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Article

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Abstract: The Great Reef of Toliara, on the southwestern coast of Madagascar, has been documented as harbouring flourishing reef communities in the 1960s, but has since been affected by various threats, causing a coral decline last reported in 2008. In 2017, we examined the spatial heterogeneity in coral community structure in the region of Toliara. Coral assemblages were characterized by a marked spatial variability, with significant variation for most of the descriptors among the three major habitats and also among stations within habitats. We recorded high coral cover, with values >40% at six of the 10 stations, which was associated with high abundance of coral colonies. We also documented the return to an *Acropora*-dominated coral assemblage. While these positive results suggest a recent return to healthier coral assemblages, they must be tempered, as the diversity that we recorded was lower than in the 1960s. Moreover, we found a high cover of algae at several stations, suggesting that the ecosystem is likely close to the tipping point toward a phase shift. Finally, the population size-structure of major coral taxa was positively skewed, with few large colonies to ensure the replenishment of local populations. The marked spatial variation suggests that marine protected areas should integrate a sufficiently large area to capture the scale of this spatial heterogeneity.

Keywords: coral reefs; scleractinian corals; community structure; spatial variability; Madagascar

1. Introduction

Surrounded by ~2400 km² of coral reefs distributed along 1400 km of coastline, Madagascar is a hotspot of biodiversity in the Western Indian Ocean [1–3]. With 380 coral and 788 reef-associated fish species, the overall diversity of Madagascar coral reefs is comparable to that of the coral triangle [2,4–6]. This high diversity of reef organisms is probably due to the size and diversity of reef habitats that are particularly well-developed on the northeast, northwest, and southwest coasts [7–9]. With ~33 km² of shallow reef area, the Great Reef of Toliara (GRT), in the southwest coast, is the largest reef complex of Madagascar and the Western Indian Ocean, and has been a refuge for diverse reef taxa, including 714 species of reef fishes [10,11] and 135 species of scleractinian corals [12,13]. This coral reef provides both costal protection and an artisanal fishery for the city of Toliara [14–16]. The GRT was intensively surveyed in the 1960s–1970s, following the establishment of a marine research center in 1961 (currently Institut Halieutique et des Sciences Marines).

The diversity and zonation of scleractinian coral assemblages, the primary reef-building species, was first studied by Pichon [12].

However, like most coral reefs worldwide, those of Madagascar have been increasingly exposed to various types of large-scale natural and anthropogenic perturbations and local stressors that have worsened their socio-ecological vulnerability and resilience [5,9,17–19]. Overfishing, sedimentation, and thermally induced coral bleaching events have particularly affected the island's coral reefs located around populated cities [20–22]. Some coral habitats of the GRT have been affected by high sedimentation caused by discharge of the Fiherenana river in the north and Onilahy river in the south [23], favoring the prevalence of coral diseases [24]. Since the 1980s, overfishing, destructive fishing, water pollution, and gleaning activities, all linked to the rapid growth of the human population (53% between 1993 and 2008), have also been a major concern for the health of the GRT [25–27]. In addition, bleaching episodes associated to El Niño events have affected coral and other reef associated species, particularly in 1998 and 2015–2016 [9,21,28]. All these episodic disturbances and chronic stressors have caused a decline in coral cover and abundance in the last 50 years, particularly for architecturally complex coral taxa such as *Acropora* and *Pocillopora*, with coral cover decreasing from ~50% to 5% during this period at several shallow habitats [25–27,29]. This decline has been associated with the increase of fleshy macroalgae or other non-reef building species, such as zoanthids and soft corals in habitats previously dominated by *Acropora* [8,25,30], an undesirable state which provides fewer ecosystem goods and services. Coral diversity has also been affected, with a decline from 38 to 30 genera in shallow habitats, and a loss of 18 genera in seagrass beds over the past 40 years [26,29].

Despite these increasing threats and the general trend of coral decline, no quantitative studies have recently examined the spatial patterns and community structure of coral assemblages, thus precluding a precise indication of the current status and the resilience capacities of the GRT. Moreover, information on the spatial variability among and within major coral reef habitats, that are often characterized by contrasting environmental conditions [31–33], is lacking for this reef. This type of information is however crucial to implement adequate conservation measures that are critically needed considering ongoing human development and importance of reef resources in this area [25]. Though some Locally Managed Marine Areas (LMMA) have been implemented in the region of the GRT with some success, they focused on fisheries and did not address coral assemblages [34,35].

In this context, the major aim of the present study was to investigate spatial patterns and community structure of coral assemblages among major reef habitats in the region of Toliara, including the GRT. Composition, generic richness, cover (including other benthic taxa), and size-structure of coral assemblages have been quantified and compared among 10 stations. Implications of our results in terms of conservation and management actions are also discussed. The original data set examined here constitutes a reference baseline for evaluating future changes in coral communities, and may help identify effective conservation actions.

2. Materials and Methods

2.1. Study Area

The present study was conducted in Madagascar's southwestern region of Toliara, including the Great Reef of Toliara (GRT), located 2 km seaward of Toliara city (Figure 1). Approximately 19 km long and 1–3 km wide, the GRT is a major barrier reef system of the SW Indian Ocean. High sedimentation comes from mining activities in the highland by the region's two main rivers, Fiherenana in the north and Onilahy in the south. Madagascar is characterized by two main seasons: winter from April to September, when sea surface temperature (SST) falls down to 18 °C, and summer from October to March, when rainfall and SST (up to ~30 °C) are higher. Dominant winds are from the SW direction. Tropical storms and cyclones generally hit Madagascar from November to May, and are common in the northern and eastern part of the island (94 tropical cyclones recorded from 1948 to

