Coral Reefs (2012) 31:919–927
DOI 10.1007/s00338-012-0920-1

REPORT

Interactive effects of live coral and structural complexity on the recruitment of reef fishes

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Received: 22 December 2011 / Accepted: 17 May 2012 / Published online: 7 June 2012

Abstract Corals reefs are subjected to multiple disturbances that modify levels of coral cover and structural complexity of the reef matrix, and in turn influence the structure of associated fish communities. With disturbances predicted to increase, insight into how changes in substrate condition will influence the recruitment of many fishes is essential for understanding the recovery of reef fish populations following biological and physical disturbances. While studies have revealed that both live coral cover and structural complexity are important for many fishes, there is a lack of understanding regarding how a combination of these changes will impact the recruitment of fishes. This study used experimentally constructed patch reefs consisting of six different habitat treatments; three levels of live coral cover (high, medium, low) crossed with two levels of structural complexity (high, low), to test the independent and combined effects of live coral cover and structural complexity on the recruitment and recovery of fish communities. The abundance and species diversity of fishes varied significantly among the six habitat treatments, but differences were not clearly associated with either coral cover or structural complexity and varied through time. More striking, however, was a significant difference in the composition of fish assemblages among treatments, due mostly to disproportionate abundance of coral-dwelling fishes on high coral cover, high complexity reefs. Overall, it appears that coral cover had a more important influence than structural complexity, at least for the contrasting levels of structural complexity achieved on experimental patch reefs. Furthermore, we found that live coral cover is important for the recruitment of some non-coral-dependent fishes. This study confirms that live coral cover is critical for the maintenance of high biodiversity on tropical coral reefs, and that sustained and ongoing declines in coral cover will adversely affect recruitment for many different species of reef fishes.

Keywords Recruitment · Settlement · Coral reef fish · Coral reef ecology · Disturbances · Resilience

Introduction

Coral reef ecosystems are subjected to a multitude of different disturbances that vary in scale and intensity. It is predicted that coral reefs will experience an increase in anthropogenic disturbances over coming decades resulting in declines of quality and quantity of coral dominated habitats (Hoegh-Guldberg 2004; Wilson et al. 2006; Hughes et al. 2010). Cyclones, storms and bioeroders change the physical architecture of reefs, while mass coral bleaching, outbreaks of crown-of-thorns starfish (*Acanthaster planci*) and coral disease reduce live coral cover (Sano et al. 1987; Willis et al. 2004; Garpe et al. 2006). Reductions in live coral cover and structural complexity of the benthos can lead to fundamental changes in reef fish communities. Coral-dependent fishes typically experience the greatest declines in abundance, but structural complexity loss can further affect other groups of fishes (Munday 2004; Wilson et al. 2006; Pratchett et al. 2008a;

Communicated by Biology Editor Dr. Stephen Swearer

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Graham et al. 2009). While disturbances to coral habitats can have a strong effect on adult fishes, studies have also observed long-term population declines as a result of the decline of suitable settlement habitats (Jones et al. 2004). Therefore, it is important to understand how changes in live coral cover and structural complexity influence the recruitment of fish larvae, especially given settling fish have very specific habitat requirements (Sale et al. 1984; Öhman et al. 1998; Holbrook et al. 2000; Booth and Beretta 2002).

The substrate of coral reefs is important for the survivorship of existing fishes, but also for the replenishment of fish communities to reefs (Jones et al. 2004; Feary et al. 2007). Live coral cover and structurally complex reefs provide essential resources for fishes by supplying them with food and refuge space and helping to mediate important biological interactions such as competition and predation (Syms and Jones 2000; Cole et al. 2008; Coker et al. 2009). Following multiple disturbances and declines in fish abundances, replenishment of fishes to these impacted reefs is essential for recovery processes and maintenance of key functional groups that help sustain reef health, promote recovery and provide resilience by preventing phase shifts (Bellwood et al. 2004; Hughes et al. 2010).

