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Coral size, health and structural complexity: effects on the ecology of a coral reef damselfish

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ABSTRACT: The structure and dynamics of animal populations are strongly influenced by the physical and biotic characteristics of their habitats. However, in complex habitats such as coral reefs, the particular habitat features that are important and the mechanisms that impact on populations are poorly understood. This study investigates the influence of coral colony size, health and branching structure of the host coral *Seriatopora hystrix* on the ecology of the resident damselfish *Chromis retrofasciata*. Field observations indicated *C. retrofasciata* preferentially occupied larger *S. hystrix* colonies, but among occupied corals, group size was greatest on colonies of an intermediate size and with wider branch spacing. Healthy corals were observed to support higher abundances. The effects of both coral health (live vs. dead) and coral complexity (fine, medium and coarse branching) on survivorship of stocked juvenile *C. retrofasciata* were examined in a patch reef experiment. Survival was 20% higher in living colonies compared to dead ones, and fish in medium complexity coral exhibited approximately 10 and 20% greater survival than those in both the low and high complexity categories, respectively. These factors had an additive effect with the highest survival observed on healthy colonies with intermediate complexity (95%) and the lowest on highly complex, dead corals (55%). Body size distributions were also reduced on corals with the narrowest branch spacing. During habitat selection trials, juveniles were observed to preferentially occupy colonies with intermediate branch spacing. Prey may prefer corals of intermediate spacing and survive better as such habitats provide shelter that obstructs predator access. This study provides evidence that suggests small reef fish species will be sensitive to disturbances that result in the loss of live coral and alter preferred structural complexity of habitats.

KEY WORDS: *Chromis retrofasciata* · Coral reef · Reef fish · Habitat structure · Habitat complexity · Predation · *Seriatopora* · Survivorship

INTRODUCTION

It is widely acknowledged that habitat characteristics can be major drivers of the structure and dynamics of animal communities and their constituent populations (Bell & Galzin 1984, Wiens 1989). The quality of a habitat for any species can depend on numerous characteristics such as patch size, structural complexity and habitat condition (Anderson 1978, Gorman & Karr 1978, McIntyre 1995, Wilson et al. 2006, Thompson et al. 2007). These different habitat features can vary in their importance and differ in their influence on key ecological processes such as habitat selection and predation (Tolimieri 1995, Almany 2004b). Habitat characteristics appear to be particularly important in complex biotic habitats, such as rainforests (McIntyre 1995) and coral reefs (Friedlander & Parrish 1998, Jones & Syms 1998). However, given that there are numerous attributes of complex habitats that are potentially important, the key factors and the actual mechanisms by which they impact on populations are not always known, which limits our understanding of how populations will respond to habitat change.

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Variable patch size, coral health and physical structure have all been shown to influence population dynamics of coral-associated reef fishes (Tolimieri 1995, Holbrook et al. 2000, Holbrook & Schmitt 2003, Aburto-Oropeza et al. 2007, Thompson et al. 2007, Schiemer et al. 2008, Bonin et al. 2012). To date a range of responses have been observed for different habitat attributes. For example, patch size appears to determine group size for some coral-dwelling fishes (Schmitt & Holbrook 1999, Thompson et al. 2007), while for others, fewer, larger individuals control larger patches (Munday et al. 1998, Kane et al. 2009). Susceptibility to predation, recruitment success and sub-lethal condition have all been linked to changes in coral health, even for species that have no direct dependence on live coral (Feary et al. 2007b, Coker et al. 2009, McCormick 2009, McCormick et al. 2010). The shelter habitat structure affords an inhabitant results from the relative sizes of predators and prey, and the space each has access to (Hacker & Steneck 1990, Eggleston & Lipcius 1992, Wahle 1992, Hixon & Beets 1993). As such, the shelter provided by a given coral will differ both between fishes and between ontogenetic stages of single species (Dahlgren & Eggleston 2000, Pratchett et al. 2008a, Schmitt et al. 2009).

