

## ***Scleractinian coral communities of the inner Seychelles 10 years after the 1998 mortality event***

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### ABSTRACT

1. The size structure and taxonomic composition of coral communities in the inner (Granitic) Seychelles were studied 10 years after a thermal stress-induced mass mortality event.

2. A survey of the abundance, population size structure and community composition of hard corals across 21 sites from three different geomorphological reef types on the Seychelles Bank provided high resolution data for discriminating coral communities based on diversity, taxonomic composition, colony abundance, surface area and size frequency distributions.

3. Results emphasize the severely impoverished and depauperate nature of inner Seychelles hard coral communities, which had lower generic diversity (40 genera recorded), and lower abundance (3.3 colonies m<sup>-2</sup>) of hard corals (excluding juveniles) than other coral reef regions of the Indian Ocean for which comparable data are currently available.

4. Analysis of coral communities indicated that management had no appreciable effect on juvenile or adult coral abundance at this point in time, and that low juvenile density (9.9 colonies m<sup>-2</sup>) may severely limit recovery of many individual reefs in the inner Seychelles.

5. While some sites were found to have appreciable coral cover (>20%), others, including long-standing protected areas with no fishing, are now in an advanced state of erosion and framework collapse with very low juvenile coral replenishment and negligible available hard substratum suitable for coral settlement.

6. Some of these reefs may have passed the threshold of viable recovery, now being in a self-reinforcing, non-coral dominated erosional phase.

7. These findings indicate variable coral community condition, with many sites showing little sign of recovery. If persistence of live hard coral is a management goal, the existing protected areas within the Seychelles Bank may require review to ensure protection of sites with high recovery potential, while a suite of other management tools should be implemented in the remaining areas.

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## INTRODUCTION

Dramatic mortality events throughout the world's coral reefs in recent years have caused a marked decline in global reef condition (Gardner *et al.*, 2003; Bruno and Selig, 2007; Wilkinson, 2008; Ateweberhan *et al.*, 2011). In addition to reducing absolute coral cover, increasing climatic and direct anthropogenic stresses are driving shifts in coral community composition worldwide (Berumen and Pratchett, 2006; McClanahan *et al.*, 2007). Changes in the composition of coral communities have profound ecological impacts on reefs (Wilson *et al.*, 2006, 2012; Pratchett *et al.*, 2008; Chong-Seng *et al.*, 2012); approximately one third of coral species are at an elevated risk of extinction, with the family Acroporidae – the primary architect of Indo-Pacific reefs – showing a higher proportion of threatened and near-threatened species than other families with dominant reef-building species (Carpenter *et al.*, 2008). Furthermore, approximately one third of reef fish species are at risk of local extinction owing to the indirect effects of coral loss (Graham *et al.*, 2011). Changes in coral communities can also adversely affect reef architecture, habitat complexity and reef growth, and are in turn likely to weaken the resilience of reefs and diminish their recovery potential from future climatic and anthropogenic impacts, with potentially grave consequences for coral reef-derived ecosystem services (Nyström *et al.*, 2008; Hughes *et al.*, 2010).

Past studies of Indian Ocean hard corals have generally employed methods that have focused either on the taxonomic richness of corals or the benthic composition of reefs, generally grouping scleractinian taxa into total coral cover or into broad benthic categories, such as physical growth form (Graham *et al.*, 2006). Although valuable in interpreting certain aspects of reef structure and health, several important dimensions of hard coral community structure are not captured with this approach, notably taxonomic composition and the size frequency dynamics of individual populations (Bak and Meesters, 1998; Done *et al.*, 2010). Coral communities are highly dynamic, particularly in the aftermath of environmental disturbances, with different coral taxa and colony sizes showing highly variable responses to thermal stress based on

evolutionary and environmental history, physiological acclimatization ability, growth form and depth (Gates and Edmunds, 1999; Marshall and Baird, 2000; McClanahan *et al.*, 2004). Indeed, interpreting reef condition based on coral cover data alone may be inadequate, since cover values may fail to detect ecologically significant differences between different coral communities (Done *et al.*, 2010; Hughes *et al.*, 2010; McClanahan *et al.*, 2011).

In terms of hard coral community composition, the reefs of the western Indian Ocean (WIO) are among the least studied (Fisher *et al.*, 2011), as well as being among the most stressed from direct human impacts such as overfishing (McClanahan, 1994; Halpern *et al.*, 2008; Cinner *et al.*, 2009). The WIO was also the most severely affected coral reef region during the 1998 coral bleaching event (Wilkinson, 1998). Across the WIO, ~45% of coral cover was lost in 1998 (Ateweberhan *et al.*, 2011), however, the impacts and subsequent recovery responses varied widely (Goreau *et al.*, 2000; McClanahan *et al.*, 2007; Graham *et al.*, 2008; Harris and Sheppard, 2008; Smith *et al.*, 2008). The reefs of the inner Seychelles, an oceanographically remote, shallow carbonate platform at the northern limit of the Mascarene Ridge, were severely affected, with estimates of 70–95% coral mortality (Goreau *et al.*, 2000), and limited subsequent recovery (Sheppard *et al.*, 2005; Graham *et al.*, 2006; Wilson *et al.*, 2012).

This study assessed the composition of inner Seychelles coral communities 10 years after the 1998 mortality event. A survey of the genus-specific size frequency distribution of hard corals was undertaken to identify potential differences in scleractinian communities and populations between different islands and geomorphological reef types. The implications of these findings are discussed with respect to reef management within the inner Seychelles.

## METHODS

Twenty-one sites around the islands of Mahé (n=9) and Praslin (n=12) in the inner Seychelles were surveyed in April 2008. Site selection and categorization followed Jennings *et al.* (1996), in which reefs were classified based on the underlying substratum, as either patch (coral patch reef habitats

on sand, rubble, or rock base), carbonate (continuous carbonate fringing reefs), or granite (granitic rocky reefs with coral growth on the granite substrate).