2010) [36]. The southwest region is less affected as the passage or formation of cyclones in the Mozambique channel is relatively rare [37,38]. Malagasy coral reefs have suffered from bleaching events caused by abnormal increases in SST, with major events in 1998 and 2015–2016. These bleaching events have caused an important decrease in coral cover (~20 and 25%, respectively) associated to an increase in algal cover [17,21]. In contrast to some other regions of the Western Indian Ocean [39], no evidence of significant degradations by outbreaks of the coral predator sea star *Acanthaster* spp. have been reported in Madagascar [40].
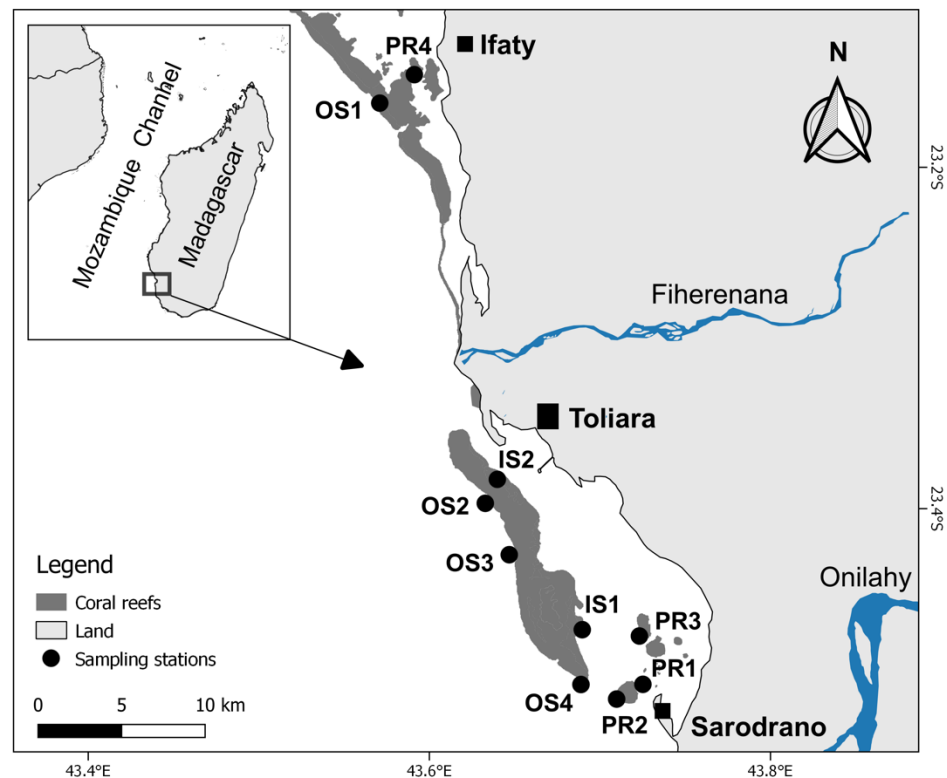
Figure 1. Map of the southwest coast of Madagascar showing the location of the 10 sampling stations in the Toliara region, including the Great Reef of Toliara (GRT). Stations were located on the three major habitat types: patch reefs (PR), inner slope (IS), and outer slope (OS).

2.2. Sampling Strategy

Sampling was undertaken from February to July 2017. A total of 10 stations were located between the village of Ifaty in the north and the village of Sarodrano in the south, on the three major habitat types: four stations on patch reefs (PR1 to PR4), two stations on the inner reef slope (IS1 and IS2), and four stations on the outer slope (OS1 to OS4; Figure 1). Initially, the 10 stations were to be placed at 10 m depth, but at some locations, coral communities were not sufficiently developed at this depth to establish a station. In the end, our stations were located between 6 and 12 m in order to be representative of the local coral communities (Supplementary Table S1). The percent cover of major living and abiotic substrate was estimated using the photoquadrat method [41]. At each station, 30 photoquadrats of 0.25 m^2 (50 × 50 cm) were taken along three transects of 10 m length with an underwater camera (W300, Nikon, Tokyo, Japan). Percent cover was estimated using the Coral Point Count with Excel extension (CPCE 4.1) [41] software. On each photo, 100 random points were used to quantify percent cover of major benthic categories: hard corals (scleractinian corals and the calcareous hydrocoral *Millepora*), dead corals (defined as recently dead coral with skeletons covered by thin layer of turf algae), soft corals (Alcyonacea, mainly represented by *Xenia* sp. and *Sarcophyton* sp.), algae (coralline algae,

macroalgae, turf), other living taxa (including sponges, hydroids, zoanthids, corallimorphs, tunicates and sea anemones), and abiotic substrates (rubble, and sand).

In addition, generic richness and abundance of adult coral colonies (>5 cm in diameter) were estimated at each station using three randomly replicated belt-transects of 10 m² (10 × 1 m), laid parallel to depth contours and separated by ~1 m, following the method described in Adjeroud et al. [42]. The size-structure of the major coral genera was recorded using the same belt-transects. Coral colonies with >50% of their living tissue area contained within each belt-transect were assigned to the following size classes for maximum diameter: 6–10, 11–20, 21–40, 41–80, 81–160, and 161–320 cm.

2.3. Data Analysis

Spatial variations of percent cover of benthic categories, generic richness (GR), and abundance of coral colonies among habitats and stations were explored using nested ANOVA, with habitat and station as fixed factors. Data were appropriately transformed ($\log(x + 1)$) for GR and abundance, and $\arcsin(x)$ for percent cover, to meet the assumptions of normality and homogeneity of variance. ANOVA were complemented by pairwise *t*-test comparisons to determine which samples showed significant differences. To explore relationships between spatial distribution of percent cover of corals and other benthic categories, Pearson (R) correlation analyses were conducted. The overall spatial variation in the composition and abundance of coral assemblages among the 10 stations was analyzed using nonmetric multidimensional scaling (nMDS), based on the Bray-Curtis dissimilarity index, and followed by ANOSIM to identify significant differences among habitats. ANOVA per permutation was used to compare the size frequency distribution among each habitat based on the colony abundances.

3. Results

Overall, benthic substrate was dominated by hard corals ($46.8 \pm 3.4\%$, mean $\pm$ SE), turf algae ($17.3 \pm 3.8\%$), macroalgae ($12.7 \pm 4.0\%$), and rubble ($12.1 \pm 4.9\%$). Percent cover of corals was significantly variable among habitats (ANOVA, F = 3.4, *p* = 0.036) and among stations within habitats (ANOVA, F = 4.8, *p* = 0.002; Supplementary Table S2; Figure 2). Coral cover was lower at the inner slope ($34.2 \pm 3.5\%$, mean $\pm$ SE) compared to the outer slope ($52.0 \pm 4.6\%$) and patch reefs ($48.0 \pm 6.5\%$; pairwise *t*-test, all *p* < 0.05; Supplementary Table S3). At the station level, coral cover values were highly variable, ranging from $22.7 \pm 13.2\%$ at PR4 to $69.9 \pm 3.7\%$ at OS3 (Supplementary Table S4). High values were also recorded at PR1 ($66.3 \pm 3.3\%$) and PR2 ($62.3 \pm 10.7\%$).