There is a need to better understand the role habitat characteristics play in structuring reef fish populations, particularly as coral reefs are now under pressure from a suite of threats that impact on a range of habitat characteristics (Jones & Syms 1998, Hughes et al. 2003, Bellwood et al. 2004, Munday et al. 2008, Pratchett et al. 2008b). Fish communities may respond to both changes in live coral cover and change in the physical structure of the habitat (Pratchett et al. 2008b), but the relative importance of these factors is not known. Distinguishing between the influence of live coral cover and structural complexity is not straightforward as these 2 components of habitat may be inextricably linked. That is, as the cover of complex coral increases, so does the overall complexity. Furthermore, corals that are most structurally complex are often those which are most susceptible to disturbances (De'ath & Moran 1998, Graham et al. 2006, Pratchett et al. 2008b), and rapid erosion and structural loss of the exposed skeleton soon follows tissue loss (Marshall & Baird 2000, Graham et al. 2006, Alvarez-Filip et al. 2009). For species of fish that occupy a structurally and biologically diverse range of habitat types, the influence of live coral cover is predicted to be minimal and habitat associations to be primarily governed by the need to shelter (Munday 2004, Wilson et al. 2008). However, the relative importance of these 2 critical components of habitat remains to be demonstrated.

To date, experimental studies that have examined the influence of coral habitat structure on associated fishes have compared structural differences between species of coral (see Jones 1988, Beukers & Jones 1998, Nemeth 1998, Almany 2004a,b, Bonin et al. 2008). The use of different coral species makes it difficult to isolate the effects of differences in structure from other potential differences between coral species. Many coral species exhibit substantial intraspecific morphological variation (Veron & Pichon 1976, Vytopil & Willis 2001, Schiemer et al. 2008, Kane et al. 2009) that may have a dramatic influence on the quality of the shelter they provide to fishes.

This study combined observational and experimental approaches to examine the significance of coral colony size, coral partial mortality and coral branching structure on the ecology of an associated damselfish. It utilised the naturally occurring morphological variation of a single coral species to examine the effects of microhabitat structure on the distribution and demography of the black bar chromis *Chromis retrofasciata*. Field surveys were employed to test whether patterns of *C. retrofasciata* abundance related to characteristics of the needle coral *Seriatopora hystrix* habitat. Experimental studies were then undertaken to test whether these habitat factors influence habitat selection, body condition and survival. An experiment using patch reefs was undertaken to understand how coral structural and health variants influenced predation rates and physiological condition of stocked early post-settlement *C. retrofasciata* recruits. We predicted that both habitat factors would be influential, but that the effects of coral health would be less than that of branching structure. A second experiment examined habitat selection preferences, based on structural variation, by early post-settlement *C. retrofasciata* recruits. We predicted individuals would show a preference for the branch structure for which maximum survivorship was observed.

MATERIALS AND METHODS

Study site and species

The study was conducted during October and November 2009 in Kimbe Bay, West New Britain Provence, Papua New Guinea (5° 30′ S, 150° 15′ E). Surveys and patch reef experiments were performed on the fringing reefs on the western side of the bay, adjacent to the Mahonia Na Dari (MND) research and conservation centre (Fig. 1). The region has a history of habitat disturbance; destructive fishing techniques were once common practice: extensive land clearance of low-lying coastal areas has led to increased sedimentation levels from terrestrial runoff; and coral bleaching and crown of thorns starfish outbreaks have also been recorded in recent years (Jones et al. 2004, Munday 2004).

The needle coral *Seriatopora hystrix* (Dana, 1846) is an abundant scleractinian coral of the family Pocilloporidae (Veron 1986). *S. hystrix* displays marked morphological variation in its branching structure, in response to the microenvironment in which it grows (Veron & Pichon 1976), ranging from those which are very compact, being composed of short branches that frequently bifurcate, to those which are more elongate and bifurcate infrequently (Veron & Pichon 1976). The morphological variation within this species is much larger than differences between some congenerics (e.g. *Acropora*) and is expected to influence patterns of habitat use by coral-dwelling fishes (Kane et al. 2009, Messmer et al. 2011).

The black bar chromis *Chromis retrofasciata* (Weber, 1913) is an abundant planktivorous damselfish (Pomacentridae), commonly found throughout Kimbe Bay. Although *C. retrofasciata* tend to associate with a broad range of scleractinian and non-scleractinian corals, as well as branching sponges, most individuals (62%) associate with *Seriatopora hystrix*. This is more than expected given *S. hystrix* abundance (Bonin 2012). Individuals are seen to forage above the colony during the day and retreat within the branching structure when threatened.