Three sites, one of each substrate category, were located in each of two no-take marine reserves from which all forms of fishing are prohibited: St Anne marine national park (gazetted in 1973) off the island of Mahé; and Cousin island special reserve off Praslin (established in 1968 with fishing banned since 1975). Thus six sites were protected, while 15 were outside protected areas (Figure 1).

### Adult colonies

Adult colonies were defined as those with a maximum colony diameter greater than 10 cm. This size distinction between adult and juvenile corals is arbitrary, and should not be taken to imply a specific stage of colony maturity, however, it is intended to separate all adult colonies from juveniles. The genus and longest diametric axis (cm) of all hard corals >10 cm lying within a randomly-placed 10 m × 1 m belt at 3 to 10 m

depth were recorded. The largest diameter of each colony was measured with a tape or ruler *in situ* over the surface of the colony (Bak and Engel, 1979). Count-based colony-sampling methods can lead to significantly biased evaluations of colony abundance as a result of the 'boundary effect' around the sampled area. It must be acknowledged that some biases may exist with this methodology (Zvuloni *et al.*, 2008), however, for comparative purposes among locations using the same methods, it provides powerful data. Potential biases were reduced by measuring only colonies lying with more than 50% of the colony surface area within the 10 m<sup>2</sup> belt transect. Between nine and 14 (median 10) replicate transects were sampled per site. This approach to surveying coral size classes and population structure is similar to that described in the IUCN coral reef resilience assessment protocol (Obura and Grimsditch, 2009), however, it captures greater detail of the entire hard coral community by measuring corals to the nearest cm and by surveying all taxa rather than a pre-defined subset of genera.

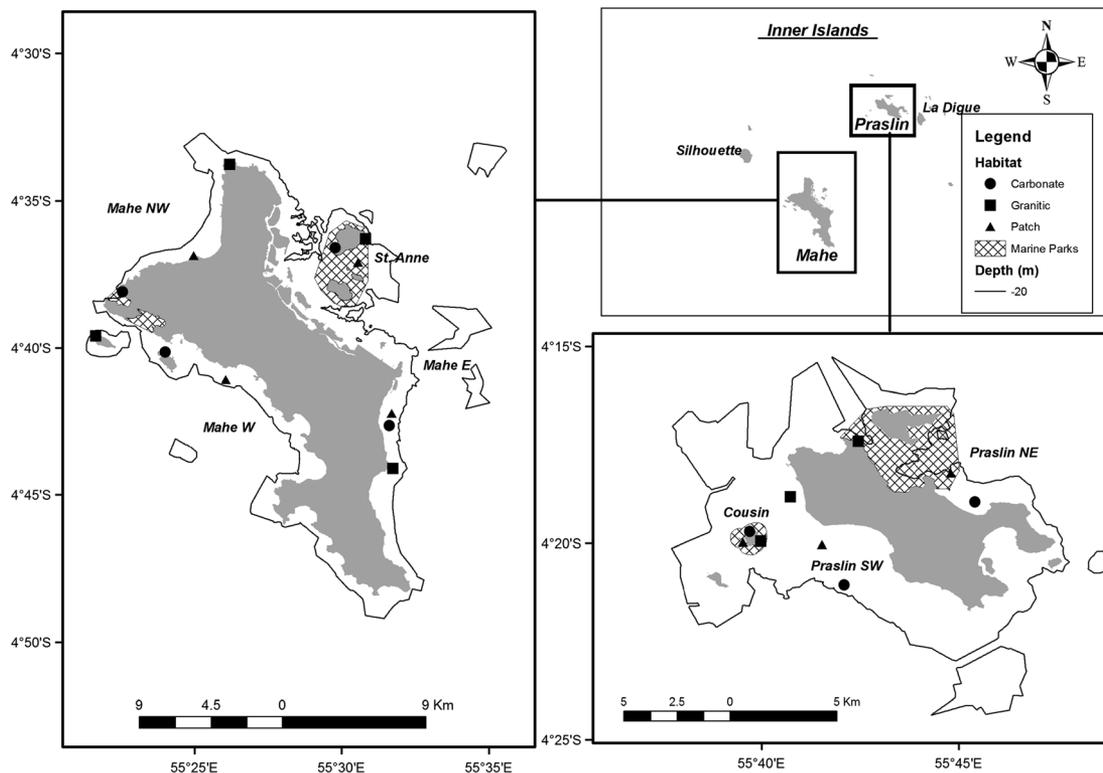


Figure 1. Survey sites across the inner Seychelles.

### Juvenile colonies

The size and genus of all juvenile hard corals ( $\leq 10$  cm diameter) found within haphazardly placed  $0.11 \text{ m}^2$  ( $33 \text{ cm} \times 33 \text{ cm}$ ) quadrats *in situ* was recorded. Colonies within each quadrat were measured along the longest axis with callipers or tape. This small quadrat size was selected since recruitment estimates generated by studies using large quadrats ( $1 \text{ m}^2$ ) greatly under-sample true juvenile coral abundance (Miller *et al.*, 2000). Between 28 and 170 (median 90) replicate  $0.11 \text{ m}^2$  quadrats were sampled per site within the same reef area covered by the belt transects. As with adult colonies, only those with more than 50% of their surface area within the quadrat area were assessed.

### Calculation of surface area

Both for adult and juvenile corals, colony surface area was modelled as approximately equivalent to  $\pi r^2$ ,  $r$  being half the maximum diametric axis measured for each colony. For conical-shaped massive colonies with a raised central feature,  $r$  was measured directly along the colony from the central point, rather than from above or as an 'aerial footprint' measurement. For overhanging, plate or table colonies, only the upper surface of corals was measured.