Recovery of fish communities can occur through the emigration of fishes from surrounding reefs or through the recruitment of larval fishes from the pelagic environment. While emigration of fishes is limited to small scales and only relevant to local disturbances, recovery through recruitment is, while an infrequent demographic event, able to repopulate communities over larger distances. Live coral cover and structural complexity are important for settling fishes through the provision of settlement cues and shelter (Sweatman 1988; Jones and Syms 1998; McCormick et al. 2010). Furthermore, some juvenile fish require specific dietary requirements (e.g., algae, live coral tissue), which influence their settlement site. An understanding of how impacts through the change in substrate health and complexity will influence the recruitment of many fishes is essential. Studies have shown that live coral and structural complexity are important for many juvenile fishes (e.g., Caley and St John 1996; Booth and Beretta 2002; Feary et al. 2007; McCormick et al. 2010), but we still lack a solid understanding of how biological and physical changes in habitat combine to impact fish recruitment.

While it is important to understand how substrate condition influences the replenishment of reef fish communities, this is difficult to study on natural reefs. Factors like larvae supply, coral composition and existing fish communities can confound differences in recruitment (Cowen 1985; Booth 1992; Messmer et al. 2011). Patch reefs are a natural component on many reefs, especially in lagoons and back reefs, and can be easily constructed and manipulated. As such, patch reefs have been used extensively to study the relationship between substrate and fish recruitment, diversity indices, mortality and offer the ability to control variables (e.g., Williams 1980; Sale et al. 1984; Syms and Jones 2000; Almany 2004; Messmer et al. 2011). Furthermore, removal of all fish prior to an experiment allows assessment of replenishment of fish due to substrate characteristics without the influence of resident fish, which may vary between patch reefs, influencing recruitment through settlement cues, competition and predation (Sweatman 1985; Booth 1995; Kent et al. 2006). While some studies have looked at the recruitment of fishes to reefs with varying coral cover (e.g., Feary et al. 2007; McCormick et al. 2010) and structural complexity (e.g., Caley and St John 1996), the interactive effects of these two attributes have not been investigated. While some species of fishes are dependent on live coral (Munday et al. 1997; Cole et al. 2008), and structural complexity can influence competition and predation (e.g., Hixon and Beets 1993), the effect of disturbances on the recovery of degraded reefs may be determined by disturbances that differentially or in combination modify both coral cover and structural complexity (Graham et al. 2011a).

The presence of living coral tissue is considered by many to be a critical factor in shaping patterns of recruitment or early post-settlement survivorship (Beukers and Jones 1998; Öhman et al. 1998; Holbrook et al. 2000). Conversely, structural complexity is important in increasing survivorship of larval fishes, providing increased number of refuge sites from predators and competitors (Syms and Jones 2000), and some authors perceive that live coral is largely irrelevant, except in providing habitat diversity (Lindahl et al. 2001; Garpe et al. 2006). Ultimately, both coral cover and topographical complexity may both be critical elements of coral-reef habitats, although they may influence different components of reef fish assemblages (Graham et al. 2009). This study used experimental manipulations to examine the recruitment of fishes to patch reefs with varying levels of live coral cover and structural complexity, to test the relative importance of these two features of coral habitats in modifying the structure of fish assemblages.

Methods

Study location and experimental design

Experimental patch reefs were constructed on a shallow sand flat situated in the lagoon behind an exposed reef flat at Lizard Island (LI) on the Great Barrier Reef, Australia (14°41′S, 145°27′E). All patch reefs were constructed from four species of live and recently dead (algal covered), but still structurally intact branching corals (*Acropora nasuta, Acropora formosa* (Fam. Acropoidae), *Pocillopora damicornis* (Fam. Pocolloporidae) and *Porities cylindrical* (Fam. Poritidae)) from nearby reefs. Coral species were the same on all reefs because studies have shown that coral diversity can influence the diversity and abundance of fishes on reefs (Munday et al. 1997; Messmer et al. 2011). These four species of corals were selected for their high abundance on surrounding reefs as well as their high susceptibility to both physical and biological disturbances (e.g., cyclones, crown of thorns, bleaching) (Marshall and Baird 2000). All reefs were 1 m^2 and constructed with an equal volume of rubble base and live and dead coral structure. Reefs were constructed to six different treatments of high, medium and low coral cover crossed with high and low structural complexity. The six treatments are labelled as; High H, High L, Med H, Med L, Low H and Low L with High, Med and Low representing three levels of coral cover and H and L representing high and low complexity, respectively. A block design was used where each of the six treatments were replicated five times and mixed across the sand flat. All reefs were first constructed as high complexity reefs and then reefs selected as low complexity treatments were physically degraded with the use of a hammer and chisel until the desired complexity was achieved. Patch reefs were situated in two rows running parallel to the reef crest at a depth of approximately 3 m. Patch reefs were 10 m apart and 30-50 m from the nearby reef edge.

