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Habitat choice, recruitment and the response of coral reef fishes to coral degradation

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Abstract The global degradation of coral reefs is having profound effects on the structure and species richness of associated reef fish assemblages. Historically, variation in the composition of fish communities has largely been attributed to factors affecting settlement of reef fish larvae. However, the mechanisms that determine how fish settlers respond to different stages of coral stress and the extent of coral loss on fish settlement are poorly understood. Here, we examined the effects of habitat degradation on fish settlement using a two-stage experimental approach. First, we employed laboratory choice experiments to test how settlers responded to early and terminal stages of coral degradation. We then quantified the settlement response of the whole reef fish assemblage in a field perturbation experiment. The laboratory choice experiments tested how juveniles from nine common Indo-Pacific fishes chose among live colonies, partially degraded colonies, and dead colonies with recent algal growth. Many species did not distinguish between live and partially degraded colonies, suggesting settlement patterns are resilient to the early stages of declining coral health. Several species preferred live or degraded corals, and none preferred to associate with dead, algal-covered colonies. In the field experiment, fish recruitment to coral colonies was monitored before and after the introduction of a coral predator (the crown-of-thorns starfish) and compared with undisturbed control colonies.

Starfish reduced live coral cover by 95–100%, causing persistent negative effects on the recruitment of coral-associated fishes. Rapid reductions in new recruit abundance, greater numbers of unoccupied colonies and a shift in the recruit community structure from one dominated by coral-associated fishes before degradation to one predominantly composed of algal-associated fish species were observed. Our results suggest that while resistant to coral stress, coral death alters the process of replenishment of coral reef fish communities.

Keywords Coral reef fishes · Habitat loss · Settlement

Introduction

Habitat loss and degradation have been major factors responsible for declining populations (Vitousek et al. 1997), loss of biodiversity (Brooks et al. 2002) and the disruption of ecosystem services (McCarty 2001; Malcolm et al. 2006) in terrestrial environments. It has been estimated that almost one-half of the land surface has been modified by human activities (Vitousek et al. 1997) and more extinctions have been attributed to habitat loss than any other factor (Dirzo and Raven 2003). Terrestrial habitat loss or alteration has been caused by a number of mechanisms, including human predation and extinction of important predators and herbivores (Lyons et al. 2004), habitat transformation for farming or development (Vitousek et al. 1997), introduction of exotic species (Seabloom et al. 2006) and most recently climate change (Sala et al. 2000; Walther et al. 2002).

One of the central issues in conservation biology has been to identify the characteristics that render species prone to habitat change (Lampila et al. 2005; Cushman 2006). A key

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factor appears to be their level of specialisation, particularly a strong association with features of a habitat that are susceptible to anthropogenic disturbance (McKinney 1997; Hughes et al. 2000; Kotze and O'Hara 2003). Habitat specialists may be highly dependent on particular habitats throughout their lives or they may pass through critical stages in their life cycle that render them highly responsive to changes in the quantity or quality of their habitat (Halpern et al. 2005; Moore and Elmendorf 2006). For open populations, the decline and extirpation of suitable recruitment habitat can potentially be a major determinant of population decline.

There is increasing evidence of the widespread loss or modification of a range of habitats in shallow marine environments (e.g. Farnsworth and Ellison 1997; Alongi 2002; Duarte 2002; McClanahan 2002; Steneck et al. 2002). The risk to biodiversity from loss of marine habitats is increasing as the scale of habitat loss expands (Dulvy et al. 2003; Munday 2004b; Kappel 2005). Coral reefs appear to be particularly susceptible to a range of natural and anthropogenic disturbances that have reduced coral cover on a global scale (Hoegh-Guldberg 1999; McClanahan 2002; Gardner et al. 2003; Hughes et al. 2003). While clearly significant for corals, recent work also indicates that coral reef fish assemblages often exhibit dramatic changes in structure and loss of biodiversity in relation to declining coral cover (Jones and Syms 1998; Halford et al. 2004; Jones et al. 2004; Graham et al. 2006; Wilson et al. 2006). While coral reef fish communities comprise the full spectrum of coral dependency, from specialists in obligate association with a single coral species (Munday et al. 1997; Munday 2004a), to those found on almost any substratum (Green 1996), the magnitude of the changes in fish communities in response to habitat change suggests a widespread reliance on the underlying coral reef habitat. However, the demographic mechanisms responsible for changes in fish community structure in response to habitat disturbance are poorly understood.