### Benthic composition

Sixteen replicate line intercept transects (LIT) (English *et al.*, 1997) were conducted at each site to record the overall biotic cover on the substrate. The LIT method was used to allow rapid assessment of the composition of target benthic and substrate groups, identifying coral taxa to genus.

### Analyses

Differences in juvenile coral abundances were assessed using a two-way crossed ANOVA with island (Mahé and Praslin) and habitat (carbonate, patch and granitic) as factors. Size frequency distributions were calculated, based on both the numerical abundance and total surface area of colonies for juvenile ( $\leq 10$  cm) and adult ( $> 10$  cm) corals, to examine life history and growth patterns exhibited by different populations and communities.

In addition, colony size frequency data from all sites for each taxon were pooled to provide a large sample size of each population.

Multivariate analyses were used to investigate the effect of various factors including management and reef geomorphology on coral communities. Non-metric multi-dimensional scaling (MDS) ordinations based on Bray–Curtis dissimilarities of square root-transformed multivariate sample data were used to assess differences in taxonomic composition among sites. Analysis of similarities (ANOSIM) were then used to identify significant differences between groups of samples based on management (marine protected areas that exclude fishing vs. fished sites), location (Mahé vs Praslin), and reef geomorphology (granitic, patch or carbonate). Finally, SIMPER analysis was used to identify the genera of corals for both adult and juvenile communities that contributed the most to differences between Mahé and Praslin and between different reef geomorphologies for juvenile communities (the significant factors identified in ANOSIM testing).

Multivariate analyses were repeated with two sets of values calculated from the raw data: colony density values, defined as the mean number of colonies per taxon per unit area ( $\text{colonies genus}^{-1} \text{ m}^{-2}$ ) per site; and colony surface area values, defined as the mean total surface area of colonies per taxon per unit area ( $\text{m}^2 \text{ m}^{-2}$ ) per site. In each case values for each sample used in analyses were calculated as the mean for each site from all replicates. Univariate and multivariate statistical analyses were carried out using PASW 18.0 (SPSS Inc.), Minitab 14.20 (Minitab Inc.) and Primer 6.1 (Primer-E Ltd.).

## RESULTS

### Overview of coral reef condition

Coral communities were generally situated on flat patch reef or continuous carbonate substrata at the survey depth, or on steeply shelving granite boulders on a sand substrate, at a maximum depth of 10–12 m. Most reefs on patch or carbonate substrata were extremely depauperate (Figure 2), with low coral cover, heavily eroded reef frameworks, and highly variable abundance of erect macroalgae; ranging from absence of seaweeds at nine of 21 sites, to 70%

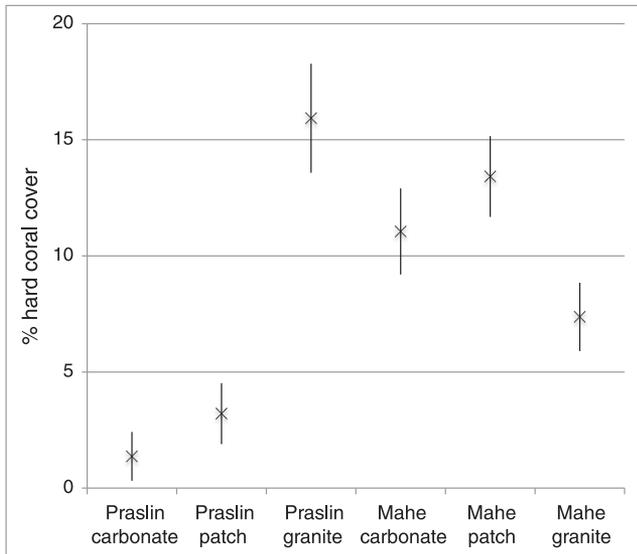


Figure 2. Mean percentage benthic cover of hard coral ( $\pm$  standard error of mean) based on line intercept measurements, across patch, carbonate and granitic reef sites at Mahé and Praslin islands, ranked in order of increasing coral cover.

( $\pm 3\%$  SE) – predominantly *Sargassum* and *Lobophora* spp. – at one carbonate site at Praslin island. Reefs on hard granitic substrata generally supported much higher abundance, cover and complexity of corals. The density of small encrusting faviids growing directly on granite boulders was particularly high, predominantly of *Favia* spp., *Favites pentagona* and *Goniastrea* spp.. Several of these sites also showed prolific growth of branching and tabular *Acropora* species, notably *Acropora clathrata*, *Acropora abrotanoides*, and *Acropora pulchra*.

### Coral communities

In total, 40 genera from 14 scleractinian families were recorded. Surveys showed little variation in either generic or family diversity among sites (mean number of adult taxa per site 17.8 ( $\pm 1.5$  standard error) and 8.7 ( $\pm 0.6$  SE) respectively) as well as low variation between transects across all sites (mean number of adult taxa per transect 7.3 ( $\pm 0.3$  standard error) and 4.6 ( $\pm 0.1$  SE) respectively).

Across all sites, adult colony density ranged from 0.3 to 7.4 colonies  $m^{-2}$ , both extremes being around Praslin Island, with a mean colony density across all sites of 3.3 colonies  $m^{-2} \pm 0.3$  SE). Total adult colony surface area ranged from 0.01 to 1.45  $m^2$  per planar  $m^2$  (mean 0.3  $\pm 0.1$  SE). Extremely high

coral surface area estimates ( $>1m^2$ ) are due to surface area estimates of large non-planar corals within two-dimensional survey belts and tiering of some colonies.