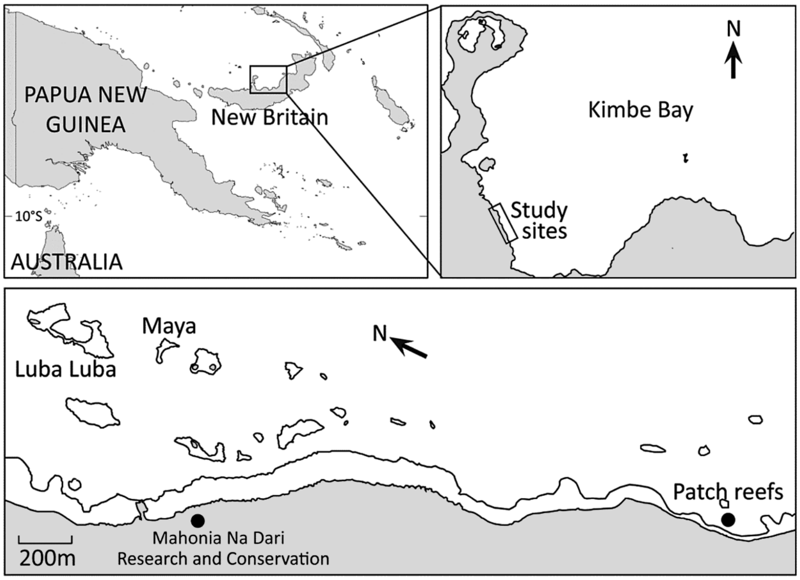

Fig. 1. Study site on the western side of Kimbe Bay, New Britain, Papua New Guinea. Location of the patch reef experiments and the 2 reefs surveyed are indicated

Patterns of habitat use

To assess patterns of habitat use in the wild, surveys were conducted on SCUBA at 2 reefs, Maya's and Luba Luba, in Kimbe Bay (Fig. 1). Surveys were conducted over a depth range of 1 to 25 m around the entire circumference of both reefs. Surveys commenced at a depth where a pair of divers following the contour of the reef encountered the deepest *Seriatopora hystrix*, and systematic sampling of all shallower colonies followed. Microhabitat characteristics of all *S. hystrix* colonies encountered, regardless of the presence or absence of *Chromis retrofasciata* individuals (n = 154 colonies), as well as visual estimates of the size and number of any associating *C. retrofasciata* were recorded. The error in size estimations of *C. retrofasciata* individuals was examined before the surveys proper commenced. To do so, the observer visually estimated the size of all *C. retrofasciata* inhabiting a colony of *S. hystrix* before capturing them with a net and clove oil-ethanol mixture and measuring them *in situ* with callipers. Surveys commenced once error in size estimation was consistently <10%. Throughout the study a single observer estimated *C. retrofasciata* size to minimise bias.

The depth below the surface, size, extent of partial mortality and structural characteristics were recorded for every colony of *Seriatopora hystrix* encountered. Coral size was estimated as a hemisphere (Jokiel & Morrissey 1986) using the mean of the maximum colony diameter, a perpendicular central diameter and height. This geometric estimation was used to quantify the size of colonies at its peripheries where fish larger than the branch spacing would be excluded. Coral mortality was visually estimated to the nearest 10%. A quantitative index of habitat complexity was obtained by counting the number of branch tips that occurred within a 10 × 10 cm quadrat placed over the centre of the colony, whereby the higher the number of branch tips per quadrat, the tighter the branch spacing. Colony height was recorded as the distance from the base of the colony to the top. For each coral colony, branch depth and spacing measurements were recorded with the wire end and nose of a pair of callipers, respectively, for 5 branch pairs. The 5 replicates of each branch metric were later averaged to give a single value for each per colony. Survey data were later used to compare characteristics of *S. hystrix* that contained resident *Chromis retrofasciata* to those which did not.

A multiple regression was carried out to determine the extent to which colony size, percent mortality, complexity, depth, height, branch spacing, branch depth, mean *Chromis retrofasciata* size and the number of other damselfishes as predictor variables explained variation in the group size of *C. retrofasciata* between colonies. Multiple regression models were optimised using a forward stepwise protocol and autocorrelations were considered visually with a correlation matrix. Those colonies supporting resident *C. retrofasciata* were classified as occupied, while those without were unoccupied. Data were pooled between reefs as there was no difference in the mean number of *C. retrofasciata* per colony of *Seriatopora hystrix* between the reefs (ANOVA: $F_{(1,152)} = 2.37$, $p > 0.1$). ANOVA was used to compare colonies based on their occupancy or various characteristics of habitat. Where appropriate, Type I sum of squares was used in unbalanced ANOVA. All reported ANOVA results satisfied the assumptions of homoscedasticity, Gaussian distributions and independence.