Coral cover was dominated by *Acropora* colonies (>50% of overall coral cover), with highest values recorded at the inner slope ($37.9 \pm 15.4\%$) and, to a lesser degree, at patch reefs ($28.8 \pm 6.9\%$), whereas cover was lower at the outer slope ($12.8 \pm 2.7\%$; Figure 3). *Pavona* cover was also high at the inner slope ($27.2 \pm 13.1\%$), whereas values were greatly reduced at patch reefs ($1.5 \pm 0.5\%$) and the outer slope ($1.1 \pm 0.5\%$). Percent cover of other coral genera was lower than *Acropora* and *Pavona* (<7%). For *Echinopora* ($4.9 \pm 2.2\%$), *Seriatopora* ($4.9 \pm 1.5\%$), and *Porites* ($3.8 \pm 0.9\%$), highest values were recorded on the outer slope. Cover of *Seriatopora* ($4.2 \pm 2.0\%$) was also relatively important at patch reefs, together with *Galaxea* ($6.4 \pm 6.2\%$) and *Montipora* ($4.0 \pm 3.5\%$).
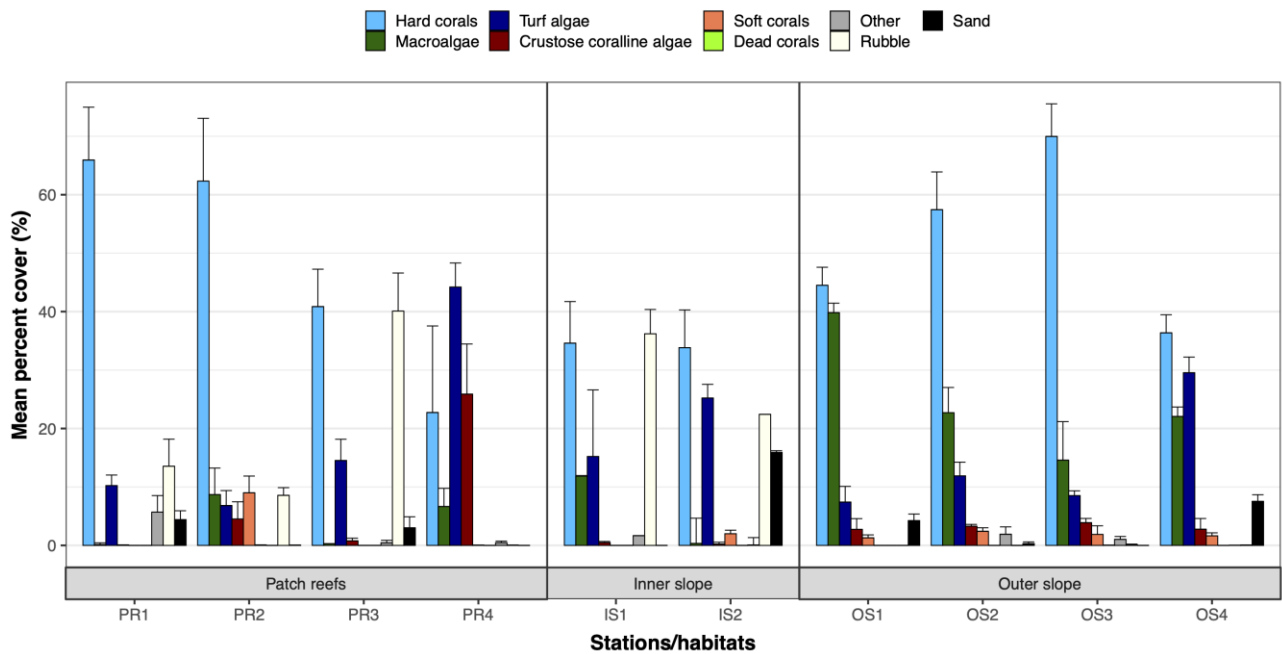
Figure 2. Mean percent cover of major substrate categories at the 10 stations located on the three major habitats (PR: patch reefs, IS: inner slope, and OS: outer slope). Error bars represent standard error.
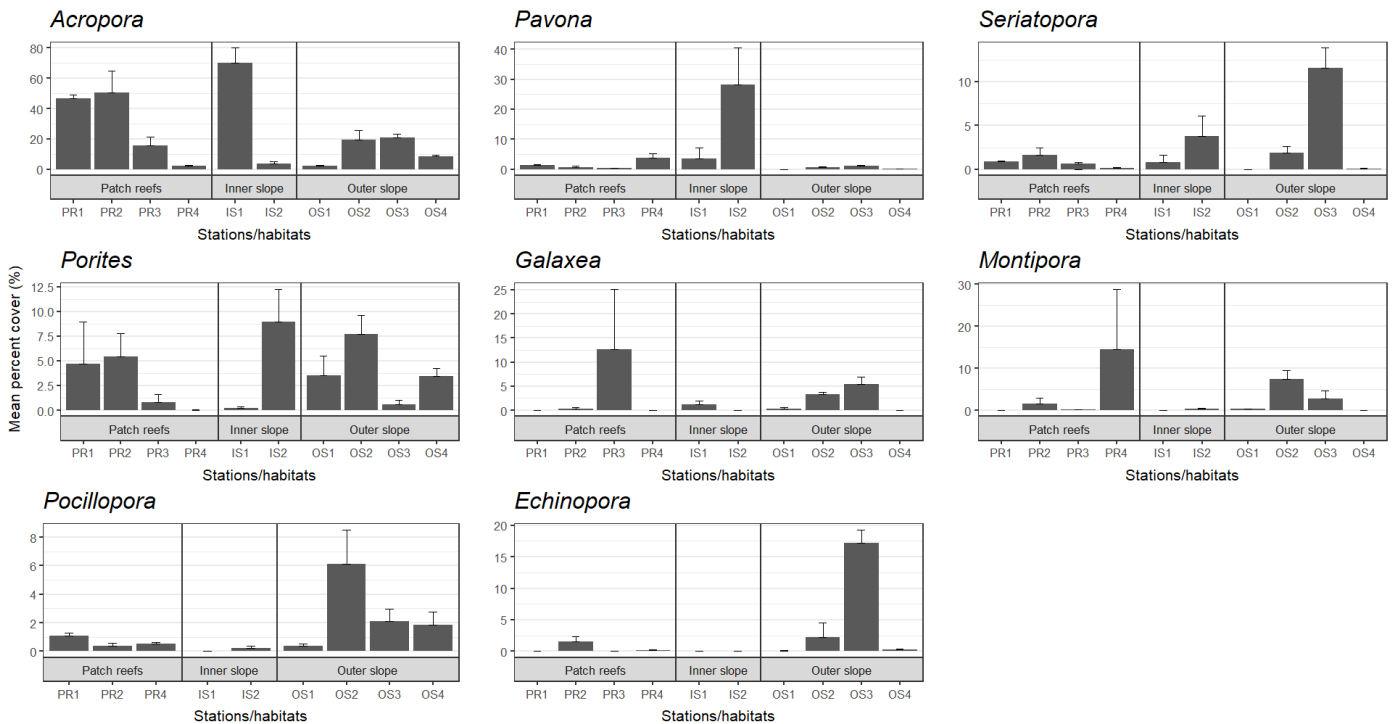
Figure 3. Mean percent cover of the eight major coral genera at the 10 stations located on the three major habitats (PR: patch reefs, IS: inner slope, and OS: outer slope). Error bars represent standard error.