Juvenile colony density ranged over two orders of magnitude between sites, from 0.4 colonies  $m^{-2}$  (equivalent to a total coral area of 0.0005  $m^2$ ), again at the same highly depauperate site at Praslin Island, to a maximum of 37.0 colonies  $m^{-2}$  (equivalent to a total coral area of 0.07  $m^2$ ) at a granite site on Mahé. Mean juvenile density across all sites was 9.9 colonies  $m^{-2} \pm 0.02$  SE, with higher densities recorded on reefs around Mahé (Figure 3(a);  $F_{1,15} = 3.86$ ,  $P = 0.068$ ) as well as on granitic reefs rather than carbonate reefs (Figure 3 (b);  $F_{2,15} = 3.35$ ,  $P = 0.063$ ).

Total colony surface area was dominated by large corals (41–160 cm), whereas the considerably higher numerical abundance of smaller colonies makes only a small contribution to overall coral surface area. Similarly the density of small juvenile corals (2–3 cm) is high, declining as colony size increases (Figure 4(a)). A comparatively low abundance of very small corals ( $\sim 1$  cm) is indicative of the difficulty in detecting these individuals. Surface area occupied by juvenile corals increased in a linear fashion with colony

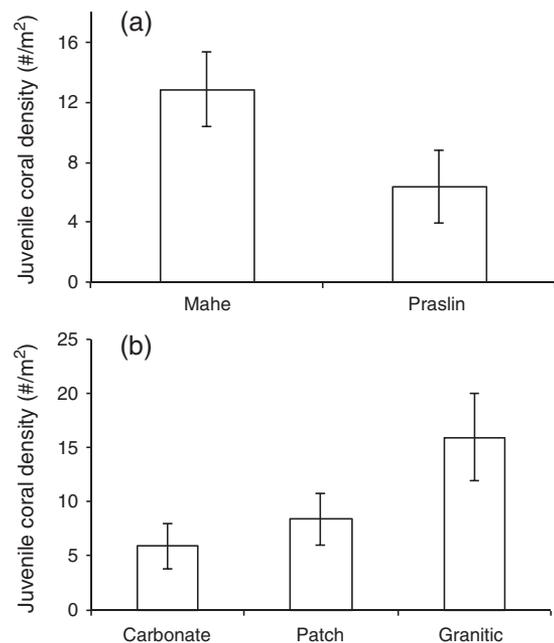


Figure 3. Mean juvenile coral density (number per  $m^2$ ) at Mahé and Praslin islands (a), and in the three habitat types surveyed (b). Error bars are 1 standard error of the mean.

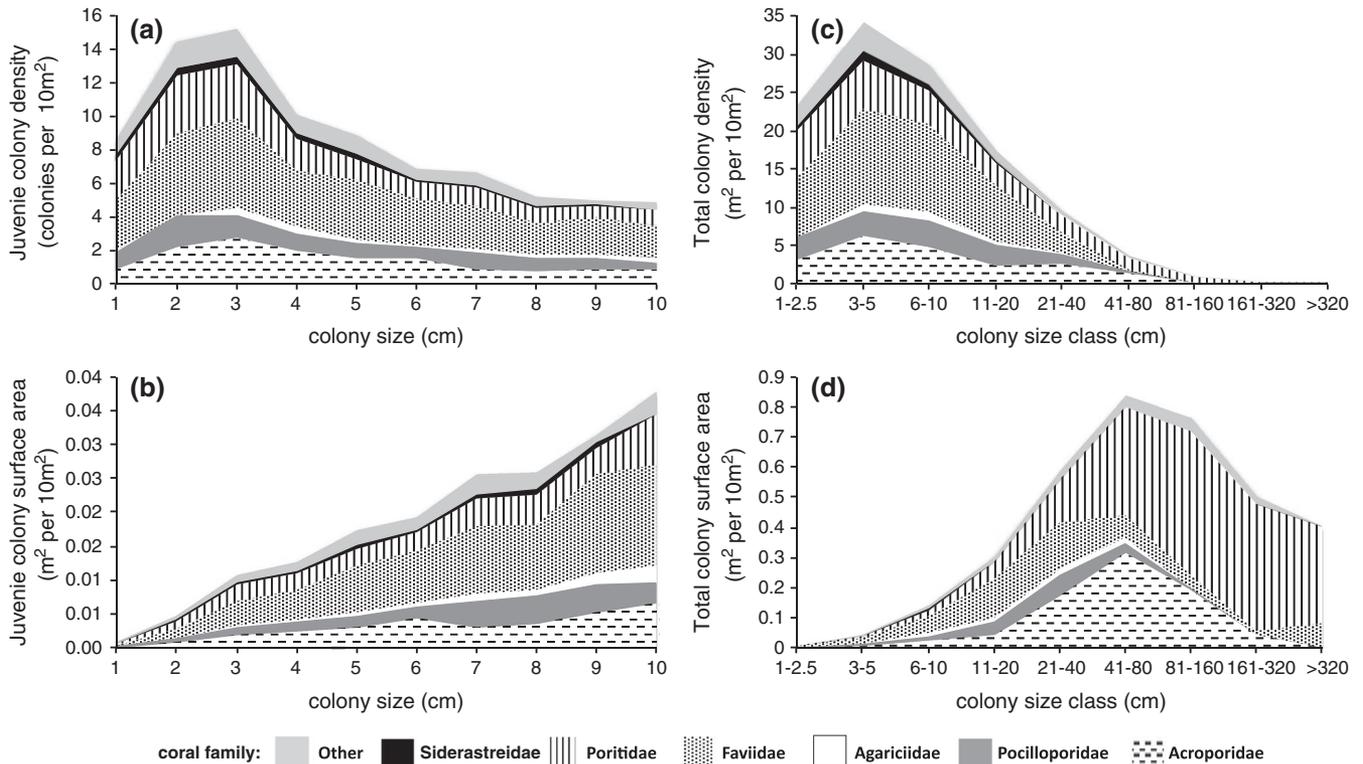


Figure 4. Mean colony density (left) and total hard coral surface area (right) by colony size showing contribution of dominant scleractinian families to size frequency distributions (all taxa, all sites), based on: juvenile colony density (a); juvenile colony surface area (b); adult and juvenile colony density (c); and adult and juvenile colony surface area (d). Juvenile and adult size frequency distribution data are combined in (c) and (d) to display results from the two sampling approaches (transects and quadrats) as a continuous average size frequency distribution across nine size classes.

size but made only a minor contribution to the overall area coverage (Figure 4(b)).

