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Spatial variability in habitat structure and heterogenic coral reef fish assemblages inside a small-scale marine reserve after a coral mass mortality event

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ABSTRACT

Coral reefs at the inner granitic islands in the Seychelles were heavily affected by the worldwide bleaching event in 1998, which led to subsequent coral mortality and widespread phase shifts to macroalgae dominated reefs. In this study, five sites within a small, but well enforced marine reserve at Cousin Island, were investigate using various methods to explore differences in coral habitat quality, coral recruitment, fish assemblages, key invertebrate grazers, and rugosity. The objective of the study was to collect a broad set of scientific data, which could be useful to describe linkage between coral reef and fish assemblages after a large-scale disturbance, as well as for future management decisions regarding marine resources, in terms of MPA protection and recovery abilities. The results showed high spatial variation in coral coverage between sites (from 1.5% to 43.2%), which were higher than previously reported, as well as high variation in dispersal of coral recruits. Furthermore, there were large heterogenic differences in fish densities and composition, which were directly linked to coral habitat quality, e.g. total fish abundance was 15 times higher on sites with high coral coverage in comparison to sites with low coral cover. In summary, this study demonstrates that coral reef habitat and fish assemblage may display high spatial variability and heterogenic differences after large-scale disturbances and suggests that potential recovery from coral mass mortality may occur in a non-linear and patchy procedure, which in turn may depend on underlying stocastical processes that affect coral recruitment and survivorship.

1. Introduction

Degradation, fragmentation, and loss of habitats have been suggested as some of the most critical threats to global terrestrial and marine biodiversity (Musick, 1999; Bellwood et al., 2004; Carpenter et al., 2008; Graham et al., 2011). During the last couple of decades coral reef habitats, which have the highest biodiversity of all marine ecosystems (Birkeland, 1997), have declined at an alarming rate due to a combination of both anthropogenic and natural disturbances (Bruno and Selig, 2007; Gamfeldt et al., 2014). Threats to coral reef habitats and associated fish communities include: over-exploitation (Myers and Worm, 2003; Berkes et al., 2006; Knowlton and Jackson, 2008), decreases in water quality (Wooldridge, 2009), outbreaks of crown-of-thorns starfish (*Acanthaster planci*) (Wilson et al., 2008; De'ath et al., 2012), sedimentation, (Fabricius, 2005; Halpern et al., 2013), and more recently severe large-scale effects from climate change (reviewed by Pratchett et al., 2011; Hoegh-Guldberg, 2012; Wernberg et al., 2012; Hughes et al., 2013).

While the coral reefs in the Seychelles have been considered to be one of the least affected areas by local anthropogenic disturbances in the Western Indian Ocean (Cinner et al., 2009; Burke et al., 2011), the coral reefs at the inner granitic islands at the Seychelles were one of the most severely affected areas by the worldwide 1998 bleaching event (Wilkinson, 2004), with up to 95% coral mortality (Bigot et al., 2000; Graham et al., 2006; Wilson et al., 2012). The coral bleaching event in 1998 occurred as a result of the interaction of the El Niño Southern Oscillation (ENSO) and Indian Ocean Dipole (IOD), which led to global increased sea surface

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temperatures and large-scale coral bleaching, which was followed by coral mass mortality and widespread phase shifts to macroalgae dominated reefs (Goreau et al., 2000; Spalding and Jarvis, 2002; Graham et al., 2006), defined as an extensive decrease in coral cover coinciding with substantial increases in some alternative benthic organism, which have persisted for more than five years (Norström et al., 2009).

Before 1998, coral coverage at the inner granitic islands at the Seychelles was reported to reach in average 28% and surveys conducted within the marine reserve at Cousin Island described the coral reefs within the MPA to be in good condition, with high percentage of coral cover (Wilson et al., 2012) and high levels of fish biomass (Jennings et al., 1996). However, the coral reefs around Mahe and Praslin suffered extensive damage and mortality from the 1998 bleaching event and mean coral cover within the reserve at Cousin Island decreased with 95–99% coverage (Wilson et al., 2012) and covered only approximately 1% of the benthic substrate in to 2005 (Ledlie et al., 2007).

The aims of this study was to investigate spatial variability in coral reef habitat and fish community, as well as examine ecological linkages between habitat quality and coral reef fish assemblages within a small well-protected MPA. Scientific information regarding recovery rates of coral reefs and associated fish assemblages in small marine reserves may have important implications for both the local fishery, as well as for continuing support and coastal management decisions (Halpern and Warner, 2002; Roberts et al., 2003; McClanahan et al., 2006).

Five sites were selected for extensive surveys within the marine reserve at Cousin Island and by using various methods investigate differences in: (1) biotic and abiotic benthic substrate, (2) rugosity, (3) coral recruitment, (4) fish density and functional groups, and (5) key invertebrate grazers.

2. Material and methods

2.1. Study area

The study was carried out inside the no-take MPA around Cousin Island in the Seychelles. Cousin Island is a part of the inner granitic archipelago of the Seychelles and was declared a nature reserve by the government of the Seychelles in 1968 (Jennings, 1998). The area received further legal protection in 1975 and became a 'Special reserve' when the surrounding water, from 400 m from the high tide water mark in all directions around the island covering in total approximately 1.2 km^2 was protected (Francis et al., 2002), which makes it one of the longest established no-take marine reserves in the Western Indian Ocean (McClanahan et al., 2009). The MPA is well enforced (Jennings et al., 1996) by local wardens and the science officer, who lives permanently on the island, and during the turtle season all beaches are frequently patrolled.

The marine area around Cousin Island is characterised by fringing carbonate reef, granite reefs, patch reefs, and extensive areas of sand and *Sargassum* sp., a late succession algae species (McClanahan, 1997). The coral reefs around Cousin Island are affected by large seasonal variation due to the regional monsoon weather system, and the sandy area is repeatedly shifting between the eastern and northern beaches, which during certain times can result in low visibility. All of the reefs within the MPA are located fairly shallow (<20 m).

Five different sites around Cousin Island were surveyed for this study (Fig. 1). Site 1: carbonate reef mainly dominated by a combination of macroalgae and turf algae, but with patches of high coral cover; Site 2: carbonate reef dominated by turf algae and underlying substrate of stable coral rubble, which is being recolonised by coral recruits; Site 3: granitic and carbonate reef mainly dominated by algae and patches of corals; Site 4: carbonate reef flat dominated by high coverage of turf algae and with low structural complexity; Site 5: carbonate reef slope dominated by corals (Fig. 2a, b).

12 and 15 sub-locations were randomly selected for surveying at each site (15 sub-locations at Site 1, 2, and 3; and 12 sub-locations and Site 4 and 5). All sites were located within the 400 m zone where all fishing activities and all other extraction of marine organism are completely prohibited.

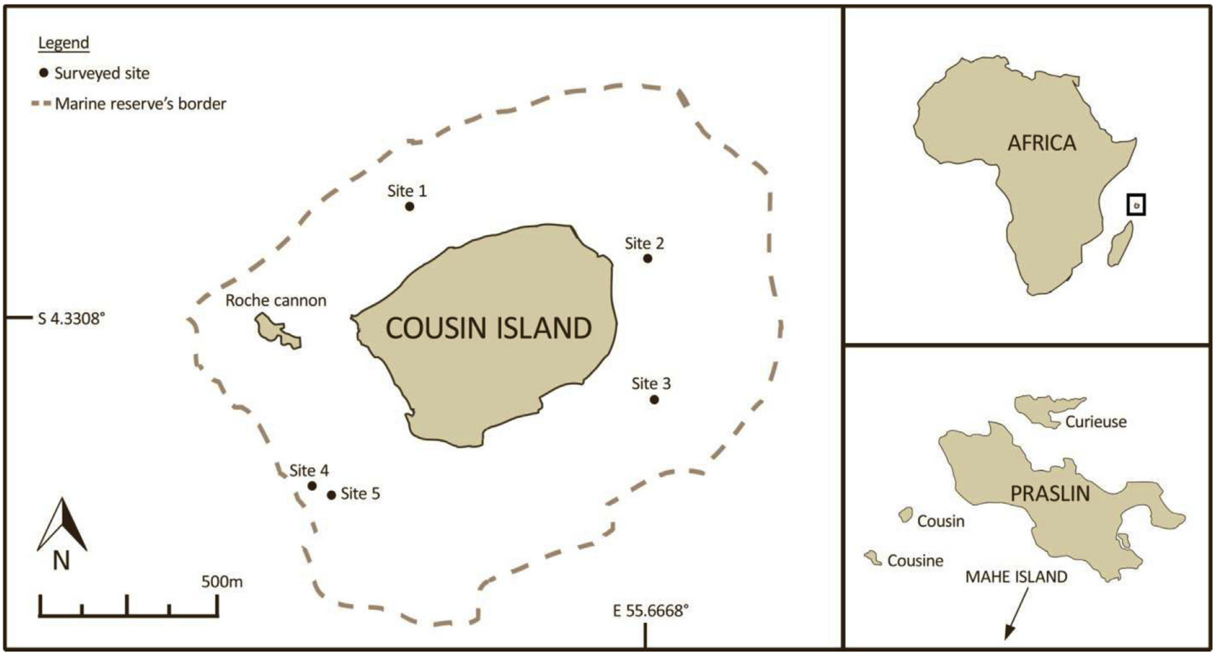

Fig. 1. Map of Cousin Island Special Reserve with the five surveyed sites marked out. Dashed line indicate border of the marine protected area.