In contrast, *Porites* (4.5 ± 2.4%) and *Pocillopora* (3.7 ± 2.0%) cover were the highest on the inner slope. It is interesting to note that despite similar overall coral cover, some stations of the same habitat may have contrasting cover at the generic level, such as inner slope stations (Figure 3).

Macroalgal cover varied significantly among habitats (ANOVA, F = 60.5, *p* = 0.001) and stations (ANOVA, F = 7.7, *p* = 0.001), with values ranging from 0.1 ± 0.3% at PR1 to

39.8 ± 1.6% at OS1 (Figure 2). Cover of turf algae showed a strong variation among stations (ANOVA, F = 7.3, p = 0.0003), with values between 6.8 ± 2.5% at PR2 to 44.1 ± 4.1% at PR4, though no difference was found among habitats (ANOVA, F = 2.2, p = 0.1). Similarly, cover of crustose coralline algae was variable among stations (ANOVA, F = 1259.7, p = 0.01), with a maximal value of 25.8 ± 8.4% recorded at PR4, but was not significantly different among habitats (ANOVA, F = 53.1, p = 0.5). Soft corals were not recorded at stations PR1, PR3, and IS1 and cover values were relatively low (<2%) at most other stations, except at PR2 where cover reached 9.0 ± 2.8%. Comparisons among habitats and stations did not reveal significant differences (ANOVA, all p > 0.05). Cover of other invertebrates (sponges, zoanthids and tunicates) was also low at most stations (<2%), with highest value recorded at PR1 (5.6 ± 2.8%), whereas no significant variation was recorded among habitats (ANOVA, F = 0.3 p = 0.7) and stations (ANOVA, F = 2.3 p = 0.06). Percent cover of rubbles was significantly different among habitats (ANOVA, F = 3.7, p = 0.04) and stations (ANOVA, F = 2.3, p = 0.001), with highest values recorded at PR3 (40.0 ± 6.5%), while almost no rubbles were recorded at outer reef stations. Sand cover was highly variable among stations (ANOVA, F = 7.4, p = 0.0003), with values up to 15.9 ± 0.3% at IS2, but not among habitats (ANOVA, F = 2.6, p = 0.09). The spatial distribution of coral cover was positively correlated with variation in turf algae (R = −0.655, p < 0.001) and crustose coralline algae (R = −0.462, p < 0.010; Supplementary Figure S1). Although significant, a positive correlation was found with dead corals (R = 0.487, p = 0.006), but this relationship is difficult to interpret as only 2 stations have dead coral cover greater than 0. No significant correlations were recorded with other benthic categories (macroalgae, soft corals, other invertebrates, rubbles, and sand; Supplementary Figure S1).

A total of 43 coral genera were recorded from the 10 stations, with an overall mean of 20.1 ± 1.2 genera.10 m^{-2}. Generic richness (GR) was significantly variable among habitats (ANOVA, F = 6.2, p = 0.008) and among stations within habitats (ANOVA, F = 5.2, p = 0.001; Supplementary Table S5; Figure 4). GR values ranged from 11.3 ± 1.2 genera.10 m^{-2} at PR1 to 28.6 ± 2.0 genera.10 m^{-2} at OS2, with high values (>20 genera.10 m^{-2}) also recorded at PR2, PR3, and OS4 (Supplementary Tables S6 and S7). In terms of colony abundance, coral assemblages were mainly composed of eight genera (*Acropora*, *Seriatopora*, *Galaxea*, *Porites*, *Pocillopora*, *Montipora*, *Dipsastraea*, and *Favites*), while other genera such as *Blastomussa*, *Plesiastrea*, *Turbinaria*, *Astrea*, and *Diploastrea* were rarely recorded (all together <4%) at the 10 stations (Supplementary Figure S2). The relative contribution of these eight major genera was highly similar among the three habitats, and *Acropora* was clearly the dominant genera at all habitats and stations.

