance of recruitment and post-settlement processes in the maintenance of coral assemblages in an insular, fragmented reef system. *Mar. Ecol. Prog. Ser.* **2013**, 473, 149–162. [CrossRef]
- 70. Baird, A.H.; Babcock, R.C.; Mundy, C.P. Habitat selection by larvae influences the depth distribution of six common coral species. *Mar. Ecol. Prog. Ser.* **2003**, 252, 289–293. [CrossRef]
- 71. Penin, L.; Adjeroud, M.; Pratchett, M.S.; Hughes, T.P. Spatial distribution of juvenile and adult corals around Moorea (French Polynesia): Implications for population regulation. *Bull. Mar. Sci.* 2007, *80*, 379–389.
- 72. Pichon, M.; Morrissey, J. Benthic zonation and community structure of South Island Reef, Lizard Island (Great Barrier Reef). *Bull. Mar. Sci.* **1981**, *31*, 581–593.
- 73. Jupiter, S.; Roff, G.; Marion, G.; Henderson, M.; Schrameyer, V.; McCulloch, M.; Hoegh-Guldberg, O. Linkages between coral assemblages and coral proxies of terrestrial exposure along a cross-shelf gradient on the southern Great Barrier Reef. *Coral Reefs* **2008**, *27*, 887–903. [CrossRef]
- 74. Baum, G.; Januar, H.I.; Ferse, S.C.A.; Kunzmann, A. Local and regional impacts of pollution on coral reefs along the Thousand Islands North of the megacity Jakarta, Indonesia. *PLoS ONE* 2015, 10, e0138271. [CrossRef] [PubMed]
- 75. Kayal, M.; Vercelloni, J.; Lison de Loma, T.; Bosserelle, P.; Chancerelle, Y.; Geoffroy, S.; Stievenart, C.; Michonneau, F.; Penin, L.; Planes, S.; et al. Predator Crown-of-Thorns Starfish (*Acanthaster planci*) outbreak, mass mortality of corals, and cascading effects on reef fish and benthic communities. *PLoS ONE* 2012, 7, e47363. [CrossRef] [PubMed]
- 76. Darling, E.S.; Alvarez-Filip, L.; Oliver, T.A.; McClanahan, T.R.; Côté, I.M. Evaluating life-history strategies of reef corals from species traits. *Ecol. Lett.* **2012**, *15*, 1378–1386. [CrossRef]
- Kayal, M.; Vercelloni, J.; Wand, M.P.; Adjeroud, M. Searching for the best bet in life-strategy: A quantitative approach to individual performance and population dynamics in reef-building corals. *Ecol. Complex.* 2015, 23, 73–84. [CrossRef]
- 78. Dollar, S.J.; Grigg, R.W. Anthropogenic and natural stresses on selected coral reefs in Hawai'i: A multidecade synthesis of impact and recovery. *Pac. Sci.* **2004**, *58*, 281–304. [CrossRef]
- 79. Dumas, P.; Jimenez, H.; Peignon, C.; Wantiez, L.; Adjeroud, M. Small-scale habitat structure modulates the effects of no-take marine reserves for coral reef macroinvertebrates. *PLoS ONE* **2013**, *8*, e58998. [CrossRef]



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