The life history transition during which larvae undergo metamorphosis into juveniles and take up residence on coral reefs is a critical period for reef fishes. Juveniles can exhibit strong habitat selection at settlement, including selection for particular coral substrata (Tolimieri 1995; Öhman et al. 1998; Holbrook et al. 2002) or particular depths or reef zones (Srinivasan 2003) and can also use the presence or absence of conspecifics or other fishes as settlement cues (Jones 1987; Sweatman 1988; Booth 1992, 1995). The dynamics and distribution of adult fish populations, and how they ultimately respond to disturbance, may be strongly influenced by habitat-limited recruitment (Schmitt and Holbrook 2000; Syms and Jones 2000; Booth and Beretta 2002). Recent work suggests that

a large proportion of reef fishes may preferentially recruit into live branching corals, even many of those not necessarily associated with corals as adults (Jones et al. 2004). Species-specific differences in coral preferences and levels of specialisation are likely to influence how fish assemblages respond to live coral loss (Syms and Jones 2000; Munday 2004b; Gardiner and Jones 2005; Feary et al. 2007). However, our understanding of the extent of habitat selection at the time of recruitment, and the effects of coral death on fish recruitment require further investigation.

Although phase shifts in the structure of coral reef fish communities may begin with the effects of habitat change on recruitment, support for this hypothesis has been limited to a few monitoring studies (Lewis 1998; Booth and Beretta 2002; Jones et al. 2004) and a laboratory-based study (Öhman et al. 1998). Further experimental studies are needed to understand the extent of the relationship between fish recruitment and coral degradation. For example, while we know that reef fishes are choosy at settlement, we do not know at what stage of declining coral health they begin discriminating among corals. That is, do they avoid settling into bleached corals (which may recover) or do they only distinguish among living and dead (algal covered) substrata? Also, Wilson et al. (2006) showed that the nature of fish community changes depends upon the type of disturbance, distinguishing among disturbances that kill corals while leaving the structure intact [e.g. bleaching, crown-of-thorns starfish (COTS)] from those that destroy the structure as well (e.g. storms, mechanical damage). While several studies have experimentally established the response of fishes to the mechanical disturbance of reefs (Lewis 1998; Syms and Jones 2000), there have been no experimental demonstrations of the effects of the loss of living coral tissue only.

The aims of this study were two fold. Firstly, we set out to test whether the selection of benthic microhabitats by larvae of several common Indo-Pacific reef fishes was influenced by the health of coral colonies. To do this, habitat choice experiments were conducted in laboratory aquaria to examine the degree to which juveniles distinguished between live colonies, partially degraded colonies, and dead colonies with recent algal growth. We hypothesised that habitat specialists were more likely to distinguish between habitats within the aquaria than habitat generalists. We also hypothesised that the nature and strength of association between newly settled fishes and healthy coral would determine how they responded to habitat degradation. We tested this second hypothesis in an experiment conducted in the field. Coral colonies were experimentally degraded by introducing a coral predator, the COTS, and we monitored and compared natural settlement to degraded and control colonies.

Materials and methods

Laboratory preference experiment

Settlement-stage larvae of several common Indo-Pacific damselfishes (Pomacentridae) were collected using light traps (Stobutzki and Bellwood 1998) from the lagoon at Lizard Island on the northern Great Barrier Reef, Australia (14°40′S; 145°28′E). The species collected were assigned to three habitat use categories based on patterns of adult habitat use (Randall et al. 1997; Allen et al. 2003): live coral-associated species (*Chromis viridis*, *Pomacentrus moluccensis*), degraded coral associates (*Chrysiptera flavipinnis*, *Chrysiptera rollandi*, *Pomacentrus amboinensis*, *Pomacentrus nagasakiensis*), and species associated with dead, algal-covered corals (*Dischistodus prosopotaenia*, *Pomacentrus chrysurus* and *Pomacentrus wardi*). Larvae were held prior to trials in featureless glass aquaria supplied with filtered seawater and aeration.

In each trial, three coral colonies (*Acropora cerealis*), each in a different category of health, were placed in a large, circular 300-l tank filled with filtered seawater. All colonies were collected from the field in their natural state of health; there was no experimental manipulation of live coral cover. The three coral colonies were randomly arranged in a triangular configuration along the sides of the tank with equal distance between colonies. The condition of the three colonies was as follows: live (100% live coral cover), degraded (>75% reduction in live coral) and algal-covered (dead coral with 1- to 2-week-old algal growth) (personal observation). All colonies were 20–30 cm^2 in diameter. Three larvae of the same species were utilised within each trial. Monthly peaks in pomacentrid settlement occur over a few nights each month (Milicich et al. 1992). During these temporal periods extremely large numbers of larvae will settle onto the reef and it is unlikely that for the majority of species settlement will occur in isolation from other individuals. Using three larvae within each trial ensured that species' natural behaviour at settlement was shown. Larvae were introduced into the centre of the tank between 2000 and 2100 hours and their colony choice was recorded the following morning at 0500 hours, and subsequently every 30 min until 1300 hours. Twenty-one individuals of each species were tested over seven trials (*n* = 7). Individuals <10 cm from a colony were deemed to be associated with that colony. Coral colonies were only used in a single trial and tanks were cleaned between trials.