Figure 4. Mean generic richness of corals at the 10 stations located on the three major habitats (PR: patch reefs, IS: inner slope, and OS: outer slope). Error bars represent standard error.
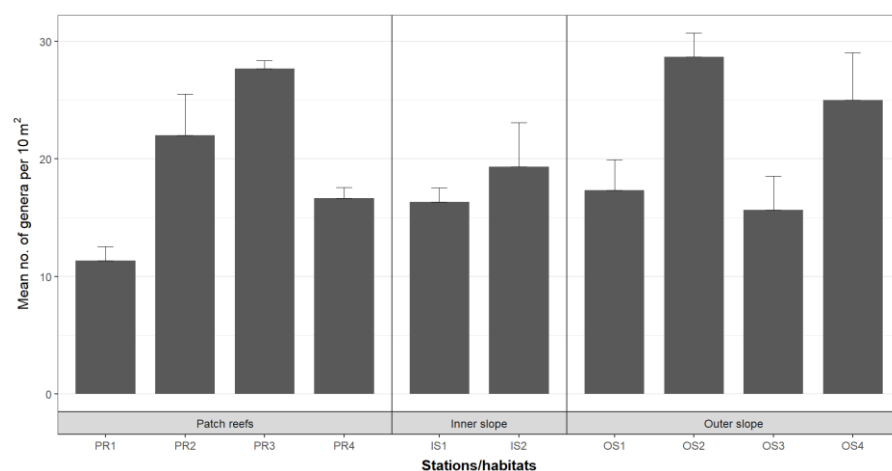
A total of 4644 coral colonies were recorded at the 10 stations, representing an over-all mean abundance of 150.4 ± 11.1 colonies.10 m^{-2}. Coral colony abundance was significantly variable among habitats (ANOVA, F = 4.0, *p* = 0.03), and among stations within habitats (ANOVA, F = 3.8, *p* = 0.005; Supplementary Table S8; Figure 5). Values ranged from 91.0 ± 13.0 at PR1 to 224.6 ± 18.3 colonies.10 m^{-2} at OS3, with low values (<100 colonies.10 m^{-2}) also recorded at IS3 and OS1 (Supplementary Tables S9 and S10). All eight major coral genera showed a significant spatial variation in abundance across habitats (ANOVA, all *p* < 0.001) and across stations within habitats (ANOVA, all *p* < 0.001; Figure 6). For *Acropora*, *Seriatopora*, *Galaxea*, *Pocillopora*, *Dipsastraea*, *Favites*, and *Montipora*, highest values of abundance were recorded at outer slope stations, though two to ten times lower values were also found in this habitat. Relatively high abundance of coral colonies was also recorded in other habitats, including *Pocillopora*, *Dipsastraea*, *Favites*, *Montipora*, and *Porites* in patch reefs, and *Seriatopora*, *Galaxea*, and *Porites* on the inner slope.
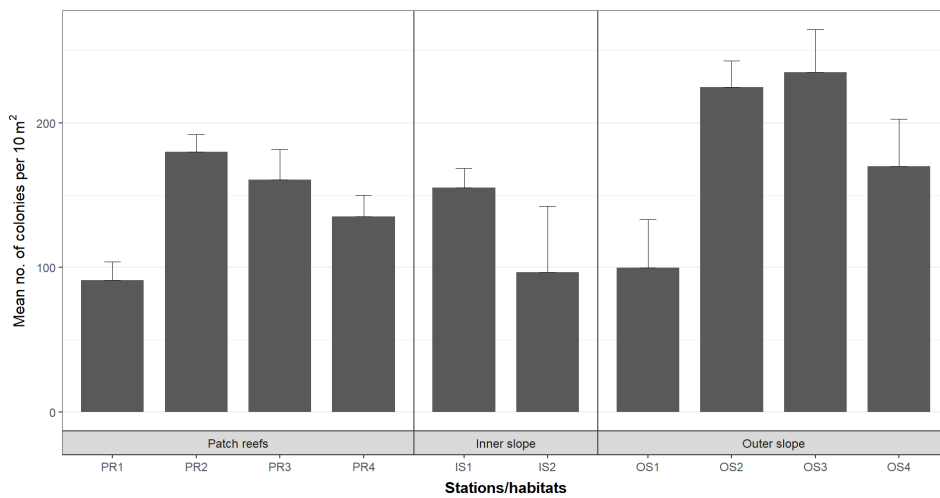
Figure 5. Mean abundance of overall coral colonies (all genera pooled) at the 10 stations located on the three major habitats (PR: patch reefs, IS: inner slope, and OS: outer slope). Error bars represent standard error.
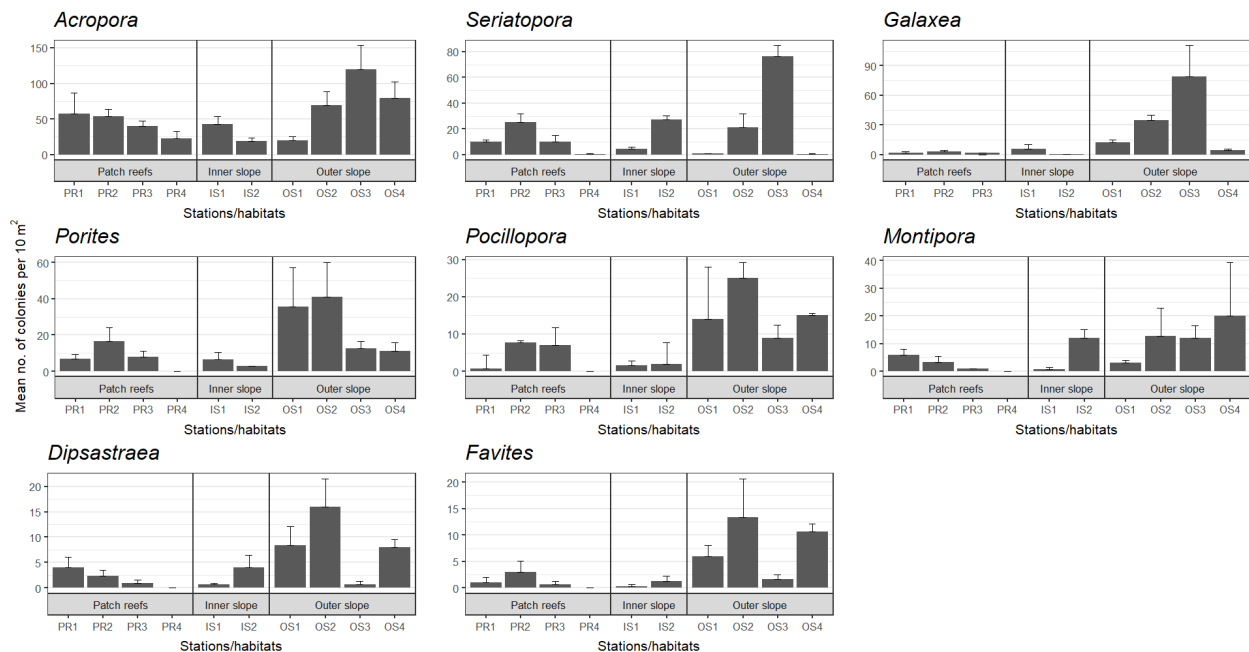
Figure 6. Mean abundance of colonies of the eight major coral genera at the 10 stations located on the three major habitats (PR: patch reefs, IS: inner slope, and OS: outer slope). Error bars represent standard error.