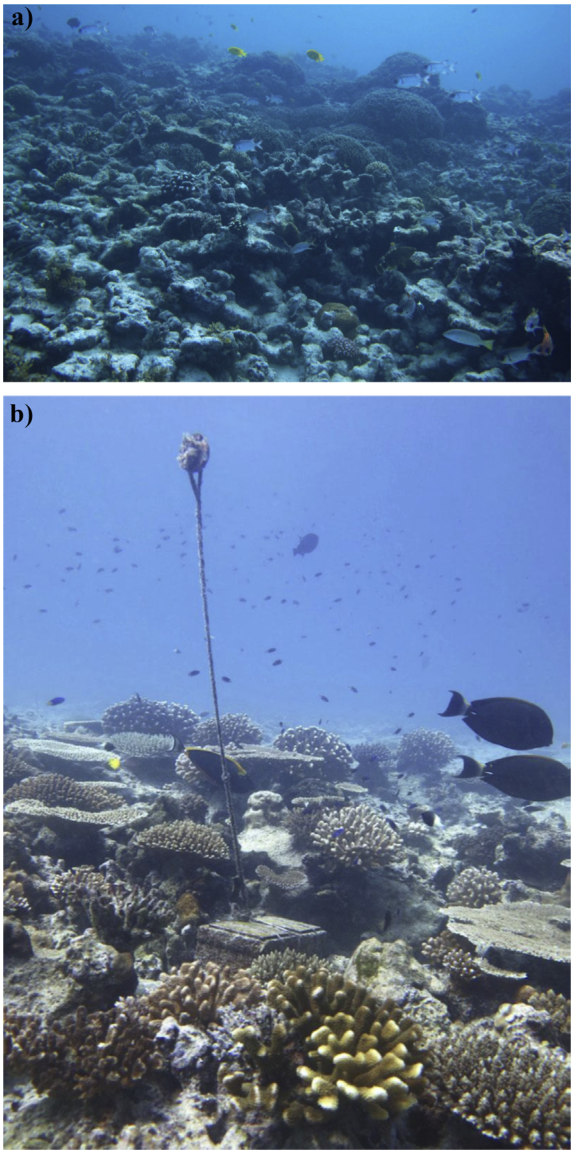

Fig. 2. a. Stable coral rubble, which is slowly being recolonised with corals. Photo: April J. Burt. b. High coral coverage at one of the investigated sites (Site 5) at Cousin Island special reserve, which were severely damaged by the 1998 coral mortality event. Photo: April J. Burt.

2.2. Collection of data

The following survey methods were used to collect data for this study: line intercept transects (LIT), coral recruit quadrates, belt transects for fish abundance and key invertebrate grazers, and rugosity, i.e. the three dimensional complexity of the benthic substrate on a small defined spatial scale (Wilson et al., 2008).

All data was collected during October 2013 to April 2014 using SCUBA and recorded by the same persons during the study (AJB and ECM) to reduce personal bias, which has shown to affect accuracy of data collection (Samoilys and Carlos, 2000; Nadon et al., 2012; McCauley et al., 2012).

Benthic substrate was recorded using 10 m LIT transect. Transects were placed haphazardly parallel to the shore at approximately the same depth (6 m–10 m) according to English et al. (1997). Biotic substrate was classified into the following categories: live hard coral, soft coral, coralline algae, turf algae, macroalgae, algal assemblage, sponge, and other (including zooanthids and sea anemones) (Leujak and Ormond, 2007). Hard coral was further classified to genus and morphology according to the literature (Veron, 2000). In addition, the underlying abiotic substrate was noted included sand, rock, rubble, and dead coral. In total 69 LIT transects were completed for the study and the same transects were used for counting fish and invertebrates. Each transect was separated by a random number of fin kicks (with a minimum of approximately 10 m interspacing).

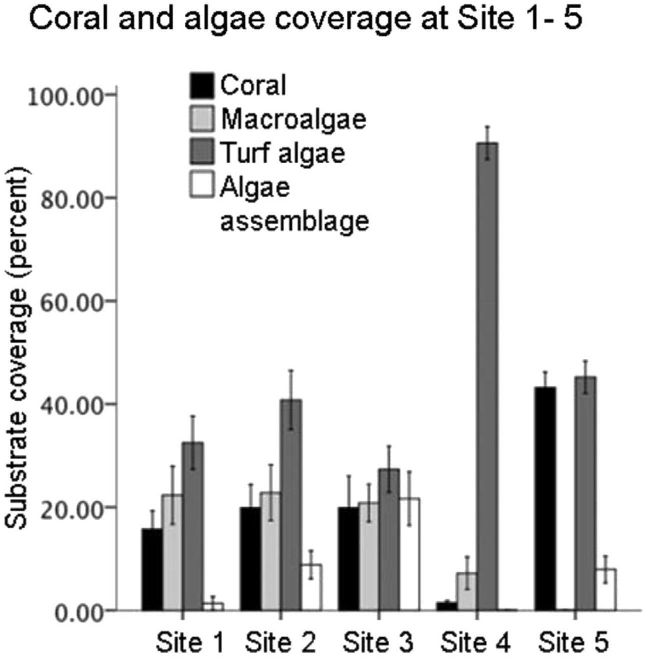

Fig. 3. Differences in coral and algae coverage at the five surveyed site inside the marine reserve at Cousin Island. Error bars denotes ±SE errors of the mean.

Coral recruitment was surveyed at each site by counting the number of recruits within a 1 m^2 quadrate. Three quadrates were randomly placed at each sub-location, resulting in 36–45 quadrates surveyed at each site. Coral recruits were classified as corals smaller than 5 cm diameter, which represent approximately 2 years growth (Wendling et al., 2003). For each quadrate, the substrate was meticulously examined and any present algae were carefully parted in order to locate small and concealed recruits. In total 207 quadrates were surveyed during the study.

Coral reef fish assemblage were surveyed using 20 m belt transect (English et al., 1997). A transect tape was laid parallel to shore by one diver while the surveyor swam in front, recording fish abundances 2.5 m from each side of the tape. Samoilys and Gribble (1997) recommend this technique of simultaneously counting fish while rolling out the transect tape, since it increases the accuracy of data collection. Fish were identified to family level and later categorised into functional groups (Froese and Pauly, 2014), which has been defined as a group of species that perform a similar function, regardless of their taxonomic affinities (Steneck and Dethier, 1994; Bellwood et al., 2004). At each site 12–15 belt transects were completed, covering in total 6900 m^2.

Surveying of key invertebrate grazers (*Diadema* sp.) were carried out along the same transects as the fish belt transects, where one observer searched and counted all individuals of sea urchins.

Finally, the small-scale complexity of the benthic substrate (rugosity) was measured using the 'chain-and-tape' method (Risk, 1972; Luckhurst and Luckhurst, 1978; McCormick, 1994).

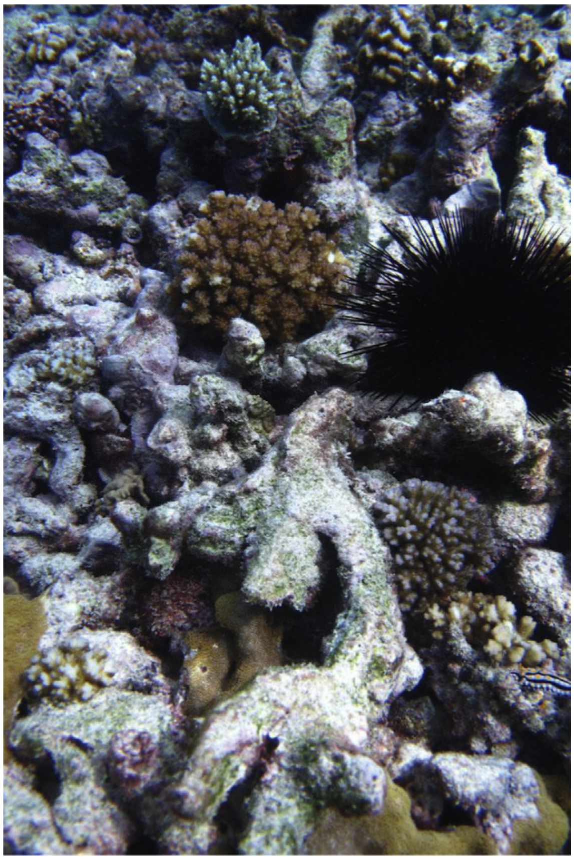

Fig. 4. Various types of coral recruits growing on top of stabilised coral rubble. Photo: April J. Burt.