Since individuals within each trial could not be separately identified, the average abundance of all individuals (within each fish species) associating with each of the three colony categories was quantified over all seven trials. As the data did not satisfy the assumptions of normality and homogeneity of variance required by ANOVA, Kruskal–Wallis

ANOVA on ranks was used to examine whether significant differences in habitat association were apparent within each fish species. Any significant differences found in habitat associations within species were then examined using post hoc Mann–Whitney *U*-tests, to determine the importance of each habitat in influencing species habitat associations. The Mann–Whitney *U*-test is a nonparametric alternative to the *t*-test for comparing differences in population means and has the advantage of not requiring normal probability distribution for the data. We identified potential metrics when these tests showed significant differences ($P \leq 0.05$).

Field disturbance experiment

The field experiment was conducted in Kimbe Bay, West New Britain, Papua New Guinea (5°30′S, 150°05′E). All invertebrate predators were removed from ten colonies of *A. cerealis* (20–30 cm^2 diameter) on each of three reef complexes (A, B, C). Over a 2- to 3-month period, naturally settling fishes were collected every 3–4 days from each colony using hand nets and clove oil as an anaesthetic (Munday and Wilson 1997). Surveys and collections were conducted at reef C from April to June 2005 and at reefs A and B from August to September 2005. After this 2- to 3-month period, all colonies on each reef were completely caged with small wire-mesh cages. On each reef a single COTS was introduced into each of five randomly selected cages (experimental), whereas the remaining five colonies were left unmanipulated (control). Cages remained in place for 2 days and were then removed. Experimental colonies lost from 95 to 100% of live coral cover, whereas there was no reduction in live coral on control colonies. Natural settlement of fishes was then quantified every 3–4 days from June to November 2005 on reef C, and September to November 2005 on reefs A and B. Recent work has shown that despite seasonal fluctuations in the abundance of fish larvae settling into reefs within Kimbe Bay coinciding with wet seasons (February–November) (Srinivasan and Jones 2006), the majority of common coral reef fishes show little fluctuation in successful settlement throughout the year. Thus, natural settlement rate was expected to vary little throughout the year, allowing us to compare new settler composition between collections throughout the experimental time period.

The average abundance and species richness of new settlers associated with replicate coral colonies (between experimental and control) was quantified within each reef, based on the entire sampling time before and then after introduction of COTS. Both the average abundance and average species richness of new settlers associated with coral colonies within each reef, over each sampling period, were then analysed using repeated measures multivariate ANOVA, with the average abundance and average species

richness of new settlers as dependent variables. Factors in each repeated measures model were reefs (A, B, C), treatment (control, experimental) and colony surveys through time as the repeated measure.

Results

Laboratory preference experiment

Significant differences in habitat association were apparent within the majority of study species, when comparing the average abundance of all individuals (within each fish species) associating with each of the three colony categories throughout trials (Table 1). Mann–Whitney *U*-tests showed that within the species showing significant differences in habitat association, several groups were apparent; species preferentially using the live habitat, species associating with both live and degraded habitats and species preferentially found in the degraded habitat (Table 2). The habitat use of *P. moluccensis* and *C. viridis* both conformed to

adult categories, with both using live habitats. In comparison, both *C. flavipinnis* and *P. amboinensis* were more dependent on the live coral than adult categories would predict. Adults of both species consistently associate with degraded habitats, though within laboratory aquaria both species preferentially used either live or degraded habitats (Table 2). *Pomacentrus chrysurus* were predominantly found using the live habitat, while *P. wardi* associated with the degraded habitat (Table 2)

Temporal changes in habitat association between 0500 and 1300 hours were apparent between species (Fig. 1). High levels of movement between habitats were apparent during the first temporal period, with the majority of species associated with all three habitats in the first temporal period (Fig. 1). By the second or third temporal periods, however, the majority of species had associated with a particular habitat and invariably remained in that habitat for the duration of the trial (Fig. 1). Nevertheless, differences in movement between habitats were found between the study species (Fig. 1). Species not closely associating with the live habitat were less likely to remain in distinct habitats within the aquaria, moving more frequently throughout the habitats during trials, while those associating with the live habitat would move into this habitat in the first or second temporal period and remain in this habitat for the duration of the trial (Fig. 1).