The composition and abundance of coral assemblages showed a significant difference among the three habitats. The nMDS, based on the Bray-Curtis dissimilarity index, first discriminated stations of the outer slope from those of the two other habitats (20% similarity; Figure 7A; ANOSIM, R > 0.50, Supplementary Table S11), whereas stations of the inner slope and patch reefs were highly similar (ANOSIM, R < 0.25). Stations of the outer slope were characterized by higher abundance of *Acropora* and *Galaxea*, and a particularly high value of *Seriatopora* at OS3 (Supplementary Table S12), distinguishing this station from the three others at a higher similarity level (40%).
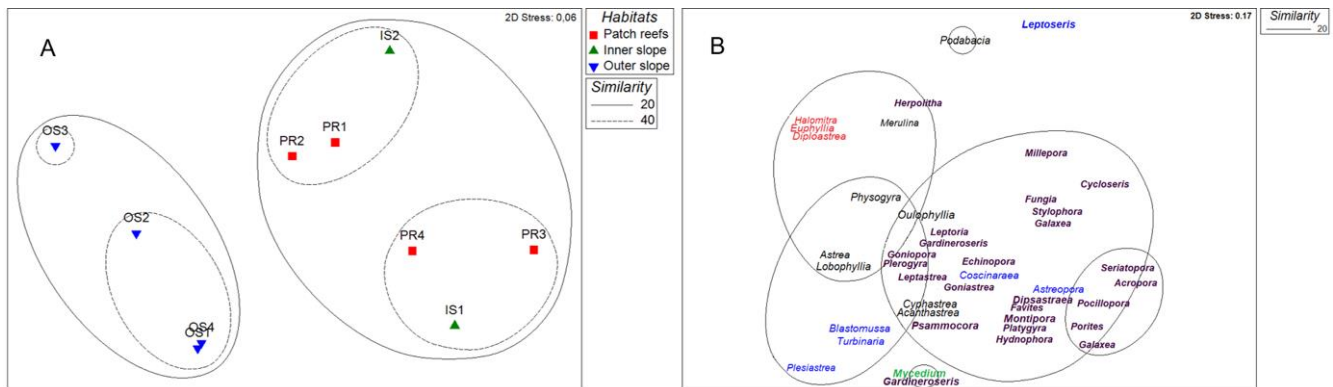
Figure 7. Non-metric multidimensional scaling (nMDS), based on the Bray-Curtis dissimilarity index, showing the spatial variation in the composition and abundance of coral assemblages among the 10 stations located on the three major habitats (PR: patch reefs, IS: inner slope, and OS: outer slope). Position of the 10 stations (**A**) and of the 43 genera (**B**) on the first two axes of the nMDS. The color code is as follows: red for patch reefs stations and coral genera exclusively recorded on this habitat, green for inner slope stations and coral genera exclusively recorded on this habitat, blue for outer slope stations and coral genera exclusively recorded on this habitat, coral genera recorded at all three habitats are indicated in purple, and coral genera recorded on more than two habitats are in black.

At this similarity level, two other groups of stations were discriminated; PR1, PR2, and IS2 were characterized by a high abundance of *Fungia*, *Herpolitha*, *Stylophora*, and *Seriatopora*, whereas IS1, PR3, and PR4 were distinguished from the other patch reefs and inner slope stations by their high abundance of *Cycloseris* and *Pavona* (Figure 7B; Supplementary Table S12).

Coral assemblages at the 10 surveyed stations were dominated by colonies of <20 cm in maximum diameter, representing 73% of the colonies recorded (Figure 8). Size frequency distribution of the eight dominant genera followed a right skewed pattern with higher abundance of small size colonies (6–10 cm and 11–20 cm in diameter) and a decrease in abundance of higher size classes (Supplementary Tables S13–S15). For most coral genera and at all three habitats, size-structure was dominated by the 11–20 cm size class, except for *Seriatopora*, *Galaxea*, and *Favites*, which had more colonies of 6–10 cm in diameter at patch reefs. The largest colonies were rare, mainly represented by branching colonies of *Acropora*, and *Seriatopora*, and massive *Galaxea*. A significant difference in the size structure was recorded among habitats (Permutational ANOVA, $p < 0.001$; Supplementary Table S13), except between patch reefs and inner slope (pairwise *t*-test, $p > 0.05$; Supplementary Table S14).
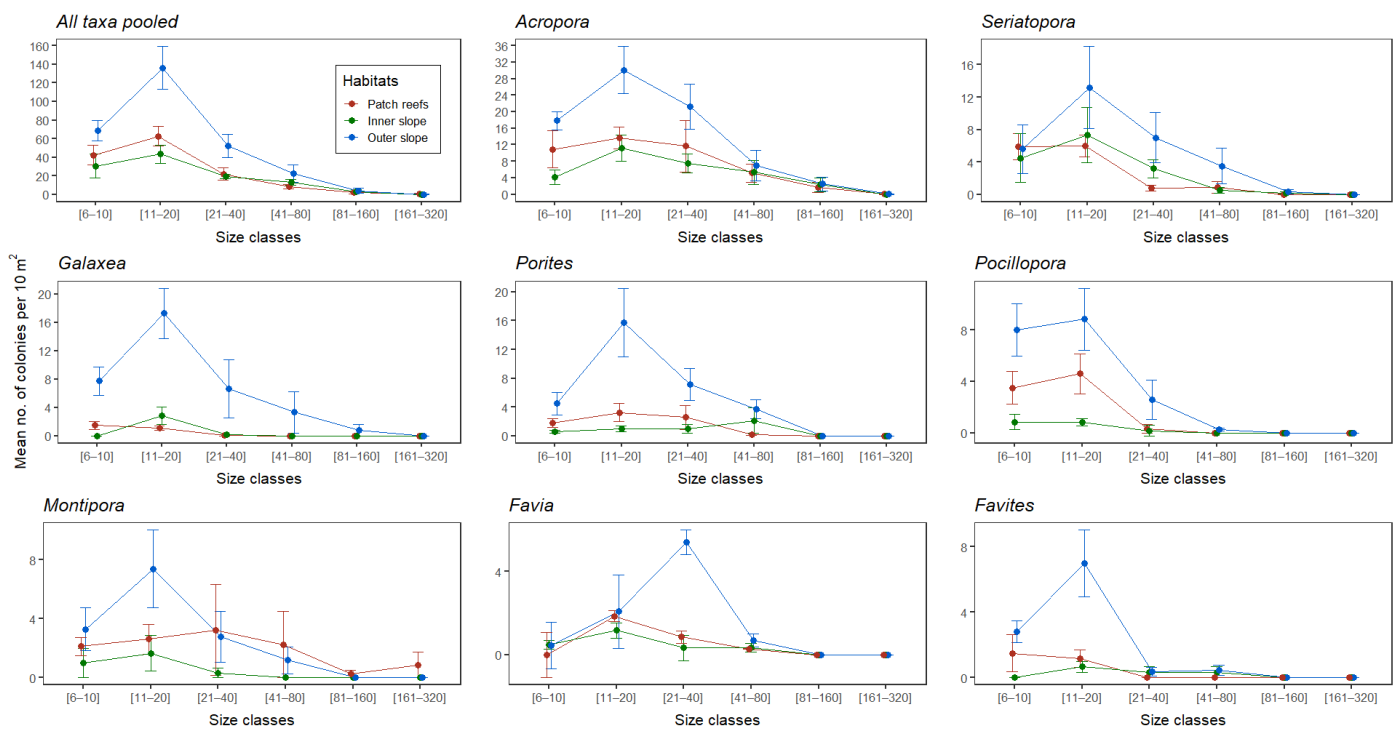
Figure 8. Size-structure of the eight major coral genera at each of the three major habitats (PR: patch reefs, IS: inner slope, and OS: outer slope) surveyed (all stations pooled). Error bars represent standard error.