Across all sites the largest colony observed was a *Porites solida* colony measuring 525 cm across the colony surface. Median adult coral size was 18 cm; less than one quarter of the colony diameter that accounted for half the cumulative surface area of adult colonies (78 cm), on account of the non-linearity between colony diameter and area. Between-site analyses showed that granitic sites exhibited lower mean colony sizes than reef sites on non-granitic substrata ( $23.3 \pm 0.3$  cm SE maximum diameter on granitic reefs compared with  $28.9 \pm 0.6$  cm SE and  $31.7 \pm 0.9$  cm for patch and carbonate reefs respectively; ANOVA  $P < 0.01$ ).

Faviid colonies dominated both adult and juvenile coral communities when abundance was assessed in terms of density of colonies (Table 1, Figure 4(a), (c)). Other prominent families were (in order of decreasing density) poritids, acroporids and pocilloporids. Conversely, total surface area

of adults was dominated by poritids, followed by acroporids then faviids, while the juvenile coral communities were dominated by faviids, followed by acroporids and poritids (Table 1; Figure 4(b), (d)).

#### Relationship between juvenile colony density and benthic cover

Positive correlations between juvenile settlement space and juvenile colony density were recorded, despite the generally very low values of juvenile coral abundance observed. Higher coverage of hard benthic substrate groups suitable for larval settlement (calculated as combined cover of calcareous encrusting algae and uncolonized standing dead coral) favoured higher levels of juvenile density (Pearson  $r = 0.50$ ,  $P = 0.02$ ). Due to co-linearity between combined hard 'settleable' substrata and combined live benthic groups unsuitable for juvenile settlement, this correlation also reflects a negative relationship with live benthic cover (calculated as combined cover of

Table 1. Mean family density and surface area for adult and juvenile colonies, and percentage of total (adults and juveniles combined). Dominant families highlighted in each case

	Size	Acroporidae	Pocilloporidae	Agariciidae	Faviidae	Poritidae	Siderastreae	Other	Total
Mean colony density (colonies per m <sup>2</sup> )	≤10 cm	139 (12%)	97 (8%)	24 (2%)	<b>315 (27%)</b>	168 (14%)	24 (2%)	89 (8%)	856 (73%)
	>10 cm	64 (6%)	40 (3%)	9 (1%)	<b>105 (9%)</b>	72 (6%)	1 (0%)	19 (2%)	310 (27%)
Mean colony surface area (m <sup>2</sup> per transect)	≤10 cm	0.03 (1%)	0.02 (1%)	0.01 (0%)	<b>0.07 (2%)</b>	0.03 (1%)	0.00 (0%)	0.02 (0%)	0.19 (5%)
	>10 cm	0.77 (22%)	0.15 (4%)	0.04 (1%)	0.50 (14%)	<b>1.7 (50%)</b>	0.00 (0%)	0.15 (4%)	3.40 (95%)

live hard and soft coral, macroalgae and turf algae, sponges and other live benthic groups) (Pearson  $r = -0.50$ ,  $P = 0.02$ ).

### Multivariate analysis of coral communities

Analysis of taxonomic composition of communities showed differences in generic composition of juveniles between geomorphological substrate classes (carbonate, patch or granite), but not of adult corals (within-region ANOSIM Global R values for juvenile and adult communities based on colony density values by genera 0.176 ( $P < 0.002$ ) and 0.091 ( $P = 0.08$ ) respectively). Pairwise tests showed differences between granitic habitats and both patch and carbonate habitats for juvenile coral composition, and no differences between patch and carbonate habitat types.

Coral communities showed no difference between protected and unprotected sites, for either adult or juvenile coral communities (within-region ANOSIM Global R values based on colony density values by genera 0.15 ( $P = 0.10$ ) and 0.10 ( $P = 0.21$ )). However, results do show a clear separation of all sites from Mahé from all but two of the Praslin sites for adult corals and all but four Praslin sites for juvenile corals based on a similarity level of 40 (Figure 5). This separation between the two islands is highly significant and indicates profound differences in their scleractinian communities, largely the result of very low colony abundance at Praslin relative to Mahé (between-island Global R for juvenile and adult communities based on colony density data 0.29 ( $P < 0.001$ ) and 0.46 ( $P < 0.001$ ) respectively).

For adult coral communities, nine genera make up 60% of the difference between the island groups, with all genera having a higher abundance around Mahé (Table 2). Similarly, for juvenile coral communities eight genera make up 60% of the difference, and all have higher abundance around Mahé (Table 2). The relative abundances of coral genera within and between the two islands indicate subtle differences in the composition of coral communities on Mahé and Praslin. Bubble plots showing the density of the two dominant coral genera for both adults and juveniles (*Porites* and *Acropora*) demonstrate the spatial variability in abundance among sites and show that