To confirm distinct differences in coral cover and structural complexity at the start and throughout the course of the experiment, measurements of coral cover and substrate composition were made using a 100 point grid on an aerial photograph to calculate a percentage cover. Coral cover for the three levels were: High = 56.5 % (SE ± 2.0), Med = 33.5 (SE ± 2.0) and Low = 10.6 (SE ± 0.9). Substrate was recorded as live coral, algal, soft coral, sand and rubble. Habitat complexity was measured by recording the height of the reef at five random points (Wilson et al. 2007), rugosity as the linear distance covered by a 3 m chain fitted to the patch reef contour (replicated 3 times) (Risk 1972) and the number of refuge holes (diameters <5 cm, 5–10 cm, >10 cm) (Graham et al. 2003) of each individual patch reef (Table 1). To display measures of patch reef complexity and composition, measures of rugosity, refuge holes (<5 cm), reef height and benthic composition were entered into a principal component analysis (PCA), based on correlation matrices (Fig. 1). High and low complexity patch reefs fall out separately with high complexity reefs containing higher levels of rugosity, sand, number of small holes and reefs were also higher. Patch reefs were also separated on a gradient driven by levels of live coral cover, algae and rubble.

Table 1 Measurements of habitat complexity for high and low complexity patch reefs (mean ± SE)

	High	Low
Height (cm)	43.5 ± 2.4	19.6 ± 0.7
Rugosity (m)	0.71 ± 0.03	0.48 ± 0.01
Holes <5 cm	185 ± 15	123 ± 10
Holes 5–10 cm	23 ± 2	35 ± 6
Holes >10 cm	12 ± 1	14 ± 1

Surveys

Fish surveys were conducted periodically on scuba from 13th November through to 14th December. All patch reefs were constructed a few days before surveying commenced and were devoid of fish upon construction. For all patch reefs, recently recruited fishes that were visible were counted and identified to species. Fishes were classified as recruits by their size and lack of pigmentation. Because recruitment of fishes at LI is patchy in time, reefs were surveyed approximately every 2 days over this period to try and capture all species of fishes recruiting to the different patch reefs. During this period, the majority of fish recruit to the reefs and settle during the night (Victor 1991), and we attempted to capture that recruitment the following day. Unfortunately, we cannot confidently distinguish between present and recently settled recruits through non-destructive sampling methods. However, while individuals may be recorded in multiple surveys, the

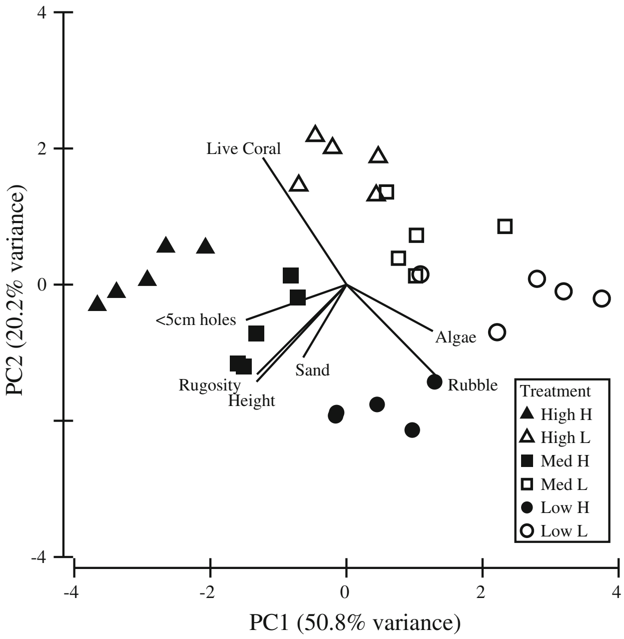


Fig. 1 Separation of six groups of patch reefs based on coral cover and structural complexity indices. Each *symbol* represents an individual patch reef