4. Discussion

This study on the spatial structure of coral assemblages has allowed the assessment of the current health of coral reefs in the region of Toliara, and represents a valuable quantitative baseline for future comparisons. At most survey stations, the substrate cover is dominated by living corals (overall mean of 46.8 ± 3.4%), with values >40% at six of the 10 stations located on patch reefs and the outer slope, and even reaching 60–70% at three stations. This high coral cover is associated with a high abundance of coral colonies (overall mean abundance of ~150 colonies.10 m^{-2}), notably at most outer reef and patch reef stations (up to ~220 colonies.10 m^{-2}). Such recent high coral cover and abundance is unexpected given the multiple large-scale disturbances and local stressors that have affected the GRT for several decades, including severe bleaching events in 1998 and 2015–2016, and important fishing and gleaning activities [5,9,21,27]. In fact, the overall coral cover that we recorded in 2017 is much higher than values reported in 2008 (~13%) [25], but similar to the ones found in the 1960s (~40%) [12]. Similarly, the abundances of coral colonies that we recorded in 2017 were much higher than the ones reported in 2008 at various GRT stations (~50 colonies.10 m^{-2}) [25]. Despite the different depth ranges and sampling techniques used by these studies that may partly explain some of the observed differences in coral cover, abundance, and diversity, our results suggest a recent trend to a return to healthier coral assemblages. Such high coral cover recorded at several sites of the GRT are in fact comparable to those in less disturbed reefs around Madagascar, such as the reef of Belo-sur-Mer (~55%) [17], Nosy Be (~50%) [43], northwest (~70%) [44], Ambodivaibe (48%) [5], or Andavadoaka (~42% on some patch reefs) [30]. The relatively good health of coral reefs in the Toliara region could be partly linked to the presence of the Southwest MAdagascar Coastal Current (SMACC), a shallow current flowing along the southwest coast toward the south, and which may facilitate larval transport from northern, less disturbed reefs and enhance the replenishment of reefs under the influence of this current [45].

However, these positive and encouraging results should be taken with caution. Firstly, even if the overall diversity of corals recorded during this study (43 genera) is higher than

the one reported in 2008 (30 genera) [25], it is still lower than the one found in the 1960s (61 genera) [12]. This decreasing trend in coral diversity was also documented by Bruggemann et al. [26] with 18 of the 61 genera reported by Pichon [12] not being recorded in 2011. Some rare genera recorded in the northwest [44], northeast [5], and southeast Madagascar [19] were not seen (*Anomastraea, Horastrea, Craterastrea, Plesiastrea, Caulastrea*) or rarely recorded (*Coscinaraea, Diploastrea, Blastomussa*) at the GRT (Supplementary Table S16). In fact, as reported by Todinanahary et al. [29], coral assemblages of the GRT have not only declined in their overall diversity, but have also changed in their composition. Secondly, turf and macroalgae are abundant at most stations, with cover higher than 20%, notably on the outer slope. This high biomass of fleshy algae is likely resulting from the decline in the abundance of herbivorous fishes recorded in the bay of Toliara and Ranobe following decades of overfishing [25,26]. This level of algal cover greatly reduces the availability of adequate substrate for coral settlement and growth, and induces a strong competition for space. A high cover of fleshy algae also suggests that the ecosystem is likely close to the tipping point toward a coral to macroalgal phase shift. Thirdly, the population size-structure of all major coral taxa in the Toliara region is positively skewed, with a large dominance of small colonies and relatively few large ones, as also documented in several other coral reefs [46–48]. Since fecundity is positively correlated to colony size [49–51], this lack of large colonies may compromise the reproduction of local coral populations and consequently their persistence, as they will mainly rely on northern sites for their replenishment [45].