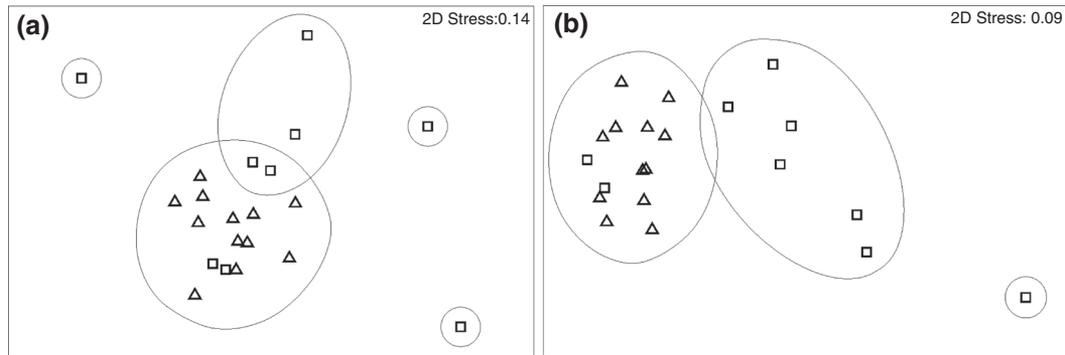


Figure 5. Non-metric MDS ordinations based on juvenile (a) and adult (b) colony density data (colonies per m<sup>2</sup>), from all genera. Squares indicate values from Praslin Island, triangles from Mahé Island. Values for each sample are the mean of all replicates within each site. Samples grouped within Bray–Curtis similarity boundaries at a similarity level of 40.

Table 2. SIMPER outputs for greatest pairwise differences between Mahé and Praslin in juvenile and adult coral genera for the genera that cumulatively contributed to 60% of the overall difference. Genera are listed in descending order of contribution

Adult coral communities				Juvenile coral communities			
Genera	Average abun. Mahé	Average abun. Praslin	Contrib. (%)	Genera	Average abun. Mahé	Average abun. Praslin	Contrib. (%)
<i>Porites</i>	0.89	0.47	10.42	<i>Porites</i>	1.37	0.86	9.98
<i>Acropora</i>	0.72	0.49	10.10	<i>Acropora</i>	1.23	0.52	9.26
<i>Favites</i>	0.71	0.32	8.96	<i>Favites</i>	1.20	0.57	8.92
<i>Favia</i>	0.55	0.17	7.18	<i>Favia</i>	1.10	0.36	7.94
<i>Pocillopora</i>	0.47	0.42	6.65	<i>Fungia</i>	0.47	0.42	7.03
<i>Goniopora</i>	0.3	0.00	5.07	<i>Pocillopora</i>	0.84	0.47	7.02
<i>Goniastrea</i>	0.48	0.25	4.67	<i>Pavona</i>	0.47	0.17	5.38
<i>Stylophora</i>	0.18	0.11	3.60	<i>Leptastrea</i>	0.47	0.53	5.23
<i>Galaxea</i>	0.21	0.03	3.56				

abundance is typically an order of magnitude higher on Mahé compared with Praslin sites (Figure 6). For juvenile coral communities four genera account for at least 60% of the similarity within each geomorphological group, although the taxa vary between geomorphological groups with *Favites* being the main influence of group similarity on granite reefs, *Pocillopora* on carbonate reefs and *Acropora* on patch reefs (Table 3).

## DISCUSSION

The highly depauperate nature of coral communities on reefs of the inner, or granitic, Seychelles is notable at a regional scale. The diversity, density and surface area of both juvenile and adult corals within the inner Seychelles were lower than any other sites surveyed across five countries in the central and western Indian Ocean between 2006

and 2009, during a regional study that employed the same methods as this research (Harris, 2010). The extremely low diversity and abundance of corals on these reefs may be compromising the ability of many inner Seychelles reefs to recover from severe bleaching and other ongoing stressors.

A comparison of generic diversity data with values from three regions of the southern Red Sea and Madagascar indicates a markedly lower taxonomic diversity of scleractinia in the inner Seychelles (Harris, 2010). Mean Shannon diversity ( $H'$ ) values across all sites surveyed in the Seychelles were 1.9 ( $\pm 0.1$  SEM), compared with 2.0, 2.4 and 2.7 ( $\pm 0.1$  SEM in all cases) in southern Saudi Arabia and two regions of western Madagascar respectively (Harris, 2010). More recent surveys have documented nine scleractinian genera not recorded in this study (Sullivan, 2009), however, it is notable that a number of formerly recorded genera were absent from the present study.