Field experiment

Significant differences in both the abundance and species richness of new settlers associating with control and experimental treatments on all three reefs were apparent (Table 3), due to large reductions in new settlers associating with experimental colonies after live coral degradation (Fig. 2). Reductions in the abundance of new settlers on experimental colonies were most apparent on both A and B, with a 95 and 97% decrease in abundance after coral degradation, respectively, while a 75% decrease in new settler abundance was also apparent on C.

Table 1 Kruskal–Wallis one-way ANOVA examining whether significant differences in habitat association in late-stage larvae of nine pomacentrid species was apparent between live, degraded and algal-covered coral habitats within aquaria

Species	χ^2	df	P
Chrysiptera flavipinnis	25.85	2	***
Chrysiptera rollandi	1.75	2	0.41
Chromis viridis	80.96	2	***
Dischistodus prosopotaenia	26.51	2	***
Pomacentrus amboinensis	67.19	2	***
Pomacentrus chrysurus	34.50	2	***
Pomacentrus moluccensis	236.65	2	***
Pomacentrus nagasakiensis	5.49	2	0.06
Pomacentrus wardi	35.37	2	***

*** $P \leq 0.001$

Table 2 Mann–Whitney *U*-tests examining the importance of live, degraded or algal-covered habitats in influencing the habitat associations in late-stage larvae of nine pomacentrid species within aquaria

Species	Live	Degraded	P	Live	Algal covered	P	Degraded	Algal covered	P	Preferred habitat in aquaria
Chromis viridis	17,754.50	10,686.50	***	18,308.00	10,133.00	***	14,823.50	13,617.50	0.1	Live
P. chrysurus	15,882.50	12,558.50	***	16,189.00	12,252.00	***	14,552.50	13,888.50	0.5	Degraded
P. wardi	12,126.50	16,314.50	***	13,904.00	14,537.00	0.5	16,282.50	12,159.00	***	Degraded
Chrysiptera flavipinnis	13,376.50	15,064.50	0.1	16,671.00	11,770.00	***	17,101.50	11,339.50	***	Live/degraded
P. amboinensis	16,860.00	11,581.00	***	19,403.00	9,037.50	***	17,079.50	11,361.50	***	Live/degraded
P. moluccensis	20,516.50	7,924.50	***	20,754.50	7,686.50	**	15,424.00	13,017.00	***	Live/degraded
D. prosopotaenia	13,427.50	15,013.50	0.1	13,413.50	15,027.50	0.1	14,356.50	14,084.50	0.8	All habitats

** $P \leq 0.01$, *** $P \leq 0.001$

Fig. 1 Mean density (± SE) of the late-stage larvae of nine pomacentrid species at four temporal periods from 0500 to 1300 hours in live, degraded and algal-covered habitats within laboratory aquaria. Larvae were released between 2000 and 2100 hours the previous night
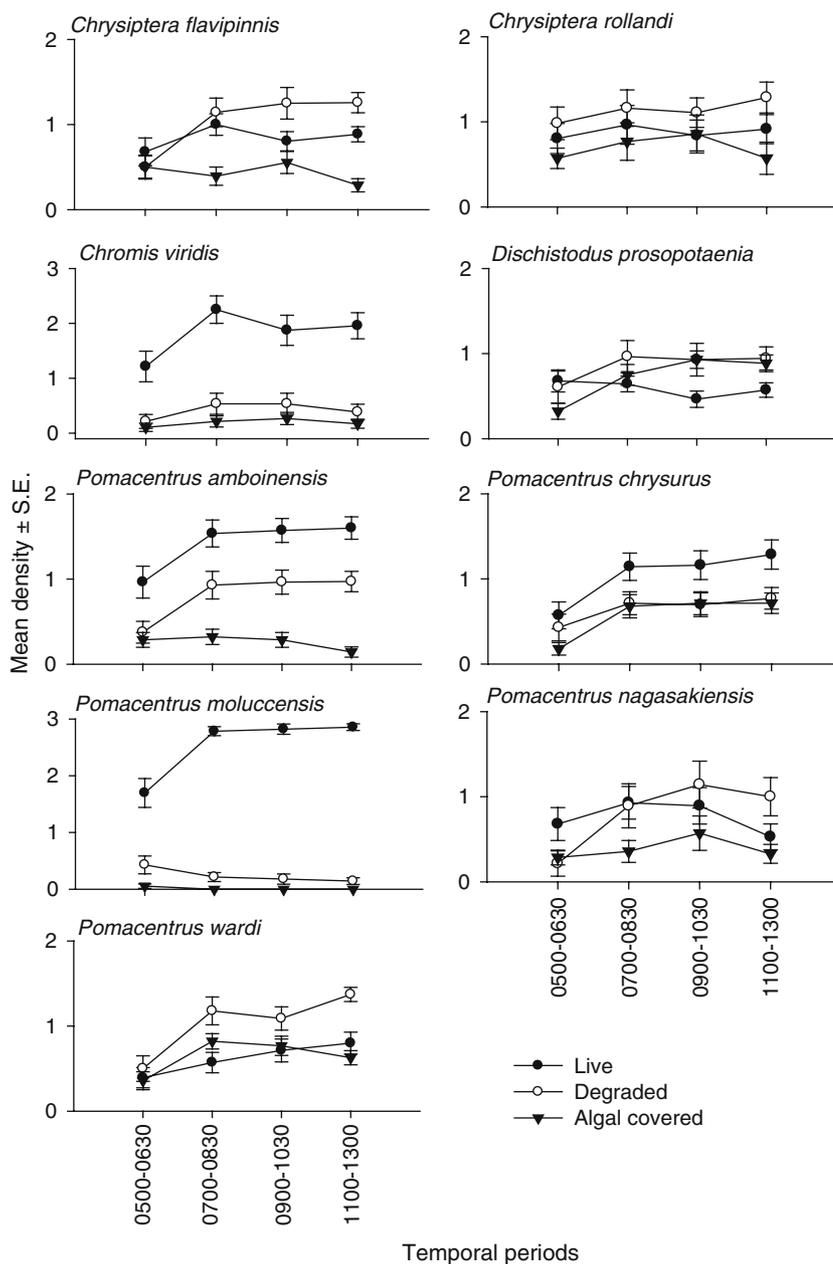
Reductions in the species richness of assemblages in experimental coral colonies were also apparent throughout reefs, with at least 40% decrease in the average species richness in experimental coral colonies on all three reefs, after caging (Fig. 2). Such large reductions in the abundance and species richness of new settlers associating with experimental colonies were largely due to reductions in the settlement of two species strongly associated with live coral, the coral goby *Gobiodon quinquestrigatus* (Gobiidae), which reduced in proportional abundance by 12% after coral loss and the damselfish, *P. moluccensis*, which decreased in proportion by 100% on degraded colonies (Fig. 3). In comparison, although fluctuations in both the abundance and species richness of newly settled fishes were observed on control colonies, the magnitude of these changes was significantly less than that observed on experimental reefs (Fig. 2).