2.3. Data analysis

One-way ANOVA was used to analyse differences between sites regarding benthic substrate, total fish density and composition, invertebrate density, coral recruitment, and rugosity. ANOVA assumptions were tested using Brown-Forsythe's test for homogeneity of variances. When necessary, transformations were applied (square, square root, log+1 transformations). To further investigate differences between sites, Tukey's unequal N HSD test was used as a post hoc test. When ANOVA assumptions were not fulfilled, non-parametric Krustal-Wallis ANOVA test was used and Krustal-Wallis multiple comparisons (2-tailed, p-value) test was carried out as a post hoc test. To examine the overall relationship and linkages between benthic substrate and coral reef fish assemblage, multiple regression and simple regression analyses were carried out.

All statistical analyses were performed using the software Statistica (version 5.5) and SPSS (version 20).

3. Results

3.1. Spatial variability in habitat characteristics

The results from the surveys showed high spatial variability in habitat characteristics, coral recruitment, fish density, key invertebrate grazers, and rugosity at the five investigate sites inside the marine reserve at Cousin Island (Tables 1–3).

Recorded coral coverage displayed significant differences between sites, covering in average 19.8% of the substrate, however coverage varied from 1.5% at Site 4–43.2% at Site 5 ($p < 0.001$; Fig. 3). Furthermore, coral recruitment was also unequal distributed at the surveyed sites, from 1.31 coral recruits/m^2 at Site 4, but was significantly higher at Site 2 with 6.98 coral recruits/m^2 and 3.72 coral recruits/m^2 at Site 5 ($p < 0.01$; Table 1a, Figs. 4, 5).

Total coverage of algae (macroalgae, turf algae, algae assemblage) was high at all sites and reached up to 97.8% at Site 4, with the lowest recorded cover at Site 1 and Site 5 (56.2% and 53.1% respectively). However, while algae coverage was the predominated substrate at all sites, the algae composition differed markedly between sites (Fig. 3). Cover of turf algae was significantly higher at Site 4 in comparison to all other sites and reached nearly 90.6%, while it varied in between 27.4 and 45.2% at the other sites ($p < 0.001$; Table 1a). In comparison, macroalgae reached 7.2% at Site 4 and varied between 20.8 and 22.8% at Site 1–3, but was not recorded at all at Site 5 ($p < 0.001$; Table 1a). Finally, algae assemblage reached the highest noted coverage of 21.7% at Site 3, but was significantly lower at Site 1 and 4, with 1.3% and 0% coverage, respectively ($p < 0.001$; Table 1a).

In addition, bare substrate (substrate with no recorded biotic coverage) was high at Site 1, reaching 24.75% and was significantly lower at Site 2, 4, and 5.

3.2. Abiotic benthic substrate and rugosity

The underlying abiotic substrate varied between the surveyed sites. Coverage of rock was highest at Site 3 (82.6%) and was significantly lower at Site 1 (57.8%) and Site 2 (55.4%) ($p < 0.01$; Table 1b). Coverage of rubble varied from 38.6% at Site 2–16.9% at Site 5 and 7.2% at Site 3 ($p < 0.01$; Table 1b). Sand was relatively uncommon, except at Site 1, which had a 21.8% coverage of sand, which was significantly higher than all other surveyed sites, which had a coverage of <5% ($p < 0.001$; Table 1b).

Rugosity was lowest at Site 4 in comparison to all other sites; however due to low number of replicates this result was not statistically significant.

3.3. Fish composition, functional groups, and key invertebrate grazers

Total fish density varied greatly between sites with 3.0 specimens/100 m^2 recorded at Site 4, which was lower in comparison to 19.9 specimens/100 m^2 at Site 1 and significantly lower in comparison to all other sites (39.6 at Site 5; 48.7 at Site 3; and 50.5 specimens/100 m^2 at Site 2) ($p < 0.001$; Table 3, Fig. 7).

Functional groups displayed high heterogenic differences between sites (Fig. 6). Numbers of piscivores were highest at Site 2 and reached 2.93 specimens/100 m^2 and were higher than numbers of piscivores at Site 1 and Site 4, which had 0.73 and 0.0 specimens/100 m^2 recorded respectively ($p < 0.001$; Table 2). In addition, invertebrate/piscivores and invertebrate feeding groups were not encountered at all at Site 4.

In comparison, herbivores were noted at all sites, but in various numbers, from 2.92 specimens/100 m^2 at Site 4, which was significantly lower in comparison to recorded numbers of herbivores at Site 2, 3, and 5 ($p < 0.001$; Table 2). Highest numbers of herbivores were encounter at Site 2 and Site 3, with 30.73 and 34.20 specimens/100 m^2 recorded respectively. Both sites had higher densities of herbivores than Site 1 and Site 4 ($p < 0.001$; Table 2).

Densities of corallivores were highest at Site 5 (5.50 specimens/100 m^2), which were significantly different from Site 2 and Site 4, which had 1.47 and 0.0 number of specimens/100 m^2 noted ($p < 0.001$; Table 2). Obligate corallivores, which are corallivore Chaetodontidae species which has a diet that is centred on coral up to 80% according to Cole et al. (2008), were most commonly found at Site 5, which also had the highest level of coral cover and were

Table 1a

Biotic substrate and coral recruitment and diversity at all surveyed sites at Cousin Island. Significant results from one-way ANOVA, Unequal N HSD, and non-parametric Kruskal–Wallis tests. Substrate presented in percentage and coral recruitment in recruits/m^2 with mean coverage and standard error in brackets.*p < 0.05; **p < 0.01; ***p < 0.001; ns (not significant).

Substrate	Site 1 (n = 15)	Site 2 (n = 15)	Site 3 (n = 15)	Site 4 (n = 12)	Site 5 (n = 12)	p-value
Coral	15.76 (3.54) Site 5: 0.017*	19.91 (4.51) Site 4: 0.025*	19.91 (6.14) Site 5: 0.034*	1.45 (0.42) Site 2: 0.025* Site 5: <0.001***	43.18 (3.02) Site 1: 0.017* Site 3: 0.034* Site 4: <0.001***	<0.001***[b]
Soft coral	0.00 (0.00) *ns*	0.53 (0.53) *ns*	0.00 (0.00) *ns*	0.00 (0.00) *ns*	0.00 (0.00) *ns*	*ns*[a,b]
Coralline algae	3.10 (1.42) *ns*	2.33 (0.83) *ns*	3.15 (1.04) *ns*	0.33 (0.19) *ns*	1.25 (0.43) *ns*	*ns*[a,b]
Turf algae	32.50 (5.16) Site 4: <0.001***	40.79 (5.73) Site 4: 0.001**	27.36 (4.47) Site 4: <0.001***	90.58 (3.19) Site 1: <0.001*** Site 2: 0.001** Site 3: <0.001*** Site 5: 0.026*	45.21 (3.15) Site 4: 0.026*	<0.001***[b]
Algal assemblage	1.33 (1.33) Site 3: <0.001***	8.82 (2.74) Site 4: 0.034*	21.67 (5.21) Site 1: <0.001*** Site 4: <0.001***	0.00 (0.00) Site 2: 0.034* Site 3: <0.001***	7.93 (2.61)	<0.001***[b]
Macroalgae	22.33 (5.63) Site 5: 0.008**	22.81 (5.41) Site 5: <0.001***	20.82 (3.65) Site 5: 0.003**	7.21 (3.15)	0.00 (0.00) Site 1: 0.008** Site 2: <0.001*** Site 3: <0.001***	<0.001***[b]
Sponge	0.23 (0.23) *ns*	0.07 (0.07) *ns*	0.33 (0.19) *ns*	0.42 (0.21) *ns*	1.66 (0.67) *ns*	*ns*[a,b]
Bare substrate	24.75 (5.71) Site 2: 0.041* Site 4: 0.001** Site 5: 0.014*	4.56 (2.86) Site 1: 0.041*	6.83 (2.90)	0.01 (0.01) Site 1: 0.001**	0.78 (0.46) Site 1: 0.014*	0.002**[b]
Coral recruits/m^2	2.89 (0.80)	6.98 (1.67) Site 4: 0.003**	2.05 (0.47)	1.31 (0.47) Site 2: 0.003** Site 5: 0.036*	3.72 (0.59) Site 4: 0.036*	0.01**[b]
Coral recruits diversity/m^2	1.67 (0.30)	2.42 (0.36) Site 4: 0.013*	1.58 (0.31)	0.97 (0.30) Site 2: 0.013* Site 5: 0.017*	2.44 (0.25) Site 4: 0.018*	<0.001***[b]

[a] One-way ANOVA.

[b] Krustal-Wallis ANOVA: Median test.

totally absent at Site 4, which had the lowest coverage of corals ($p < 0.001$; Table 2).

Planktivores were most frequently observed at Site 5 and were more than twice as numerous as on all other sites ($p < 0.001$; Table 2). Densities of omnivores were generally low, varying from 0.08 to 1.40 specimens/100 m^2 at all sites and differed significantly between Site 4, which had the lowest observed levels of omnivores to Site 2 and Site 3 ($p < 0.01$; Table 2).

Recorded numbers of key invertebrate grazers was highest at Site 5 (6.6 specimens/100 m^2) and were significantly lower at Site 1 (2.0 specimens/100 m^2) ($p < 0.01$; Table 3).