overall trends among habitat treatments would be maintained. Patch reefs were all surveyed non-destructively by visual recording on the same day by the same observer for consistency (DJC). Reefs were surveyed in three stages; (1) from a distance of ≈3 m to capture shy species as well as fish swimming in the water column and around the fringes of the reefs, (2) from the immediate edge of the reef to record the majority of species residing on the reefs and (3) reefs were searched intensively with the aid of an underwater torch to capture fishes within the intrinsic structure of the reef framework. Each reef was surveyed until no new individuals were identified, and the reef had been meticulously searched (approx 10 min per reef). Although this method may not capture cryptic species, most species would be captured visually, and any missed species would be consistent among treatments. Due to the high numbers (approx 1,000) of Apogoniidae that would recruit and school above some of the patch reefs, they were omitted from analyses as they would significantly skew the data.

Analysis

To examine common indices of fish assemblages among the different reef treatments, abundance and species diversity were compared over the survey period by repeated measures ANOVAs (RMANOVA) in SPSS V19. Measures of abundance and diversity (Shannon diversity index *H'*) for each survey were effectively paired, and a repeated measure was undertaken. Sphericity, assumptions of normality and homogeneity of variance were examined using residual analysis. Following RMANOVA, a Tukey's HSD was conducted to explore significant differences among the six reef treatments. Ordination analysis was performed in PRIMER V6. Data were square root transformed to down weight highly abundant fishes. The final five survey dates were used to represent the most advanced community of juvenile fishes and because Bray–Curtis values and an exploratory multi-dimensional scaling (MDS) plot indicated that dissimilarities in fish communities were greater between time intervals early on in the experiment than towards the end. This MDS plot of the final five survey dates was fitted with similarity slices grouping patch reefs with 70 and 75 Bray–Curtis similarity of reef fish community composition based on a hierarchical clustering analysis (Clarke 1993). All differences were analysed using ANOSIM to assess statistical difference among the treatments. SIMPER was run on the last five surveys to assess which species of fish were driving the differences and ranked in order according to their contribution (%) to the difference. From this, the species that contributed accumulatively 50 % of the differences were plotted as vectors to illustrate the differences according to the six different treatments.