INNER SEYCHELLES SCLERACTINIAN CORAL COMMUNITY COMPOSITION

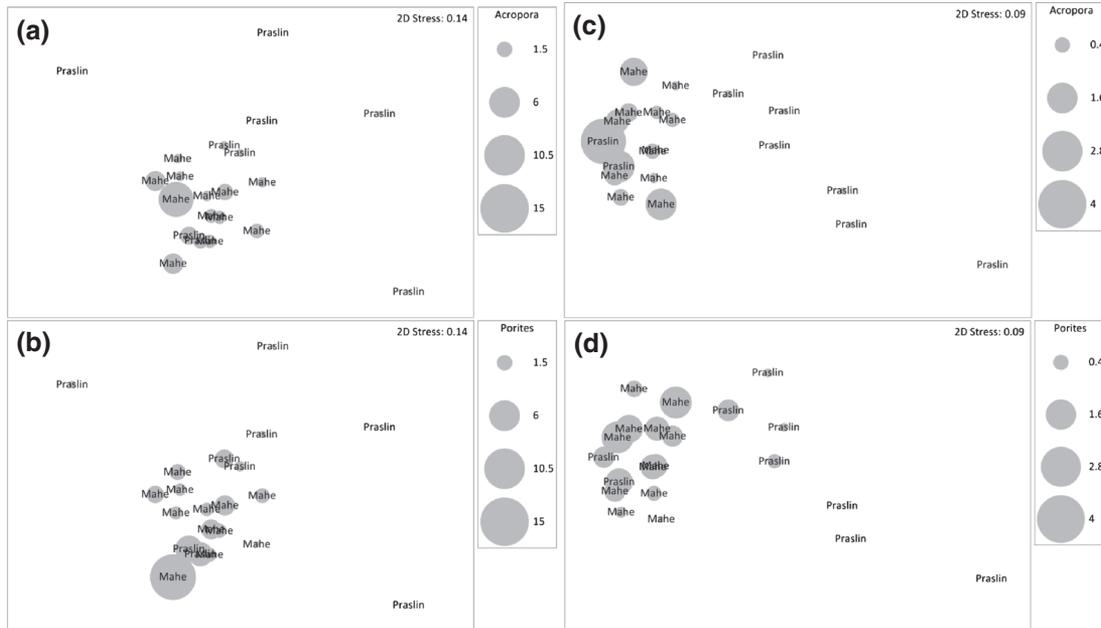


Figure 6. Bubble plots superimposing taxon-specific values of density of *Acropora* and *Porites* colonies across sites. Density values overlaid on juvenile ((a) and (b)) and adult ((c) and (d)) MDS plots from Figure 5.

Table 3. SIMPER results for one-way analysis of juvenile genus contributions to group differences between granite, carbonate and patch sites, showing only the dominant taxa that cumulatively contributed to 60% of the overall similarity within each geomorphology

Genera	Average abun. granite	Contrib. granite (%)	Average abun. patch	Contrib. patch (%)	Average abun. carb.	Contrib. carb. (%)
<i>Favites</i>	1.74	19.48			0.46	14.85
<i>Porites</i>	1.76	19.08	1.04	21.90	0.65	16.54
<i>Acropora</i>	1.16	15.27	0.80	16.97		
<i>Pocillopora</i>	0.94	11.69			0.77	18.68
<i>Favia</i>			0.57	10.55	0.48	13.48
<i>Pavona</i>			0.59	9.98		

These were *Seriatopora*, *Pachyseris*, *Echinophyllia* and *Oxypora* (one colony of *Pachyseris* was recorded at St Anne Island, Mahé). These genera have all been highlighted as taxa with high vulnerability to extinction from bleaching (McClanahan *et al.*, 2007). While *Pachyseris*, *Echinophyllia* and *Oxypora* are generally more common in deeper environments than those sampled here (and may therefore persist at reef sites not sampled in the present study), the absence of *Seriatopora* is notable, and this may be the first taxon to have been locally extirpated from the inner Seychelles reefs.

Surveys in the southern Seychelles during the 1998 warming episode recorded high levels of bleaching and mortality in branching coral species, in contrast to low levels in encrusting species (Spencer *et al.*, 2000). Such taxon-specific bleaching

patterns appear to be common across the Indian Ocean (McClanahan *et al.*, 2007). In the inner Seychelles, following the bleaching events of 2002 and 2003, slow growing corals such as massive *Porites* and *Goniopora* were observed to become increasingly dominant genera, suffering only temporarily arrested growth from bleaching that brought about significant losses in branching and encrusting taxa (Engelhardt *et al.*, 2002; Engelhardt, 2004). Surveys from 2005 to 2011 have confirmed these observations of an increasing relative abundance of encrusting and massive corals compared with the previously dominant branching habitat-forming taxa (Graham *et al.*, 2006; Wilson *et al.*, 2012). Observations of massive *Porites* colonies as the largest surviving colonies in this study lend support to these observations.

Although there were exceptions, many of the sites comprising carbonate and sandy patch reef substrata showed a pervasive structural collapse and a shift towards low diversity macroalgal-dominated states, with little available hard substratum suitable for coral settlement. Indeed, a number of sites known to have previously shown thriving reef growth (Jennings *et al.*, 1996) no longer appeared to be actively accreting, and many dead reef structures had collapsed to such an extent that little more than highly mobile rubble remained. Like profuse macroalgal cover, the existence of much rubble also precludes significant coral recovery (Sheppard, 2006; Chong-Seng *et al.*, 2012), so that prognosis for recovery of these sites in the short term remains poor. A study of the same inner Seychelles sites including data up to 2011 suggests that there has been some accelerating recovery of coral cover at some sites, while other sites continue to show little improvement, mediated largely by the extent of macroalgal expansion (Wilson *et al.*, 2012). Indeed, the condition of coral reefs across the inner Seychelles appears to vary greatly from recovering coral cover and structural complexity, to low relief reefs dominated with macroalgae (Chong-Seng *et al.*, 2012), and the ability of herbivores to reduce this macroalgae dominance appears low (Chong-Seng *et al.*, in press a)

These observations are particularly worrisome given that fishing effort on inner Seychelles reefs is fairly light and has remained relatively constant since the early 1990s, and, with the exception of isolated occurrences of chronic sedimentation and pollution, the reefs are considered to be relatively unaffected by anthropogenic disturbance in comparison with many more heavily utilized reefs in east Africa and the broader western Indian Ocean region (Cinner *et al.*, 2009). Indeed, recent analyses have suggested that at a regional level, Seychelles reefs may be considered among the least threatened from anthropogenic impacts in the Indian Ocean (Burke *et al.*, 2011).

In apparent contrast to the depletion of scleractinian communities, median colony size (in terms of contribution to cumulative colony surface area) was high; almost double that observed on thriving coral reefs in the Farasan Banks, Saudi Arabia, where mean hard coral cover across >50

sites exceeded the maximum value recorded at any site in this study (Harris, 2010). Large colonies contribute disproportionately to the overall surface area of corals in the inner Seychelles, suggesting survival of some old colonies despite low replenishment.