3.4. Interactions between habitat structure and fish composition

The final multiple linear regression model showed that coral cover was significantly correlated with the following predictors: fish density, sea urchins, and macroalgae (the latter displayed a negative correlation) ($R^2 = 0.36$; intercept $p < 0.01$).

Regarding functional feeding groups, planktivores, obligate corallivores, and invertivores correlated with coral coverage ($R^2 = 0.37$; intercept $p < 0.05$) and when separated into fish family groups surgeonfish, triggerfish, sweetlips, and parrotfish displayed similar results, although not significant ($R^2 = 0.35$; intercept $p = 0.07$).

The lowest recorded numbers of coral recruits were at the same site as the lowest observed coral coverage (Site 4), however there was no significant correlation between coral coverage and coral recruits. In contrast, numbers of coral recruits were strongly correlated with coral recruits diversity ($R^2 = 0.63$, $p < 0001$).

4. Discussion

4.1. High spatial variability in coral habitat quality and fish composition between sites

This study investigated coral reef habitat and fish assemblage at five different sites within a small (approximately 1.2 km^2), but well protected no-take MPA (Jennings et al., 1996) that was severely affected by the worldwide coral mass mortality event that occurred 1998 (Bigot et al., 2000; Wilkinson, 2004; Graham et al., 2006; Wilson et al., 2012). Coral reefs at the inner granitic islands at Seychelles were heavily damaged and average live coral cover fell from 27% to 3% after the bleaching event 1998 with a reduction of up to 90% of live coral coverage (Graham et al., 2007). While previous studies have reported little recovery inside MPAs at the inner granitic islands at the Seychelles (Ledlie et al., 2007; Wilson et al., 2012; Harris et al., 2014), the results from our study demonstrated high heterogenic variability in habitat quality between sites, including coral coverage and coral recruitment, as well as large differences in fish density and composition of functional groups. This type of information could be important for both a broader scientific understanding of coral reef recovery after a large scale disturbance, as well as for marine management decisions, e.g. in support of expansions of the current marine reserve or future designs of MPA networks. Furthermore, in areas where MPAs are being managed by local communities or NGOs, it is of great importance to demonstrate effects of reserves in order to maintain local support (Beger et al., 2004; McClanahan and Graham, 2005; Mora and Sale, 2011).

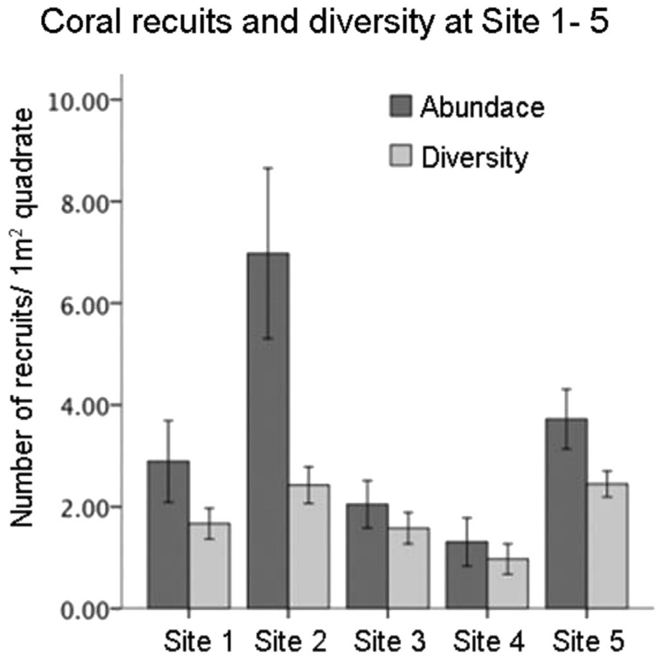

Fig. 5. Differences in coral recruitment and coral diversity at the five surveyed site inside the marine reserve at Cousin Island. Error bars denotes ±SE errors of the mean.

4.2. *Variability in coral coverage and recruitment*

Results from this study showed that coral cover varied greatly between sites, with the lowest coverage of 1.5% recorded at Site 4 and in average 43.2% coral cover at the nearby Site 5, while the remaining three sites had a coral coverage of 15.7–19.9%. Although most of the reefs around Cousin Island were dominated by various types of algae, patchy coral recovery, which has been documented in the region (Baker et al., 2008; Chong-Seng et al., 2012; Sheppard et al., 2012), seem to be occurring around Cousin Island. Coral recovery, defined as a return to coral dominance (Connell, 1997) seemed to occur at one site (Site 4), which displayed a coral coverage that was similar to pre-1998 levels in the area. In addition, coral coverage was in general higher than previous reported (Ledlie et al., 2007; Wilson et al., 2012; Harris et al., 2014).

Coral recruitment and survival have been suggested to be a vital part of coral reef recovery (Miller et al., 2000; Fox, 2004; Graham et al., 2011). In this study, there were no significant correlation between coral recruitment and coral coverage, a result which may depend on co-linearity between available substrate for coral recruitment settlement and live benthic coverage (Harris et al., 2014). However, two of the surveyed sites were located fairly close to each other (Site 4 and Site 5), but displayed large differences in both coral coverage and recruitment, a result which may indicate that coral settlement and survival may operate on small scales (Green and Edmunds, 2011; O'Leary and Potts, 2011; Sawall et al., 2013). Indeed, recent studies have shown that coral larvae may selectively settle at beneficial habitats and avoid degenerated reefs (Dixson et al., 2014). The highest numbers of coral recruits were found in areas where coverage of coral rubble had stabilised and lowest at sites with high algae coverage, a result that has been seen by other authors (Kuffner et al., 2006; Ritson-Williams et al., 2009; but see Chong-Seng et al., 2012). It is possible that as coral rubble continue to stabilise around the island, coral recruitment may be further enhanced, however recruitment success and survivorship may also depend on other stochastical processes, such as oceanographic factors and future disturbances, which are poorly understood and hard to predict (Connell et al., 1997; Hughes et al., 2012; Freeman et al., 2013). In addition, numbers of coral recruits and coral diversity were significantly correlated, which may indicate that coral recruitment most likely were not due to one single episode of recruitment success (Green and Edmunds, 2011; Sawall et al., 2013; Harris et al., 2014).

Unfortunately, baseline survey data from before 1998 including all surveyed sites have not been collected, however some of the investigated sites have shown increased coral coverage during recent years (Montoya-Maya et al., 2015). Furthermore, while some larger coral colonies (e.g. massive *Porites* sp. >2 m^2 in diameters) were encountered inside the marine reserve, a vast majority of the recorded and observed coral colonies were moderately small in sizes, in average 30–40 cm in diameter (*pers obs*). Although coral age and size relationship may vary between species (Soong, 1993; Bak and Meesters, 1999), it is not unreasonable to assume that due to the small size of encountered corals colonies, these were corals that have successfully recruited and survived after the 1998 coral mass mortality event. Average recovery of coral reefs in the region has been estimated to increase with 1% coral cover per year, but has shown to vary (Wilson et al., 2012), which is not uncommon, since coral reefs often display a dynamic response to disturbances (Graham et al., 2006; Polidoro and Carpenter, 2013; Dixson et al., 2014).

4.3. *Heterogenic differences in fish community and linkage to habitat*

Fish density and assemblage showed a high variation and

Table 1b

Abiotic substrate and rugosity at all surveyed sites at Cousin Island. Significant results from one-way ANOVA, Unequal N HSD, and non-parametric Kruskal–Wallis tests. Substrate presented in percentage with mean coverage and standard error in brackets.*p < 0.05; **p < 0.01; ***p < 0.001; ns (not significant).

Substrate	Site 1 (n = 15)	Site 2 (n = 15)	Site 3 (n = 15)	Site 4 (n = 12)	Site 5 (n = 12)	p-Value
Rock	57.87 (5.68) Site 3: 0.012*	55.40 (8.66) Site 3: 0.027*	82.57 (6.95) Site 1: 0.012* Site 2: 0.027*	78.94 (6.36)	82.68 (3.85)	0.002**[a]
Sand	21.83 (5.70) Site 4: 0.001** Site 5: 0.001**	5.93 (3.00)	3.56 (1.56)	0.00 (0.00) Site 1: 0.001**	0.00 (0.00) Site 1: 0.001**	<0.001***[b]
Rubble	20.14 (6.70)	38.60 (8.33) Site 3: 0.006** Site 5: 0.047*	7.20 (2.91) Site 2: 0.005**	21.06 (6.36)	16.91 (3.95) Site 2: 0.047*	0.007**[b]
Dead coral	0.00 (0.00) *ns*	0.07 (0.07) *ns*	0.00 (0.00) *ns*	0.00 (0.00) 0.41 (0.41) *ns*	*ns*	*ns*[a, b]
Rugosity[1] [1] n = 3	1.50 (0.17) *ns*	1.45 (0.15) *ns*	1.48 (0.07) *ns*	1.08 (0.04) *ns*	1.45 (0.21) *ns*	*ns*[a, b]

[a] One-way ANOVA.

[b] Krustal-Wallis ANOVA: Median test.