Changes in the composition of new settlers associating with experimental, opposed to control, colonies were apparent after caging (Fig. 3). Within experimental colonies, increased abundances of combtooth blennies (Blenniidae) and triplefins (Tripterygiidae) (e.g. *Ecsenius prooculis*, *Helcogramma* spp.) were observed settling into the habitats, while decreased abundances of species more closely associated with live coral were found within the habitats (Fig. 3). On experimental colonies fishes closely associated

Table 3 Repeated measures ANOVA examining whether significant differences in mean abundance (*Abundance*) and mean species richness (*Diversity*) of new settlers were apparent within each reef (*Reef*), between coral health treatments (*Treat*) over experimental trial (*Time*)

	df	F	P
Abundance			
Reef	2	3.12	0.06
Treat	1	16.94	**
Reef × Treat	2	9.37	**
Time	18	4.16	***
Time × Reef	36	4.84	***
Time × Treat	18	15.16	***
Time × Reef × Treat	36	2.12	***
Diversity			
Reef	2	10.58	***
Treat	1	43.29	***
Reef × Treat	2	5.81	**
Time	18	5.65	***
Time × Reef	36	2.71	***
Time × Treat	18	10.34	***
Time × Reef × Treat	36	1.95	***

$** P \leq 0.01$, $*** P \leq 0.001$

with algal resources (e.g. blennies and triplefins) comprised only 1.8% of the assemblage 2 weeks before live caging, which increased to 18% two weeks after cages were taken off and over 90% after 8 weeks. In comparison, little change in the composition of new settling species associating with control colonies was apparent before and after caging (Fig. 3).

Significant temporal changes in both the abundance and species richness of new settlers were apparent between treatments (Table 3). Degradation of experimental colonies led to temporal reductions in both the abundance and species richness of new settlers associating with experimental colonies 2 weeks after coral loss (Fig. 4). In comparison, little change or an increase in the abundance and a decrease

in species richness of new settlers were apparent in control colonies (Fig. 4).

Although no significant difference in percent occupancy was apparent between control and experimental colonies before caging (ANOVA, $F = 0.344$, $df = 1$, $P = 0.565$), reductions of live coral cover (following caging) on experimental colonies resulted in a significantly higher frequency of empty colonies during subsequent sampling periods than control colonies (ANOVA, $F = 60.54$, $df = 1$, $P < 0.001$). Across all three reef complexes, 4 weeks before live coral loss an average of 52% (± 7.4 SE) of experimental colonies contained at least one individual, whereas 4 weeks after caging and live coral degradation only 9% (± 4.2 SE) of experimental colonies were occupied. In contrast, the percent occupancy on control reefs increased during the experiment: 4 weeks before caging an average of 45% (± 10 SE) of control colonies were occupied by at least one individual, whereas 4 weeks after manipulation an average of 74% (± 6.4 SE) of control colonies were occupied.