Results

Patch reef indices

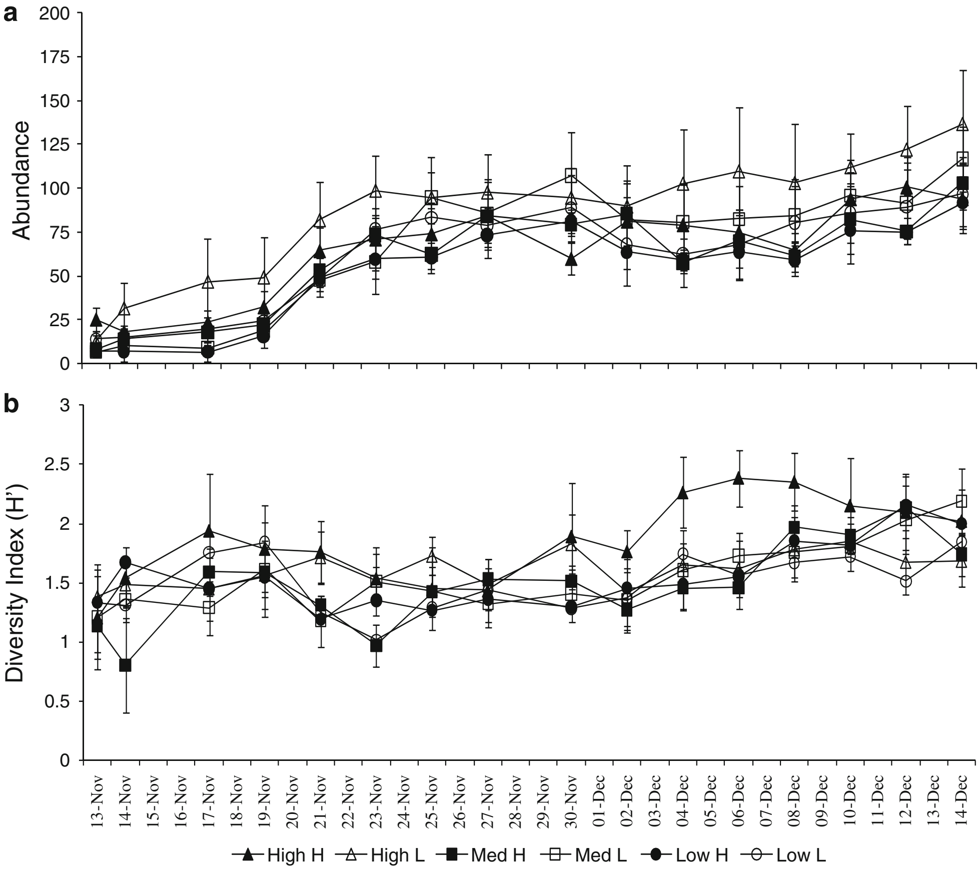
Across the 30 patch reefs, we recorded a total of 75 species of fishes from 23 families by the end of the survey period. There were some significant differences in the accumulation of fishes among the treatments ($F = 23.842$, $df = 5$, $P < 0.001$), but differences attributable to coral cover versus structural complexity were not consistent through time (Fig. 2a). Overall abundance was higher on reefs with high coral cover and low complexity (High L) with the highest abundance recorded at the end of the survey period (mean 136.6 ± 31.3 SE) and lowest on low coral cover and high complexity (Low H) with the greatest abundance recorded at the end of the survey (mean 91.6 ± 14.5 SE). Abundance for both treatments was significantly different ($P < 0.05$) to the other five habitat treatments based on Pairwise comparisons.

Significant differences were also detected among the six treatments for species diversity over time ($F = 4.954$, $df = 5$, $P = 0.013$) (Fig. 2b). This difference was driven by patch reefs with high coral cover and high complexity (High H) showing significantly higher species diversity compared to all other treatments ($P < 0.05$, Pairwise comparisons). The difference among treatments was variable through time and was particularly apparent during surveys conducted on the 4th, 6th and 8th of December where diversity was higher on high coral cover and high complexity (High H).

Patch reef fish communities

The MDS plot of the fish community composition shows clear differences among the treatments where hierarchical agglomerative clustering (70 and 75 % similarity) groups replicates within habitat treatments (Fig. 3a). An ANOSIM test of difference in community structure between the six treatments, where an *R* value of 0 states that there is no difference between groups, while an *R* value of 1 states that between-group differences are larger than all within-group differences (Clarke and Warwick 2001), revealed strong differences between treatments of high, medium and low coral cover ($R = 0.95$, $P < 0.001$) and high and low complexity ($R = 1$, $P < 0.001$). SIMPER analysis results of species contribution (%) to these dissimilarities in communities between treatments showed that the species contributing accumulatively 50 % of the differences were associated with different reef treatments (Fig. 3b). SIMPER yielded 17 species that clearly discriminated between coral cover and habitat complexity, with nine species from the family Pomacentridae contributing to the list (Fig. 3b). Of the species contributing to the differences, 82 % were

Fig. 2 Changes in mean (± SE) fish **a** abundance and **b** Shannon diversity index (H') associated with six patch reef treatments over time



associated with reefs with high or medium coral cover, including *Dascyllus aruanus, D. retriculatus, Gobiodon oculolineatus, Pomacentrus* sp. and *P. moluccensis*. Conversely, there were three species associating with low coral cover reefs: *Acanthurus* sp., *Pomacentrus amboinensis* and *P. chrysurus*. One piscivore, *Cephalopholis boenak,* and a common species of goatfish (*Mulloidichthys flavolineatus*) were associated with reefs of high coral cover and complexity showing a dependence of live coral cover at recruitment. Species contributing to differences based on the complexity of the reefs were: *Chaetodon auriga, Coris batuensis, Pomacentrus adelus, P. amboinensis* and *P. nagasakiensis*.