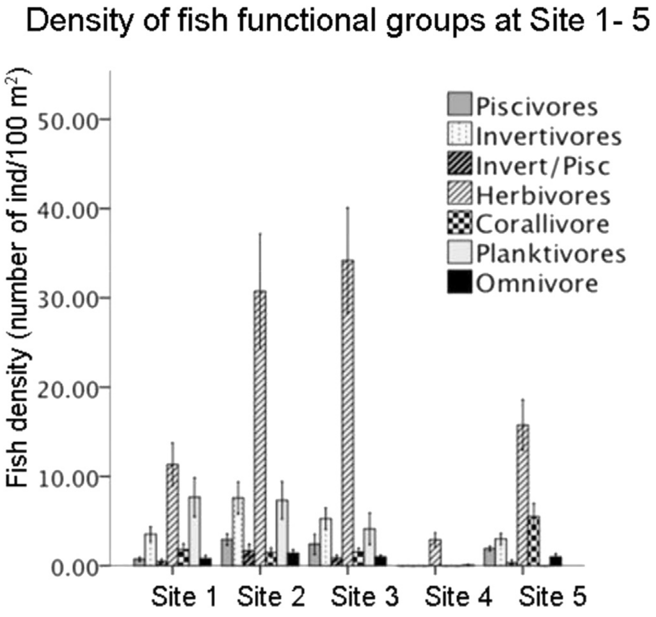

Fig. 6. Differences in fish density of functional groups at the five surveyed site inside the marine reserve at Cousin Island. Error bars denotes ±SE errors of the mean.

heterogenic pattern between sites, with the highest total abundances recorded at Site 2 (50.5 specimens/100 m^2), which was more than 15 times as many specimens than at Site 4, which only had 3.0 individuals noted per 100 m^2. Large differences in functional groups were recorded, with high numbers of piscivores and obligate corallivores at Site 5, which also had the highest level of coral coverage. Both functional fish groups were completely absent at Site 4, which only had a 1.5% coral coverage. Herbivores, which plays an important role for coral reef recovery (Bellwood et al., 2006; Hughes et al., 2007; Mumby and Harborne, 2010), were present at all sites, but were ten times as numerous at Site 2, 3, and 5 in comparison to Site 4. In addition, planktivores were more than twice as numerous as at Site 5 in comparison to all other sites.

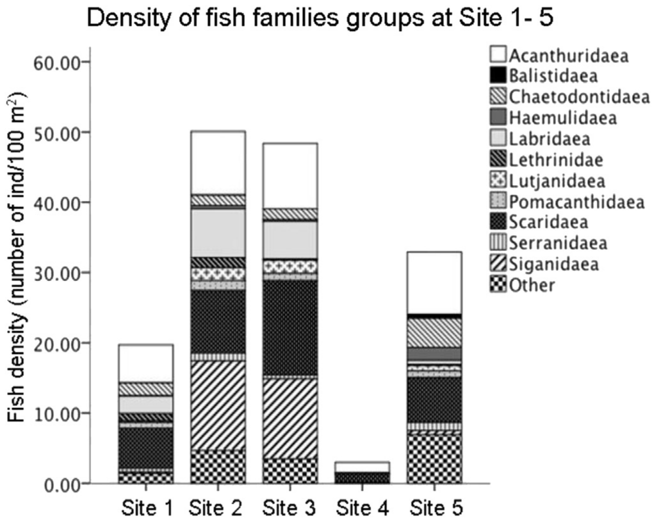

Fig. 7. Differences in fish density of family level at the five surveyed site inside the marine reserve at Cousin Island. Error bars denotes ±SE errors of the mean.

Table 2
Fish functional feeding categories at all surveyed sites at Cousin Island. Significant results from one-way ANOVA, Unequal N HSD, and non-parametric Kruskal–Wallis tests. Mean fish densities presented in species/100 m^2 and standard error in brackets.*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ns (not significant).

Feeding category	Site 1 (n = 15)	Site 2 (n = 15)	Site 3 (n = 15)	Site 4 (n = 12)	Site 5 (n = 12)	p-value
Piscivores	0.73 (0.25) Site 2: 0.011*	2.93 (0.64) Site 1: 0.011* Site 4: <0.001***	2.40 (1.15)	0.00 (0.00) Site 2: <0.001*** Site 5: <0.001***	1.92 (0.29) Site 4: <0.001***	<0.001***[b]
Invertivores	3.53 (0.85) Site 4: 0.007**	7.60 (1.80) Site 4: <0.001***	5.27 (1.20) Site 4: <0.001***	0.00 (0.00) Site 1: 0.007** Site 2: <0.001*** Site 3: <0.001*** Site 5: 0.015*	3.00 (0.66) Site 4: 0.015*	0.006**[b]
Invert/Piscivores	0.93 (0.57) *ns*	0.40 (0.19) *ns*	0.40 (0.16) *ns*	0.00 (0.00) *ns*	1.17 (0.66) *ns*	*ns*[a,b]
Herbivores	11.33 (2.42) Site 2: 0.045* Site 3: 0.013*	30.73 (6.46) Site 1: 0.044* Site 4: <0.001***	34.20 (5.90) Site 1: 0.013* Site 4: <0.001***	2.92 (0.80) Site 2: <0.001*** Site 3: <0.001*** Site 5: 0.027*	15.75 (2.83) Site 4: 0.027*	<0.001***[b]
Corallivores	1.80 (0.66)	1.47 (0.57) Site 5: 0.042*	1.53 (0.45)	0.00 (0.00) Site 5: <0.001***	5.50 (1.49) Site 2: 0.042* Site 4: <0.001***	<0.001***[b]
- *Obligate corallivores*	0.87 (0.24)	1.07 (0.54)	1.13 (0.42)	0.00 (0.00) Site 5: <0.001***	4.25 (1.02) Site 4: 0.0021**	<0.001***[b]
- *Coral/herbivores*	0.00 (0.00) *ns*	0.00 (0.00) *ns*	0.00 (0.00) *ns*	0.00 (0.00) *ns*	0.08 (0.08) *ns*	*ns*[a,b]
- *Coral/invertivores*	0.93 (0.57) *ns*	0.40 (0.19) *ns*	0.40 (0.16) *ns*	0.00 (0.00) *ns*	1.17 (0.66) *ns*	*ns*[a,b]
Planktivores	1.33 (0.99) Site 5: 0.002**	4.67 (2.28) Site 5: 0.011*	3.47 (1.35) Site 5: 0.026*	0.00 (0.00) Site 5: <0.001***	12.08 (2.13) Site 1: 0.002** Site 2: 0.011* Site 3: 0.026* Site 4: <0.001***	<0.001***[b]
Omnivores	0.80 (0.35)	1.40 (0.41) Site 4: 0.011*	1.00 (0.20) Site 4: 0.036*	0.08 (0.08) Site 2: 0.011* Site 3: 0.036*	1.00 (0.35)	0.008**[a]

[a] One-way ANOVA.
[b] Krustal-Wallis ANOVA: Median test.

Table 3

Total fish density, fish families, and key invertebrate grazers at all surveyed sites at Cousin Island. Significant results from one-way ANOVA, Unequal N HSD, and non-parametric Kruskal–Wallis tests. Mean abundance presented in species/100 m^2 and standard error in brackets.*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ns (not significant).