Discussion

Our results support an emerging view that settlement is likely to be a crucial bottleneck that determines the impact of coral degradation on reef fish biodiversity and community structure (Booth and Wellington 1998; Jones et al. 2004). For a number of coral-associated reef fish species, reductions in the availability of live coral at settlement may decrease their numerical abundance within degraded reef systems. Such changes in settlement patterns with reef degradation may then lead to a shift in the community structure of reef-associated fish communities, away from live coral specialists to degraded reef associates. This mechanism may account for the dramatic changes to coral-associated reef fish populations in response to declining live coral cover (see also Halford et al. 2004; Jones et al. 2004; Garpe et al. 2006; Graham et al. 2006; Wilson et al. 2006).

Fig. 2 Mean abundance (± SE) and mean species richness (± SE) of new settlers associated with control and experimental colonies between reefs, before and after caging
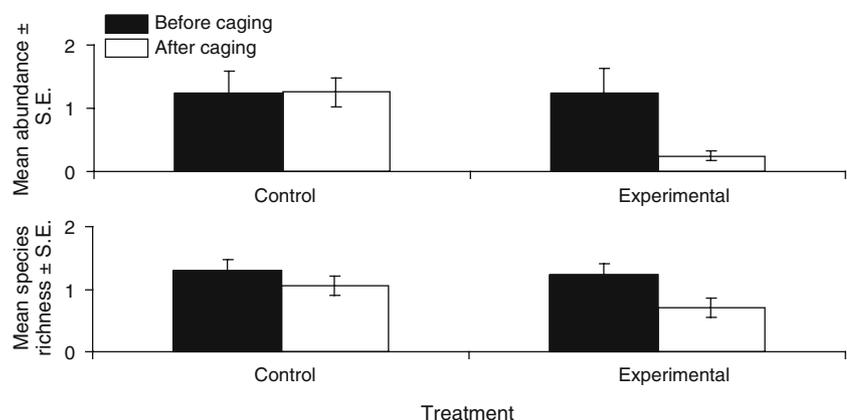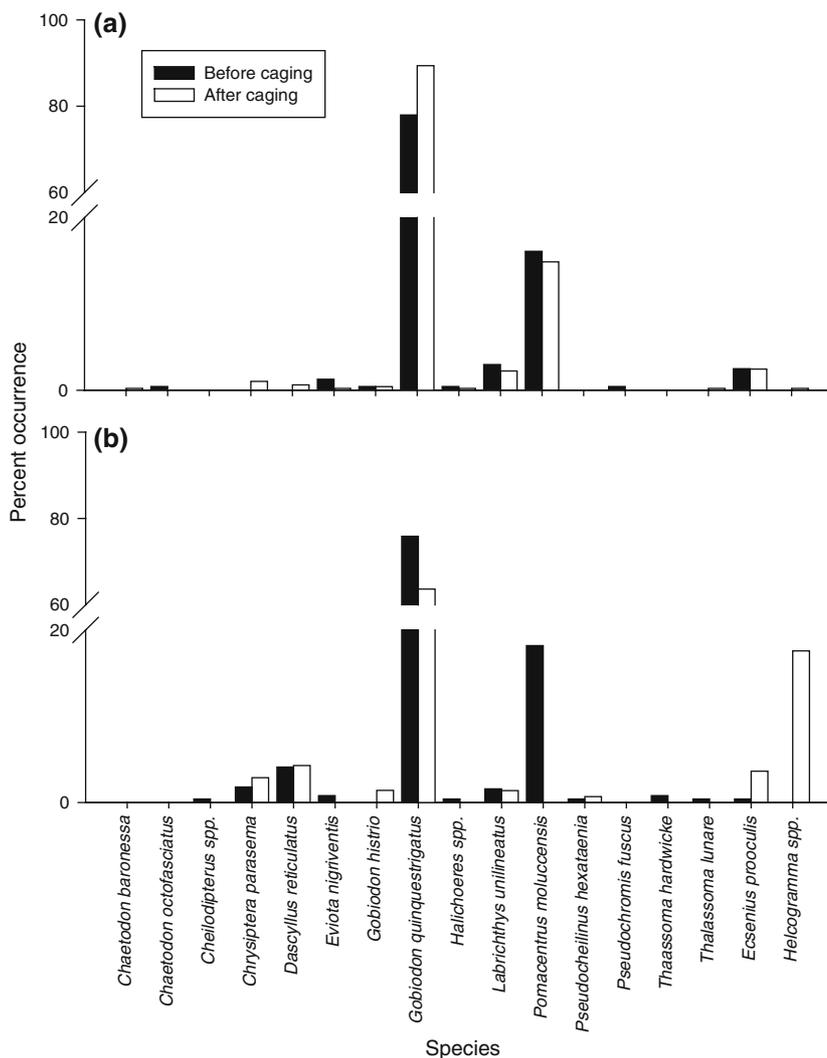
Fig. 3 Percent occurrence of all fish species associated with in situ **a** control and **b** experimental colonies before and after caging