Discussion

Scleractinian corals are the fundamental habitat-forming organisms on coral reefs, and it is well known that adult stages of many reef fishes are critically dependent on live corals for food and shelter (Munday et al. 2008; Pratchett et al. 2008a). This study shows that live coral is also important in the recruitment of many reef fishes, significantly expanding on the number of fishes that appear to be reliant on live corals. Previous studies have shown that live coral is an important settlement substrate for fishes that rely on corals as adults (Booth and Beretta 2002; Feary et al. 2007; Pratchett et al. 2008b). This study revealed that differences in fish abundance and species diversity among treatments were fairly subtle and not consistent through time, probably due to underlying stochasticity in recruitment patterns and differential survivorship. However, the abundance of fishes was highest on patch reefs with high coral cover and low complexity reefs, while diversity was highest on patch reefs with high coral cover and high complexity. This suggests that levels of live coral cover have a stronger influence on abundance and diversity than the complexity of the reef. Similarly, Caley and St John (1996), with the use of artificial reefs, found that changes in structural complexity of habitat had no effect on the abundance of new recruits, while other studies have revealed differences in abundance driven by live coral cover (Feary et al. 2007; McCormick et al. 2010). While there may be some confounding settlement and post-settlement processes associated with the abundance of recruits (e.g., predation, competition), they are predicted to be consistent between treatments. For our study, the observed differences among habitat treatments were not consistent through time. Due to this inconsistency, we cannot confidently say that coral cover or habitat complexity influences