These largest colonies are poritids and faviids, generally slow growing taxa which, given their sizes, are likely to be survivors of the 1998 and subsequent bleaching-related mortality episodes. Such large colonies would usually suggest high levels of fecundity (Babcock, 1991) and the presence of these large, highly reproductive, thermally tolerant colonies indicates viable local sources of coral larvae within the inner Seychelles. Moreover, the striking correlation between juvenile colony abundance and available hard 'settlement' substratum suggests that, where there is suitable stable substrate not occupied by macroalgae, corals are able to recolonize unoccupied reef substrata. However, notwithstanding this correlation, absolute numbers of juvenile colonies were very low, an observation that was confirmed by the use of an underwater UV lamp to enhance detection of newly recruited juveniles (*sensu* Baird *et al.*, 2006). Hence, it might be reasoned that low levels of coral settlement – and/or post-settlement survival – are limiting reef recovery in the inner Seychelles. Although the density of *Porites* recruits is twice that of any other family, dominance of *Porites* recruits is a general feature in western Indian Ocean reefs (Harris, 2010), so this result should not be interpreted as a post-bleaching change in recruit composition.

Decreased settler abundance may indicate a reduction in fertile colonies (Hughes *et al.*, 2000), a feature that might be expected after a high stress episode (Ward *et al.*, 2002). Low abundance of juveniles may also relate to high mortality caused by competing macroalgae (Kuffner *et al.*, 2006), or by physical damage from the prolific loose and abrasive coral rubble (Victor, 2008). A recent study of coral larval supply and subsequent survivorship across the inner Seychelles indicated consistent larval supply across a range of reefs, but subsequent settlement success or survivorship to juveniles and adults was negatively influenced by both macroalgae cover and mobile rubble banks (Chong-Seng *et al.*, in press b). The impact of the 2004 tsunami should

also be noted as a contributing factor exacerbating damage to reef substrates and corals before this study. The tsunami had disproportionate impacts on carbonate framework reefs in the inner Seychelles, causing the already-eroding reefs to break up further (Obura and Abdulla, 2005).

Regardless of its cause (larval supply, settlement prevention, or post-settlement mortality), recruitment failure is likely to be a factor limiting the recovery of many inner Seychelles reefs. The longer such failure persists on many of the reefs, the more fragmented the underlying substratum will become as a result of mechanical and biological erosion, in turn becoming increasingly unfavourable to coral settlement. Surveys conducted in 2004/5 showed that, relative to their pre-1998 condition, reefs of the Inner Seychelles had lost much of their coral cover and many sites had reduced structural complexity with disintegration of the shallow reef framework (Sheppard *et al.*, 2005; Graham *et al.*, 2006). At the same time macro-algae cover increased seven-fold (Graham *et al.* 2006). The present study suggests that coral communities showed limited recovery on many sites between 2005 and 2008, a situation that has since persisted until at least 2011, with hard coral cover across all sites averaging 1% increase per year between 2005 and 2011 (Wilson *et al.*, 2012).

Existing management in the form of marine protected areas (MPAs) had no demonstrable impact on juvenile or adult coral abundance in 2008. Indeed, protected sites at a strictly enforced no-take MPA situated off the coast of Praslin recorded among the lowest values of coral abundance, surface area and diversity of all sites surveyed in this study, with mean generic richness lower than at any other site surveyed in a regional study of scleractinian communities across five Indian Ocean countries (Harris 2010). This observation may lend further support to regional observations of the failure of many MPAs, especially smaller ones, to promote ecosystem recovery following large-scale disturbances (Ledlie *et al.*, 2007; Graham *et al.*, 2008). However, Wilson *et al.* (2012) found that while MPAs did not promote coral recovery when macroalgae cover was high, in cases where macroalgae was not a dominant component of the reef benthos,

there was weak evidence that the MPAs could promote some coral recovery. Encouraging recovery on the reefs where macroalgae is currently preventing coral establishment, may require some innovative management interventions to break the dominance of algae over corals (McClanahan *et al.*, 2008; Graham *et al.*, 2013).

The limited recovery within Seychelles MPAs is partially due to past zonation of protected areas around reefs previously characterized by prolific growth of thermally intolerant and/or branching coral taxa. These corals have generally shown higher susceptibility to bleaching-related mortality than more tolerant massive and encrusting colonies, consequently experiencing the greatest declines following disturbance events. As a result, some of these protected areas have lost their once profuse coral communities (Graham *et al.*, 2008), while more tolerant heterogeneous coral communities at certain other non-protected sites have experienced relatively milder declines, in some cases persisting to the point where these communities are in markedly better condition than protected reefs. These findings indicate a low likelihood of reef recovery at some sites where substrates are unfavourable for coral larval settlement and survival. Indeed, it is possible that some coral reefs located on carbonate and patch substrata within the inner Seychelles may have passed a threshold of viable recovery, now persisting in a self-reinforcing, non-coral dominated state (Hughes *et al.*, 2010).

The zoning of protected areas within the inner Seychelles may require substantial review in order to prioritize the protection of reef sites with the highest resilience and recovery potential. Safeguarding reef sites that retain heterogeneous adult coral communities growing on stable substrates should be an urgent priority. Particular emphasis should be placed on protecting granitic coral substrates, since these sites offer greater substrate stability than carbonate reefs, and their high abundance of juveniles suggests effective survivorship of coral recruits within this habitat. Indeed, granite-based coral communities within the inner Seychelles may play an increasingly crucial role as refugia for remaining coral populations, and should be prioritized for inclusion within future management decisions. Conservation and management of remaining Seychelles reefs, aimed

at enhancing recovery or reversing phase shifts to macroalgae, should draw on a variety of other tools, such as alterations in fishing gears to reduce catches of key herbivores, and reducing sediment inputs from land (Graham *et al.*, 2013). Furthermore, the Seychelles has been identified as having the adaptive capacity to trial some innovative management options such as active ecosystem manipulation and restoration (McClanahan *et al.*, 2008).

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