The majority of study species preferentially associated with either live or partially degraded coral colonies within laboratory aquaria, and none of the species examined preferentially associated with dead, algal-covered colonies. This suggests that several coral-associated reef fish species may be resilient to the early stages of degradation. For these species, the extent of coral loss may be an important factor in structuring settlement patterns. Within this study degraded treatments held up to 25% live coral cover. At this spatial scale, the degraded coral colony may have held sufficient live coral cover for species to utilise the habitat. However, once coral death and algal overgrowth had occurred there was little to no settlement of species into the habitat. Such preferences for live and degraded habitats at settlement were apparent in fishes that both associate with live coral throughout their lives (e.g. *P. moluccensis*) (Booth 2002; Booth and Beretta 2002) and for many with little to no use of live coral colonies throughout the juvenile or adult stage (e.g. *P. chrysurus*) (Allen et al. 2003). Hence,

adult responses to declining coral cover may be more a result of settlement preferences than adult habitat requirements (Jones et al. 2004).

Variations in the availability of appropriate settlement habitat may influence settlement patterns in a variety of reef-associated fishes (Holbrook et al. 2000), and can affect both local species richness and population abundance (Schmitt and Holbrook 2000). However, few studies have experimentally examined the role of habitat alteration in structuring reef fish settlement patterns, with most studies strictly observational, and therefore unable to distinguish habitat changes from other potential causative factors (Booth and Beretta 2002). In this study, reductions in live coral on experimentally degraded in situ colonies led to reductions in both the abundance and species richness of newly settling fishes, a pattern observed in other studies (Booth and Beretta 2002). Although reductions in the settlement of a range of fish species were apparent on experimentally degraded colonies, such community decline was

Fig. 4 Mean abundance (± SE) and mean species richness (± SE) of new settlers associated with control and experimental colonies between reefs every 2 weeks. *Wk* Week
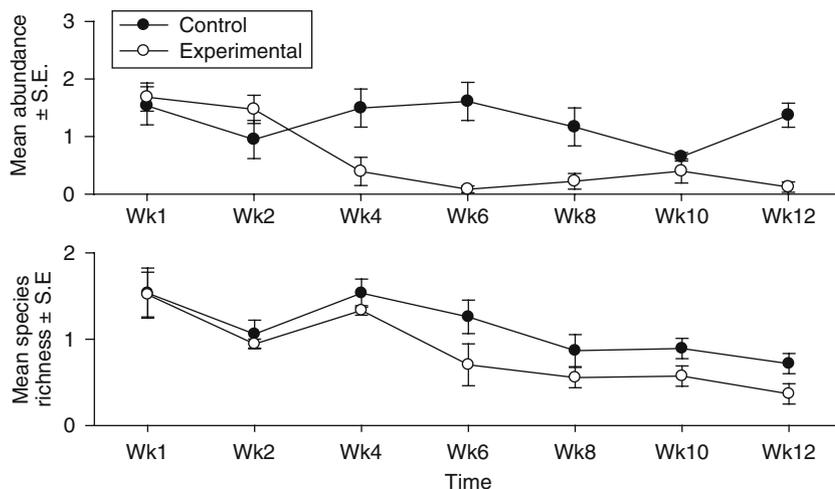
primarily due to reduced settlement of the coral-associated goby, *G. quinquestrigatus* and the coral-associated damselfish, *P. moluccensis*. Both fishes dominated live coral colonies, settling in large numbers in this habitat. Degradation of colonies by COTS predation and subsequent growth of algae reduced the number of new settlers of both fishes, with virtually no individuals of either species found on degraded colonies.