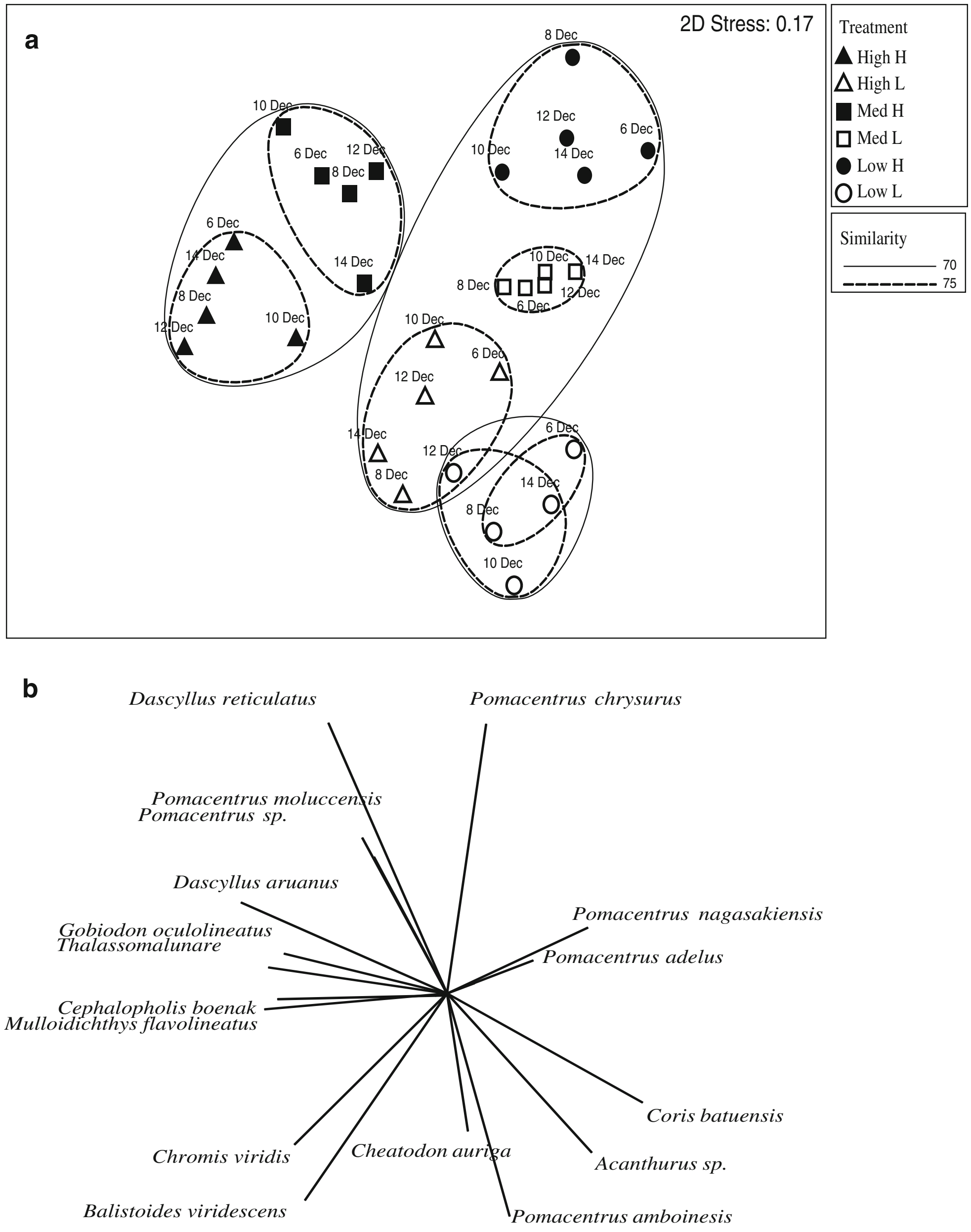


Fig. 3 Last five surveys following community stability. **a** Bi-plot of first two components of PCA with 70 and 75 % similarity groups showing a clustering of patch reefs based on fish communities. **b** Eigenvectors of fish species (top 50 % contribution), using the same Bray–Curtis similarity matrix as used for panel (**a**)

fish abundance or species diversity. Some of this variation in abundance and species diversity could be due to fluctuations in recruitment over time and post-settlement processes (Sweatman 1983, 1985; Cowen 1985; Booth 1992).

While we found small fluctuating differences in abundance and diversity among treatments, it is important to also understand species composition among treatments. Marked variation in the composition of fish assemblages associated with each of the distinct treatments was present and largely attributable to higher abundances of coral-dependent species on patch reefs with high coral cover. Differences in species composition but not common community indices show that levels of recruitment are similar, but the identity of the recruiting fishes vary with habitat condition. This community vulnerability is supported by Bellwood et al. (2006) where small crypto-benthic reef fish communities changed in composition but not abundance and diversity following habitat disturbance. Over half of the species contributing to the difference were planktivorus damselfish (Fam. Pomacentridae) with coral-dependent species associating with reefs of high and medium coral cover and high complexity, and rubble-associated species clustering with low coral cover and low complexity reefs. This shows that these fishes have the same habitat requirements at settlement as they do in adulthood. Interestingly, we found a common piscivore and a goatfish associated with high coral cover and high complexity even though both these fishes are not dependent on live coral as adults. This result suggests that these fishes depend on live coral for shelter or possibly prey attracted to this habitat, and that live coral is important for fishes at settlement even if they do not depend on it later in life. Fish communities recruiting to reefs with low levels of live coral cover and structural complexity were significantly different than those recruiting to reefs with high levels of live coral cover and structural complexity, and these treatments were dominated by a similar species complex that generally dominates as adults (Wilson et al. 2008). This suggests that coral-dependent and some non-coral-dependent fishes will not recruit in high numbers to reefs with low coral cover and structural complexity and will not replenish and replace existing species or species that declined from disturbances.

Notable differences in the abundance of fishes among experimental treatments may be driven by settlement preferences of fishes (Gutierrez 1998), or differential survivorship on patch reefs with high versus low coral cover, and high versus low complexity. Habitat characteristics have a strong influence on juvenile fishes, and settling to unsuitable habitat could result in significant effects on growth and survivorship through increased predation, competition or a decline in essential food resources (Caley and St John 1996; Beukers and Jones 1998; Munday 2001; Feary et al. 2009). Therefore, the persistence and survivorship of juvenile fish on reefs needs to be monitored through time. Furthermore, some reef fishes undergo ontogenetic shifts in habitat as they grow, with some species dependent on live corals during their early juvenile stage, but become less dependent as adults (Jones et al. 2004; Feary et al. 2007; Pratchett et al. 2008b). Further monitoring of patch reefs such as those used in this study would be necessary to answer questions regarding the persistence of fishes post-settlement and through to adulthood based on ontogenetic shifts, competition (intraspecific, interspecific) and mortality through predation and/or lack of essential resources (food, shelter).