Category	Site 1 (n = 15)	Site 2 (n = 15)	Site 3 (n = 15)	Site 4 (n = 12)	Site 5 (n = 12)	p-value
Total fish density	19.87 (3.84) Site 2: 0.012* Site 3: 0.032*	50.47 (6.91) Site 1: 0.012* Site 4: <0.001***	48.73 (7.11) Site 1: 0.032* Site 4: <0.001***	3.00 (0.80) Site 2: <0.001*** Site 3: <0.001*** Site 5: <0.001***	39.58 (3.94) Site 4: <0.001***	<0.001***[b]
Acanthuridaea (Surgeonfish)	5.40 (1.38)	9.07 (1.36) Site 4: <0.001***	9.33 (2.37) Site 4: 0.008**	1.58 (0.67) Site 2: <0.001*** Site 3: 0.008** Site 5: 0.002**	8.83 (1.57) Site 4: 0.002**	0.012*[b]
Balistidaea (Triggerfish)	0.07 (0.07) *ns*	0.00 (0.00) *ns*	0.00 (0.00) *ns*	0.00 (0.00) *ns*	0.58 (0.23) *ns*	*ns*[a,b]
Chaetodontidaea (Butterflyfish)	1.80 (0.66) Site 4: 0.044*	1.47 (0.57)	1.53 (0.45)	0.00 (0.00) Site 1: 0.04* Site 5 < 0.001***	4.17 (0.93) Site 4: <0.001***	0.004**[b]
Diodontidae (Porcupinesfish)	0.07 (0.07) *ns*	0.00 (0.00) *ns*	0.00 (0.00) *ns*	0.00 (0.00) *ns*	0.00 (0.00) *ns*	*ns*[a,b]
Haemulidaea (Sweetlips)	0.07 (0.07) Site 5: 0.005**	0.47 (0.19)	0.27 (0.21) Site 5: 0.016*	0.00 (0.00) Site 5: 0.003**	1.83 (0.56) Site 1: 0.005** Site 3: 0.016* Site 4: 0.003**	<0.001***[b]
Holocentridaea (Soldierfish)	1.33 (0.99) *ns*	4.67 (2.28) *ns*	3.47 (1.35) *ns*	0.00 (0.00) *ns*	6.92 (2.54) *ns*	*ns*[a,b]
Labridaea (Wrasse)	2.47 (0.70)	6.93 (1.07) Site 4: <0.001*** Site 5: <0.001***	5.33 (0.91) Site 4: <0.001*** Site 5: 0.002**	0.00 (0.00) Site 2: <0.001*** Site 3: <0.001***	0.58 (0.36) Site 2: <0.001*** Site 3: 0.002**	<0.001***[b]
Lethrinidae (Emperors	1.07 (0.40)	1.47 (0.70) Site 4: 0.029*	0.20 (0.14)	0.00 (0.00) Site 2: 0.029	0.17 (0.11)	0.006**[b]
Lutjanidaea (Snappers)	0.20 (0.20) Site 2: 0.030*	1.80 (0.61) Site 1: 0.030* Site 4: 0.027*	1.87 (1.09)	0.00 (0.00) Site 2: 0.027*	0.75 (0.25)	0.001**[b]
Pomacanthidaea (Angelfish)	0.80 (0.35)	1.40 (0.41) Site 4: 0.010**	1.00 (0.20) Site 4: 0.033*	0.08 (0.08) Site 2: 0.010** Site 3: 0.033*	0.92 (0.29)	0.007**[a]
Scaridaea (Parrotfish)	5.73 (1.73) Site 3: 0.011*	8.93 (1.69) Site 4: 0.004**	13.47 (1.79) Site 1: 0.011* Site 4: <0.001***	1.33 (0.64) Site 2: 0.004** Site 3: <0.001***	6.42 (1.85)	<0.001***[b]
Serranidaea (Groupers)	0.53 (0.19)	1.13 (0.22) Site 4: 0.003**	0.53 (0.19)	0.00 (0.00) Site 2: 0.003** Site 5: 0.004**	1.17 (0.24) Site 4: 0.004**	<0.001***[b]
Siganidaea (Rabbitfish)	0.20 (0.14) Site 3: 0.005**	12.73 (5.79) Site 4: 0.024*	11.40 (4.76) Site 1: 0.005** Site 4: 0.002**	0.00 (0.00) Site 2: 0.024* Site 3: 0.002**	0.58 (0.31)	<0.001***[b]
Tetradontidaea (Pufferfish)	0.00 (0.00) *ns*	0.00 (0.00) *ns*	0.00 (0.00) *ns*	0.00 (0.00) *ns*	0.00 (0.00) *ns*	*ns*[a,b]
Diadema sp. (Sea urchins)	0.20 (0.07) Site 5: 0.001**	0.44 (0.13)	0.31 (0.08)	0.39 (0.06)	0.66 (0.04) Site 1: 0.001**	<0.001***[b]

[a] One-way ANOVA.

[b] Krustal-Wallis ANOVA: Median test.

The results showed that coral cover was positively correlated with total fish density as well as with densities of sea urchins, and negatively correlated with macroalgae. This result is in agreement with other studies that have shown that coral reef fish assemblages often have been linked to coral coverage and complex three dimensional structures (Syms and Jones, 1999, Graham et al., 2006; reviewed by Pratchett et al., 2011). Furthermore, planktivores, invertivores, and obligate corallivores were directly correlated with coral coverage. Fish use coral reef habitats for food, protection, and shelter (Cox, 1994; Bozec et al., 2005; Pratchett et al., 2008) and especially obligate corallivores have shown to be directly linked to live coral coverage (Harmelin-Vivien, 1989; Pratchett, 2005), however feeding specialisation has been shown to vary widely within species of Chaetodontidaea (Sano, 2004, Berumen et al., 2005; Pratchett and Berumen, 2008).

5. Conclusions

In conclusion this study showed that coral reef habitat and associated fish assemblages may display high spatial variability and heterogenic differences within a small marine reserve and indicated that potential recovery may occur in a patchy manner (Sheppard et al., 2012; Baker et al., 2008). Since one of the most important criteria for MPAs to function has been suggested to be solid political and public support (McClanahan et al., 1997; Gell and Roberts, 2003; Bennett and Dearden, 2014), this type of collected data and results may be useful to build local support and for future management decisions regarding the MPA.

Coral recruitment and coral coverage were higher than previously reported inside the MPA at Cousin Island (Ledlie et al., 2007; Wilson et al., 2012; Harris et al., 2014) and there was a direct linkage between coral habitat and fish composition, a result which is in concordance with other authors (Rodwell et al., 2003; Ruppert et al., 2013; but see Bellwood et al., 2006). While marine reserves have shown to be beneficial in terms of protecting diversity, habitat quality, and fish biomass (Alcala and Russ, 2006; Samoilys et al., 2007; Molloy et al., 2009; Noble et al., 2013; Jörgensen et al., 2015) they cannot protect against all types of disturbances (McClanahan et al., 2001; Jones et al., 2004; Mumby et al., 2011; Selig et al., 2012; Halpern et al., 2013) and therefore investigating and assessing factors that promote coral reef recovery processes should be considered imperative for future marine ecology research.

Authors' contributions

Conceived and designed the study: TLJ, AJB. Collected data: AJB, ECM. Analysed the data: TLJ. Wrote the manuscript, prepared figures, and tables: TLJ, AJB, and ECM.

All authors contributed extensively to the work presented in this paper.

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References

Alcala, A.C., Russ, G.R., 2006. No-take marine reserves and reef fisheries management in the Philippines: a new people power revolution. Ambio 35, 245–254.

Bak, R.P., Meesters, E.H., 1999. Population structure as a response of coral communities to global change. Am. Zoologist 39 (1), 56–65.

Baker, A.C., Glynn, P.W., Riegl, B., 2008. Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. Estuar. Coast. Shelf Sci. 80 (4), 435–471.

Beger, M., Harborne, A.R., Dacles, T.P., Solandt, J.L., Ledesma, G.L., 2004. A framework of lessons learned from community-based marine reserves and its effectiveness in guiding a new coastal management initiative in the Philippines. Environ. Manag. 34, 786–801.

Bellwood, D.R., Hoey, A.S., Ackerman, J.L., Depczynski, M., 2006. Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. Glob. Change Biol. 12 (9), 1587–1594.

Bellwood, D.R., Hughes, T.P., Folke, C., Nyström, M., 2004. Confronting the coral reef crisis. Nature 429 (6994), 827–833.

Bennett, N.J., Dearden, P., 2014. Why local people do not support conservation: community perceptions of marine protected area livelihood impacts, governance and management in Thailand. Mar. Policy 44, 107–116.

Berkes, F., Hughes, T.P., Steneck, R.S., Wilson, J.A., Bellwood, D.R., Crona, B., Folke, C., Gunderson, L.H., Leslie, H.M., Norberg, J., Nyström, M., Olsson, P., Österblom, H., Scheffer, M., Worm, B., 2006. Globalization, roving bandits, and marine resources. Science 311 (5767), 1557–1558.

Berumen, M.L., Pratchett, M.S., McCormick, M.I., 2005. Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae). Mar. Ecol. Prog. Ser. 287, 217–227.

Bigot, L., Charpy, L., Maharavo, J., Rabi, F.A., Paupiah, N., Aumeeruddy, R., Villedieu, C., Lieutaud, A., 2000. Status of coral reefs of the southern Indian Ocean: the Indian ocean commission node for Comoros, Madagascar, Mauritius, Réunion and Seychelles. In: Wilkinson, C. (Ed.), Status of Coral Reefs of the World, pp. 77–94.

Birkeland, C., 1997. Implications for resource management (Chapter 14). In: Birkeland, C. (Ed.), Life and Death of Coral Reefs. Chapman and Hall. International Thomson Publishing, New York, U. S. A, pp. 298–353, 1997. 536 pp.

Bozec, Y.M., Dolédec, S., Kulbicki, M., 2005. An analysis of fish-habitat associations on disturbed coral reefs: chaetodontid fishes in New Caledonia. J. Fish Biol. 66 (4), 966–982.

Bruno, J.F., Selig, E.R., 2007. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. PLoS One 2 (8), e711.

Burke, L., Reytar, K., Spalding, M., Perry, A., 2011. Reefs at Risk Revisited. World Resources Institute, Washington, DC.

Carpenter, K.E., Abrar, M., Aeby, G., Aronson, R.B., Banks, S., Bruckner, A., Chiriboga, A., Cortés, J.J., Delbeek, C., DeVantier, L., Edgar, G.J., Edwards, A.J., Fenner, D., Guzmán, H.M., Hoeksema, B.W., Hodgson, G., Johan, O., Licuanan, W.Y., Livingstone, S.R., Lovell, E.R., Moore, J.A., Obura, D.O., Ochavillo, D., Polidoro, B.A., Precht, W.F., Quibilan, M.C., Reboton, C., Richards, Z.T., Rogers, A.D., Sanciangco, J., Sheppard, A., Sheppard, C., Smith, J., Stuart, S., Turak, E., Veron, J.E.N., Wallace, C., Weil, E., Wood, E., 2008. One- third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321 (5888), 560–563.