A physical reduction in available shelter occurs when degraded coral colonies are colonized by algae (i.e. algae reduces the amount of available space between coral branches) (Munday 2001) and this may decrease the suitability of colonies for new settlers, independent of live coral loss (Öhman et al. 1998). However, relatively immediate reductions in the abundance and species richness of new settlers on dead in situ colonies that had accumulated only light algal growth (2 weeks) were apparent in this study. This observation suggests that the loss of live coral itself was responsible for decreased settlement (Garpe et al. 2006). An increasing array of work is now showing that a variety of cues (i.e. chemical, auditory and visual) can form vital indicators for reef naïve fish larvae to initiate benthic settlement behaviour (Lecchini et al. 2005a; Lecchini et al. 2005b). In the present study, degradation of experimental coral colonies may have reduced or even negated such settlement cues, resulting in significant declines in new settlers associating with the degraded habitat.

A range of factors may have increased the loss of new settlers on algal-covered corals between surveys (every 3–4 days), such as predation or interspecific competition for resources (Steele and Forrester 2002; Webster 2002). However, post-settlement exploration and movement of new settlers into preferred habitats may have occurred, independent of ontogenetic changes in habitat use (Webster and Hixon 2000; Munday 2001). Exploration of habitats at settlement is a well-known behaviour in both terrestrial and aquatic animals (Stamps and Krishnan 1995; Leis and

Carson-Ewart 2002; Hawkins et al. 2003). Habitat exploration is thought to allow animals to examine potential habitats (Leis and Carson-Ewart 2002), targeting habitats where reproduction and survival (i.e. fitness) will be highest (Haughland and Larsen 2004). Within the present study, exploration of aquaria habitats at dawn was found, with species moving between habitats before associating with a preferred habitat. As individuals utilising preferred habitats can show increased juvenile growth (Jones 1997; Munday 2001) or survival (Wellington 1992; Munday 2001), post-settlement movement into preferred habitats may have positive effects on the demographic structure of reef fish species (Munday 2004a). It is possible that in situ settlement occurs in two phases, beginning with a coarse-scale selection of appropriate habitat, followed by early post-settlement movement into preferred substrata (sensu Finn and Kingsford 1996; McCormick and Makey 1997) and may be an important behavioural choice for successful settlement and recruitment in a range of reef-associated fishes in degraded habitats.

Associations with algal biomass (including seagrass habitats and mangroves) at settlement have been shown in a small number of taxonomic groups (e.g. Green 1998; Shima 2001; Dorenbosch et al. 2005a; Dorenbosch et al. 2005b); however, few studies have examined the response of reef fish settlement to increased algal resources following coral degradation. The majority of work has focused on the role of algal resources in structuring the abundance and species richness of adults within degraded coral reef habitats (McClanahan et al. 1999, 2001). Such work has shown that the algal biomass can provide a considerable array of resources for a range of coral reef fishes, including sites for foraging (Ceccarelli et al. 2001; Townsend and Tibbetts 2004), shelter (Wilson 2001; Clarke and Tyler 2003) and reproduction (Neat 2001). However, this study provides some of the first evidence that shifts in reef fish community structure from the numerical dominance of live coral associates to

one where algal associates numerically dominate can occur through changes in fish settlement with coral degradation and algal biomass increase (but see Booth and Beretta 2002). Such alterations in reef fish settlement patterns following reef degradation may then have strong and persistent influences on the abundance and diversity of reef fish species closely associated with live coral habitats at settlement (Schmitt and Holbrook 2000).

This work has fundamental implications in understanding the response of coral-associated reef fishes to increasing levels of live coral degradation. As the availability of suitable live coral settlement habitat decline on degraded reefs, the abundance of several species may rapidly decline and be replaced by species that preferentially associate with degraded, algal-dominated habitats (Jones et al. 2004). We can predict that such changes in recruitment for these species may then interact with their longevity to determine the time scale of effects of live coral loss on community structure. Within fishes with short life spans and high population turnover rates, substantial reductions in new settler abundance and richness with live coral loss may have relatively immediate, negative effects on community replenishment (Munday and Jones 1998; Booth and Beretta 2002). In comparison, for longer lived species, we can predict that reductions in recruit abundance with live coral loss may have little effect on their population abundance in the short term, with significant effects on the community apparent at much longer time scales (Pratchett et al. 2006). Recent research has argued that phase delays in the response of the associated reef fish community to coral loss may be due to a coupling of the adult fish with the coral reefs' physical complexity (Graham et al. 2006). Broad reductions in the structure of reef fish communities may then be linked to the breakdown of the coral reefs' physical complexity (Lewis 1998; Syms and Jones 2000; Graham et al. 2006). Although the loss of the underlying coral reef structure will have detrimental effects on the community abundance of a range of reef-associated fishes (Sano et al. 1984; Gratwicke and Speight 2005; Wilson et al. 2006), we predict that reductions in the abundance and richness of newly settling coral-associated fishes with loss of the living coral tissue only may play a substantial role in altering the replenishment and ultimately the structure of their populations within degraded reef systems.

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