As documented for several other coral reefs worldwide [42,52–54], GRT coral assemblages were characterized by a marked spatial variability, creating a heterogeneous mosaic of habitat patches. Generic richness, abundance, size-structure, and composition of adult coral assemblages were highly variable among the three major reef habitats (patch reefs, inner slope, and outer slope), but also among stations within habitats. The most diversified and abundant coral assemblages were located at several stations of patch reefs and outer slope habitats. Although our sampling was not designed to precisely identify factors controlling the observed spatial patterns, such pronounced heterogeneity of coral community structure likely results from small-scale variation in environmental conditions (sedimentation, hydrodynamic, light) and biological processes. Our correlation analyses suggest that local cover of turf algae probably influence the abundance of coral assemblages, through spatial competition and inhibition of coral larval settlement [55]. The marked spatial variation in coral recruitment recorded at the scale of the GRT is another potential major factor controlling the distribution and abundance of adult assemblages [56]. Understanding the spatial patterns of contemporary coral communities will help to construct a rigorous baseline to understand future changes, which is crucial in order to identify appropriate management actions.

In terms of colony abundance, our results highlight the marked dominance of *Acropora*. This outcome is another sign of the recent recovery to healthier coral assemblages at our study sites. In fact, *Acropora*, which was dominant in the GRT in the '60s [12], was greatly reduced in cover and abundance in 2008, to the benefit of more resistant taxa such as *Porites* and *Echinopora* [25]. There is also an abundance of other branching taxa at our study sites such as *Seriatopora, Pocillopora*, and *Stylophora*, all characterized by their susceptibility to variation in environmental conditions, notably to thermally-induced bleaching events [40,57,58]. This return to a coral assemblage dominated by *Acropora*, together with these other branching taxa, is clearly a positive indication of an ongoing recovery trend to healthier coral communities.

Despite several episodes of bleaching events, and recurrent impacts linked to overfishing, sedimentation, and gleaning activities, our results suggest that coral assemblages of the GRT still have the capacities to maintain in a healthy state, provided that large-scale disturbances or local stressors do not increase in frequency and severity in the near future. Our survey is a snapshot in a highly dynamic system and represents a valuable baseline for long-term monitoring of the GRT. Such interannual surveys of coral assemblages of the

GRT are timely for determining their status and temporal trajectories and hence, evaluating resilience capacities of this reef ecosystem. Ideally, this monitoring should not focus exclusively on corals and algae, but rather incorporate other key mechanisms of ecosystem maintenance and resilience, such as grazing pressure by herbivorous fishes and invertebrates, predation by coral-killing species of echinoids, sponges and nudibranchs [59–61], coral recruitment, and major impacts such as fishing, sedimentation, SST, and nutrient loading. Such monitoring should also include nearby mangroves and seagrass beds, as these adjacent habitats may have an important role in the functioning of the coral reef ecosystem [62,63]. In fact, identifying major drivers of the spatio-temporal variability of reef communities, which was not within the scope of the present study, is crucial, not only to improve our knowledge on their structure and dynamics, but also to identify key biophysical processes that may be prioritized in conservation actions.

Our study also has important implications for urgently needed management and conservation of the GRT. For example, the marked spatial variation that we recorded suggests that conservation measures, such as the implementation of marine protected areas (MPAs), should integrate sufficient area to capture the scale of this spatial heterogeneity. This aspect is critical, as MPA effectiveness can be obscured by important variations at small spatial scales, despite similar adjacent habitats showing opposite trends [64]. The health of the GRT and nearby coral reefs requires a drastic reduction in the fishing pressure in this area. This may be achieved by increasing the number of community-based aquaculture projects that have shown to be a successful alternative, or even principal, source of income for some coastal populations [65], and which may reduce the negative effects of overfishing on coral communities [19,22,66]. Ideally, these alternative activities must be located to minimize the impacts on nearby coral reefs and adjacent ecosystems such as mangroves and seagrass beds, and should involve end users—at least fishermen and sea farmers—in setting up the project and decision making. Furthermore, our results suggest that reef restoration activities should consider at least the genera *Acropora*, *Pocillopora*, *Seriatopora*, and *Stylophora*. These genera, which are among the most abundant in the Toliara region, have colonies with mainly branching growth forms, and are thus particularly suitable for transplantation and restoration projects [67,68]. Moreover, these genera are highly sensitive to variations in abiotic conditions, and thus may act as coral sentinels to detect environmental changes [40,57,58]. Such community-based coral farming, whose technical and social feasibility has already been demonstrated, could also improve education and awareness on the importance of corals for healthy coastal ecosystems and, consequently, on their income-generating activities [60].

The outcomes of this survey bring hope to the future of coral assemblages of the GRT by suggesting that these assemblages still have acceptable maintenance capacities, and may also be beneficial to other reef communities and the goods and services the GRT should continue to provide to local populations. But once again, this optimistic scenario can only be achieved if adequate and rigorous conservation actions are taken rapidly to limit and mitigate the local impact of disturbances that are unfortunately inevitable. In this context, the ability of local populations to become involved in community-based conservation actions is a positive aspect of their success [15,35,66]. The quantitative baseline examined here may support collaborative processes to evaluate future changes in coral communities and identify effective conservation actions.

Table S5: Summary of the nested ANOVA to test for spatial variability in generic richness among habitats and stations; Table S6: Summary of the pairwise *t*-tests to identify differences between habitats for generic richness; Table S7: Summary of the pairwise *t*-tests to identify differences between stations for generic richness; Table S8: Summary of the nested ANOVA to test for spatial variability in overall abundance of coral colonies among habitats and stations; Table S9: Summary of the pairwise *t*-tests to identify differences between habitats for abundance of coral colonies; Table S10: Summary of the pairwise *t*-tests to identify differences between stations for abundance of coral colonies; Table S11: Summary of the ANOSIM for pairwise comparison in the composition and abundance of coral genera between habitats; Table S12: Composition and abundance (mean number of colonies per station) of coral assemblages at the 10 stations used for nonmetric multidimensional scaling (nMDS); Table S13: Summary of the ANOVA per permutation for comparison of the size frequency distribution among each habitat based on the colony abundances; Table S14: Summary of the pairwise *t*-test of the size frequency distribution between habitats based on the colony abundances; Table S15: Summary of the pairwise test of the size frequency distribution based on the colony abundances; Table S16: Coral genera (scleractinians and the calcareous hydrocoral *Millepora*) recorded in the Toliara region of southwest Madagascar in 2017 (present study) and in 1961–1970 [12], in the Andavadoaka region [19], in the northwest region by Veron and Turak [4], and in the northeast region by Obura et al. [5].

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