Chong-Seng, K.M., Mannering, T.D., Pratchett, M.S., Bellwood, D.R., Graham, N.A.J., 2012. The influence of coral reef benthic condition on associated fish assemblages. PloS one 7 (8), e42167.

Cinner, J.E., McClanahan, T.R., Daw, T.M., Graham, N.A.J., Maina, J., Wilson, S.K., Hughes, T.P., 2009. Linking social and ecological systems to sustain coral reef fisheries. Curr. Biol. 19 (3), 206–212.

Cole, A.J., Pratchett, M.S., Jones, G.P., 2008. Diversity and functional importance of coral – feeding fishes on tropical coral reefs. Fish Fish. 9 (3), 286–307.

Connell, J.H., 1997. Disturbance and recovery of coral assemblages. Coral Reefs 16 (sp1), 101–113.

Connell, J.H., Hughes, T.P., Wallace, C.C., 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol. Monogr. 67 (4), 461–488.

Cox, E.F., 1994. Resource use by corallivorous butterflyfishes (family Chaetodontidae) in Hawaii. Bull. Mar. Sci. 54 (2), 535–545.

De'ath, G., Fabricius, K.E., Sweatman, H., Puotinen, M., 2012. The 27–year decline of coral cover on the Great Barrier Reef and its causes. Proc. Natl. Acad. Sci. 109 (44), 17995–17999.

Dixson, D.L., Abrego, D., Hay, M.E., 2014. Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery. Science 345 (6199), 892–897.

English, S., Wilkinson, C., Baker, V., 1997. Survey Manual for Tropical Marine Resources, second ed. Australian Institute of Marine Science, Townsville, p. 390.

Fabricius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar. Pollut. Bull. 50 (2), 125–146.

Fox, H.E., 2004. Coral recruitment in blasted and unblasted sites in Indonesia: assessing rehabilitation potential. Mar. Ecol. Prog. Ser. 269, 131–139.

Francis, J., Nilsson, A., Waruinge, D., 2002. Marine protected areas in the Eastern African region: How successful are they? Ambio 31 (7–8), 503–511.

Freeman, L.A., Kleypas, J.A., Miller, A.J., 2013. Coral reef habitat response to climate change scenarios. PloS one 8 (12), e82404.

Froese, R., Pauly, D. (Eds.), 2014. FishBase. World Wide Web electronic publication. www.fishbase.org (11/2014).

Gamfeldt, L., Lefcheck, J.S., Byrnes, J.E., Cardinale, B.J., Duffy, J.E., Griffin, J.N., 2014. Marine biodiversity and ecosystem functioning: what's known and what's next? PeerJ Prepr. 2.

Gell, F.R., Roberts, C.M., 2003. Benefits beyond boundaries: the fishery effects of marine reserves. Trends Ecol. Evol. 18 (9), 448–455.

Goreau, T., McClanahan, T., Hayes, R., Strong, A., 2000. Conservation of coral reefs after the 1998 global bleaching event. Conserv. Biol. 14 (1), 5–15.

Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Bijoux, J.P., Robinson, J., 2006. Dynamic fragility of oceanic coral reef ecosystems. Proc. Natl. Acad. Sci. U. S. A. 103 (22), 8425–8429.

Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V., Robinson, J., Bijoux, J.P., Daw, T.M., 2007. Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. Conserv. Biol. 21 (5), 1291–1300.

Graham, N.A.J., Nash, K.L., Kool, J., 2011. Coral reef recovery dynamics in a changing world. Coral Reefs 30, 283–294.

Green, D.H., Edmunds, P.J., 2011. Spatio-temporal variability of coral recruitment on shallow reefs in St. John, US Virgin Islands. J. Exp. Mar. Biol. Ecol. 397 (2), 220–229.

Halpern, B.S., Selkoe, K.A., White, C., Albert, S., Aswani, S., Lauer, M., 2013. Marine protected areas and resilience to sedimentation in the Solomon Islands. Coral Reefs 32 (1), 61–69.

Halpern, B.S., Warner, R.R., 2002. Marine reserves have rapid and lasting effects. Ecol. Lett. 5 (3), 361–366.

Harmelin-Vivien, M.L., 1989. Implications of feeding specialization on the recruitment processes and community structure of butterflyfishes. Environ. Biol. fishes 25 (1–3), 101–110.

Harris, A., Wilson, S., Graham, N., Sheppard, C., 2014. Scleractinian coral communities of the inner Seychelles 10 years after the 1998 mortality event. Aquatic Conservation: Mar. Freshw. Ecosyst. http://dx.doi.org/10.1002/aqc.2464.

Hoegh-Guldberg, O., 2012. The adaptation of coral reefs to climate change: is the Red Queen being outpaced? Sci. Mar. 76 (2), 403–408.

Hughes, T.P., Baird, A.H., Dinsdale, E.A., Moltschaniwskyj, N.A., Pratchett, M.S., Tanner, J.E., Willis, B.L., 2012. Assembly rules of reef corals are flexible along a steep climatic gradient. Curr. Biol. 22 (8), 736–741.

Hughes, T.P., Carpenter, S., Rockström, J., Scheffer, M., Walker, B., 2013. Multiscale regime shifts and planetary boundaries. Trends Ecol. Evol. 28 (7), 389–395.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr. Biol. 17 (4), 360–365.

Jennings, S., 1998. Cousin Island, Seychelles: a small, effective and internationally managed marine reserve. Coral Reefs 17 (2), 190.

Jennings, S., Marshall, S.S., Polunin, N.V.C., 1996. Seychelles' marine protected areas: comparative structure and status of reef fish communities. Biol. Conserv. 75, 201–209.

Jones, G.P., McCormick, M.I., Srinivasan, M., Eagle, J.V., 2004. Coral decline threatens fish biodiversity in marine reserves. Proc. Natl. Acad. Sci. 101 (21), 8251–8253.

Jörgensen, T.L., Gullström, M., Faxneld, S., Uychiaoco, A., Öhman, M.C., 2015. Coral Reef Fish Assemblages and Habitat Structure in Two Community-based Marine Protected Areas and Adjacent Fishing Grounds in the Northern Philippines in preparation.

Knowlton, N., Jackson, J.B.C., 2008. Shifting baselines, local impacts, and global change on coral reefs. PLoS Biol. 6 (2), e54.

Kuffner, I.B., Walters, L.J., Becerro, M.A., Paul, V.J., Ritson-Williams, R., Beach, K.S., 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. Mar. Ecol. Prog. Ser. 323, 107–117.

Ledlie, M.H., Graham, N.A.J., Bythell, J.C., Wilson, S.K., Jennings, S., Polunin, N.V.C., Hardcastle, J., 2007. Phase shifts and the role of herbivory in the resilience of coral reefs. Coral Reefs 26 (3), 641–653.

Leujak, W., Ormond, R., 2007. Comparative accuracy and efficiency of six coral community survey methods. J. Exp. Mar. Biol. Ecol. 351, 168–187.

Luckhurst, B.E., Luckhurst, K., 1978. Analysis of the influence of substrate variables on coral reef fish communities. Mar. Biol. 49 (4), 317–323.

McCauley, D.J., McLean, K.A., Bauer, J., Young, H.S., Micheli, F., 2012. Evaluating the performance of methods for estimating the abundance of rapidly declining coastal shark populations. Ecol. Appl. 22 (2), 385–392.

McClanahan, T.R., 1997. Primary succession of coral-reef algae: differing patterns of fished versus unfished reefs. J. Exp. Mar. Biol. Ecol. 218 (1), 77–102.

McClanahan, T.R., Glaesel, H., Rubens, J., Kiambo, R., 1997. The effects of traditional fisheries management on fisheries yields and the coral-reef ecosystems of southern Kenya. Environ. Conserv. 24 (02), 105–120.

McClanahan, T.R., Graham, N.A.J., 2005. Recovery trajectories of coral reef fish assemblages within Kenyan marine protected areas. Mar. Ecol. Prog. Ser. 294, 241–248.

McClanahan, T.R., Graham, N.A.J., Wilson, S.K., Letourneur, Y., Fisher, R., 2009. Effects of fisheries closure size, age, and history of compliance on coral reef fish communities in the western Indian Ocean. Mar. Ecol. Prog. Ser. 396, 99–109.

McClanahan, T.R., Marnane, M.J., Cinner, J.E., Kiene, W.E., 2006. A comparison of marine protected areas and alternative approaches to coral-reef management. Curr. Biol. 16 (14), 1408–1413.

McClanahan, T., Muthiga, N., Mangi, S., 2001. Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. Coral Reefs 19 (4), 380–391.

McCormick, M.I., 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. Mar. Ecol. Prog. Ser. Oldend. 112 (1), 87–96.

Miller, M.W., Weil, E., Szmant, A.M., 2000. Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayne National Park, USA. Coral Reefs 19 (2), 115–123.