On coral reefs, certain functional groups (e.g., herbivorous fishes) play an important role in conserving ecosystem function and resilience of coral-reef habitats (Bellwood et al. 2004; Graham et al. 2011b). Herbivorous fishes are of great importance in enhancing ecosystem resilience by regulating abundance of macroalgae, which might otherwise inhibit settlement, and growth of coral recruits (Hughes et al. 2007, 2010). In this study, we found only one species that contributed to differences in community structure that plays an important role in ecosystem function. A common herbivore *Acanthurus sp.* (Fam. Acanthuridae) was found to have strong associations with patch reefs that have low coral cover and low complexity, suggesting that recruitment of this species will be resilient to most major episodes of coral loss and habitat degradation. If this species also survives to adulthood, it may help play a role in reducing algae on these reefs and facilitate the return of live coral by reducing competition between algae and coral recruits. While one species might have limited capacity in promoting the recovery of reefs, particularly if they only form one functional group, the scale of the patch reefs may not have provided adequate space for other functionally important species to be recorded. Furthermore, this survey was only undertaken for 1 month, and therefore, we may not have captured the recruitment of other important functional species.

Declines in coral cover and structural complexity on reefs following disturbances vary dramatically depending on pre-disturbance levels and the magnitude of the impact. While some intact reefs have upwards of 95 % coral cover (Sano 2004), levels of around 50 % are more common (Sheppard et al. 2002). The levels of coral cover and structural complexity on our patch reefs represent realistic levels with respect to healthy, moderately and substantially impacted reefs. This study found that with changes in coral cover of 23 and 46 %, differences in fish composition were significantly different. Although these communities were different, treatments with low coral cover and low complexity still supported similar numbers of fish and diversity to other treatments. While low coral cover treatments had only 10.6 % coral cover and low complexity treatments were significantly degraded, this might be enough to support some species that depend on live coral for recruitment. Ultimately, there will be a threshold where reefs degrade to a point where their condition affects the recruitment of some fish species. Therefore, further degradation of our reefs to zero coral cover and pavement (flat substrate) would further increase our understanding of how disturbances will impact the recruitment of reef fishes and the importance of live coral and structural complexity.

Results from this study suggest that declines in coral cover and structural complexity will not necessarily lead to declines in overall abundance and species diversity despite coral cover being 81 % lower on low coral cover reefs than high coral cover reefs and structural complexity being significantly lower. Differences were found in species composition with the use of multivariate ordination techniques, illustrating the importance of investigating changes in species composition with habitat changes and not just basic population indices. Differences in communities are driven by coral-dependent fishes associating with reefs of high and medium coral cover and high complexity and rubble-associated fishes associating with heavily degraded reefs. Furthermore, two non-coral-dependent species were found associated with high coral cover reefs showing the importance of live coral for fishes that are non-obligately coral-dependent as adults.

Globally, coral reefs are experiencing an increase in the frequency and severity of a range of disturbances resulting in significant degradation of the benthos. This study shows that fishes will recruit and settle to degraded reefs in high numbers and high diversity following coral degradation, but that these fish communities will be significantly different compared to healthy complex reefs. These results suggest that recruiting fish communities following reef degradation will shift in composition and are unlikely to reflect pre-disturbance communities unless coral cover recovers. It is not clear from our study how longer-term survivorship of species may vary among the different treatments examined here. Some species may settle to degraded habitats but either show ontogenetic shifts or increased mortality through a lack of essential resources. It is also unclear how these changes will influence the delivery of ecosystem functions, which should be a priority area for future research.

Acknowledgments We are grateful to R. Lawton and M. Trapon for their assistance in the field and the staff at Lizard Island Research Station for logistic support. Funding was provided by AIMS@JCU and Lizard Island Ian Potter Doctorial Fellowship to D.J.C and an ARC Australian Postdoctoral Fellowship to N.A.J.G.

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