Molloy, P.P., McLean, I.B., Côté, I.M., 2009. Effects of marine reserve age on fish populations: a global meta-analysis. J. Appl. Ecol. 46, 743–751.

Montoya-Maya, P.H., Smit, K.P., Burt, A.J., Frias-Torres, S., 2015. Coral Transplantation on Damaged Reefs Enhances Coral Settlement and Recruitment in Seychelles, Indian Ocean in preparation.

Mora, C., Sale, P.F., 2011. Ongoing global biodiversity loss and the need to move beyond protected areas: a review of the technical and practical shortcomings of protected areas on land and sea. Mar. Ecol. Prog. Ser. 434, 251–266.

Mumby, P.J., Elliott, I.A., Eakin, C.M., Skirving, W., Paris, C.B., Edwards, H.J., Enríquez, S., Iglesias-Prieto, R., Cherubin, L.M., Stevens, J.R., 2011. Reserve design for uncertain responses of coral reefs to climate change. Ecol. Lett. 14 (2), 132–140.

Mumby, P.J., Harborne, A.R., 2010. Marine reserves enhance the recovery of corals on Caribbean reefs. PLoS One 5 (1), e8657.

Musick, J.A., 1999. Criteria to define extinction risk in marine fishes: the American fisheries society initiative. Fisheries 24 (12), 6–14.

Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. Nature 423 (6937), 280–283.

Nadon, M.O., Baum, J.K., Williams, I.D., McPherson, J.M., Zgliczynski, B.J., Richards, B.L., Schroeder, R.E., Brainard, R.E., 2012. Re–creating missing population baselines for Pacific reef Sharks. Conserv. Biol. 26 (3), 493–503.

Noble, M.M., van Laake, G., Berumen, M.L., Fulton, C.J., 2013. Community change within a Caribbean coral reef Marine Protected Area following two decades of local management. PloS one 8, e54069.

Norström, A.V., Nyström, M., Lokrantz, J., Folke, C., 2009. Alternative states on coral reefs: beyond coral-macroalgal phase shifts. Mar. Ecol. Prog. Ser. 376, 295–306.

O'Leary, J.K., Potts, D.C., 2011. Using hierarchical sampling to understand scales of spatial variation in early coral recruitment. Coral Reefs 30, 1013–1023.

Polidoro, B., Carpenter, K., 2013. Dynamics of coral reef recovery. Science 340 (6128), 34–35.

Pratchett, M.S., Hoey, A.S., Wilson, S.K., Messmer, V., Graham, N.A., 2011. Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. Diversity 3 (3), 424–452.

Pratchett, M.S., Berumen, M.L., 2008. Interspecific variation in distributions and diets of coral reef butterflyfishes (Teleostei: Chaetodontidae). J. Fish Biol. 73 (7), 1730–1747.

Pratchett, M.S., Munday, P.L., Wilson, S.K., 2008. Effects of climate-induced coral bleaching on coral-reef fishes. Ecol. Econ. consequences. Oceanogr. Mar. Biol. An Annu. Rev. 46, 251–296.

Pratchett, M.S., 2005. Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef. Mar. Biol. 148 (2), 373–382.

Risk, M.J., 1972. Fish diversity on a coral reef in the Virgin Islands. Smithson. Atoll Res. Bull. 153, 1–6.

Ritson-Williams, R., Arnold, S.N., Fogarty, N.D., Steneck, R.S., Vermeij, M.J., Paul, V.J., 2009. New perspectives on ecological mechanisms affecting coral recruitment on reefs. Smithson. Contributions Earth Sci. 38, 437–457.

Roberts, C.M., Andelman, S., Branch, G., Bustamante, R.H., Carlos Castilla, J., Dugan, J., Halpern, B.S., Lafferty, K.D., Leslie, H., Lubchenco, J., McArdle, D., Possingham, H.P., Ruckelshaus, M., Warner, R.R., 2003. Ecological criteria for evaluating candidate sites for marine reserves. Ecol. Appl. 13 (sp1), 199–214.

Rodwell, L.D., Barbier, E.B., Roberts, C.M., McClanahan, T.R., 2003. The importance of habitat quality for marine reserve fishery linkages. Can. J. Fish. Aquatic Sci. 60, 171–181.

Ruppert, J.L., Travers, M.J., Smith, L.L., Fortin, M.J., Meekan, M.G., 2013. Caught in the middle: combined impacts of shark removal and coral loss on the fish communities of coral reefs. PloS one 8 (9), e74648.

Samoilys, M.A., Carlos, G., 2000. Determining methods of underwater visual census for estimating the abundance of coral reef fishes. Environ. Biol. Fishes 57 (3), 289–304.

Samoilys, M., Gribble, N., 1997. Manual for Assessing Fish Stocks on Pacific Coral Reefs, Queensland Training Series. Department of Primary Industries, Brisbane.

Samoilys, M.A., Martin-Smith, K.M., Giles, B.G., Cabrera, B., Anticamara, J.A., Brunio, E.O., Vincent, A.C., 2007. Effectiveness of five small Philippines' coral reef reserves for fish populations depends on site-specific factors, particularly enforcement history. Biol. Conserv. 136, 584–601.

Sano, M., 2004. Short-term effects of a mass coral bleaching event on a reef fish assemblage at Iriomote Island, Japan. Fish. Sci. 70 (1), 41–46.

Sawall, Y., Jompa, J., Litaay, M., Maddusila, A., Richter, C., 2013. Coral recruitment and potential recovery of eutrophied and blast fishing impacted reefs in Spermonde Archipelago, Indonesia. Mar. Pollut. Bull. 74 (1), 374–382.

Selig, E.R., Casey, K.S., Bruno, J.F., 2012. Temperature-driven coral decline: the role of marine protected areas. Glob. Change Biol. 18 (5), 1561–1570.

Sheppard, C.R.C., Ateweberhan, M., Bowen, B.W., Carr, P., Chen, C.A., Clubbe, Craig, M.T., Ebinghaus, R., Eble, J., Fitzsimmons, N., Gaither, M.R., Gan, C.-H., Gollock, M., Guzman, N., Grahamn, N.A.J., Harris, A., Jones, R., Keshavmurthy, S., Koldewey, H., Lundin, C.G., Mortimer, J.A., Obura, O., Pfeiffer, M., Prince, A.R.G., Purkis, S., Raines, P., Readman, J.W., Riegl, B., Rogers, A., Schleyer, M., Seaward, M.R.D., Sheppard, A.L.S., Tamelander, J., Turner, J.R., Visram, S., Vogler, C., Vogt, S., Wolschke, H., Yanf, J.M.-C., Yang, S.-Y., Yesson, C., 2012. Reefs and islands of the Chagos Archipelago, Indian Ocean: why it is the world's largest no-take marine protected area. Aquatic Conservation: Mar. Freshw. Ecosyst. 22 (2), 232–261.

Soong, K., 1993. Colony size as a species character in massive reef corals. Coral Reefs 12 (2), 77–83.

Spalding, M.D., Jarvis, G.E., 2002. The impact of then 1998 coral mortality in reef fish communities in the Seychelles. Mar. Pollut. Bull. 44 (4), 309–321.

Steneck, R.S., Dethier, M.N., 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69 (3), 476–498.

Syms, C., Jones, G.P., 1999. Scale of disturbance and the structure of a temperate fish guild. Ecology 80 (3), 921–940.

Veron, J., 2000. Corals of the World. Australian Institute of Marine Science, Townsville, p. 295.

Wendling, B., Rosine, G., Adam, P., Alcindor, R., Louange, A., Zialor, V., 2003. Status of Carnivorous Fish and Recent Hard Coral Recruitment Rates Around Outer Islands (Seychelles). An additional survey to the Seychelles Marine Ecosystem Management Project (SEYMEMP), 5 years after the 1998 mass coral bleaching event. Technical Report.

Wernberg, T., Smale, D.A., Thomsen, M.S., 2012. A decade of climate change experiments on marine organisms: procedures, patterns and problems. Glob. Change Biol. 18 (5), 1491–1498.

Wilkinson, C., 2004. Status of Coral Reefs of the World: 2004. Australian Marine Institute of Marine Science, Townsville, Queensland, Australia.

Wilson, S.K., Fisher, R., Pratchett, M.S., Graham, N.A.J., Dulvy, N.K., Turner, R.A., Cakacaka, A., Polunin, N.V.C., Rushton, S.P., 2008. Exploitation and habitat degradation as agents of change within coral reef fish communities. Glob. Change Biol. 14, 2796–2809.

Wilson, S.K., Graham, N.A., Fisher, R., Robinson, J., Nash, K., Chong-Seng, K., Polunin, N.V.C., Aumeeruddy, R., Quatre, R., 2012. Effect of macroalgal expansion and marine protected areas on coral recovery following a climatic disturbance. Conserv. Biol. (6), 995–1004.

Wooldridge, S.A., 2009. Water quality and coral bleaching thresholds: formalising the linkage for the inshore reefs of the Great Barrier Reef, Australia. Mar. Pollut. Bull. 58 (5), 745–751.