Effect of host structure and health on survivorship and condition

An orthogonal patch reef experiment was conducted to test whether survivorship of juvenile *Chromis retrofasciata* varied with respect to 2 factors: (1) host coral health, and (2) structural complexity. The survivorship of stocked juvenile *C. retrofasciata* was monitored between *Seriatopora hystrix* patch reefs that differed in health (2 levels: alive and dead) and complexity (3 levels: low complexity = wide branch spacing; medium complexity; and high complexity = narrow branch spacing), including the fully crossed combinations of these factors. This factorial design equated to 6 separate treatments which were replicated 5 times each, resulting in 30 patch reefs. Patches consisted of a circular rubble base, with a diameter of approximately 80 cm, upon which a single colony of *S. hystrix* was affixed.

The patch reef matrix was constructed approximately 10 km south of the MND research and conservation centre, on a large sandy section approximately 100 m offshore at a depth of 3 to 7 m. A compass and tape measure were used to layout the patches, ensuring each patch was separated from other patches by at least 15 m and located no less than 20 m from other reef structure to minimise patch migration. Colonies were visually categorised into 1 of 3 complexity levels based on their branching structure, with the numbers of branch tips per quadrat of these groups then compared using the quadrat technique from the surveys and were deemed to be from statistically separate populations between complexity levels (ANOVA: $F_{(1,24)} = 38.37$, $p < 0.001$, Tukey's honestly significant difference [HSD], all $p < 0.02$).

Having sorted colonies by structure, half within each category were then placed in fresh water for 10 d to remove all live tissue with water being replaced twice daily, after which colonies were then left in direct sunlight for 8 h. These cleansing measures were imposed in an attempt to ensure dead corals were only providing structural shelter to associated fish, eliminating the contribution of live coral tissue or algal colonisation. The complexity of corals were considered homogeneous between the coral health levels (ANOVA: $F_{(1,24)} = 0.78$, $p > 0.3$).

Previous studies have shown that branch space increases with colony size (Kuwamura et al. 1994, Schiemer et al. 2008, Kane et al. 2009). To account for this, colony size was kept constant for the different treatments (largest diameter range 21 to 28 cm). Measurements indicated that colony size was not statistically different for either the complexity (ANOVA: $F_{(1,24)} = 2.98$, $p > 0.05$) or health (ANOVA: $F_{(1,24)} = 3.07$, $p > 0.05$) treatments. These colonies were then cleared of all resident fish with clove oil and placed into the experimental matrix using block randomisation. Mean patch depth was considered statistically the same for all complexity (ANOVA: $F_{(1,24)} = 0.66$, $p > 0.5$) and health levels (ANOVA: $F_{(1,24)} = 0.15$, $p > 0.5$).

Juvenile *Chromis retrofasciata* to be used in the experiment were collected from 3 reefs within 10 km of the patch reefs. All fish were tagged using a subcutaneous tag of fluorescent elastomer in the muscle block above the lateral line to uniquely identify all fish belonging to each patch. Fish were tagged 12 h prior to placement on the patch reefs to identify any immediate mortality due to this procedure. Before stocking, any other fish that were associating with the patches were removed. Each patch was then covered with a 1 m^3 mesh cage with 0.2 cm mesh, and 8 juvenile fish were stocked per patch and allowed to settle into their new habitat. Patches were stocked over a 4 d period with patches remaining under the mesh cages for a minimum of 6 h. This technique minimised any immediate emigration at stocking, which was limited to a single incident. In this case, another juvenile was stocked with an elastomer tag colour not used in the vicinity and was observed to survive for many days into the experiment (the emigrant was never relocated). The experiment was considered operational immediately after the cages were removed.

Daily counts of remaining *Chromis retrofasciata* were conducted on each patch to quantify persistence of tagged fish. Once settled, no movement of juvenile *C. retrofasciata* was observed between patches during the daily monitoring. As a result of this apparent lack of movement, any reduction in stocked numbers was attributed to *in situ* mortality. The small, vulnerable size of juveniles and their reliance on shelter habitat made it unlikely for them to traverse the great distance of open sand to other reef structures.

After 30 d of observations, any remaining juvenile *Chromis retrofasciata* were collected and euthanized with an overdose of clove oil to test for differences in physiological condition between habitat treatments, based on Fulton's condition factor, following Feary et al. (2009). Fulton's condition factor (K) was defined as $K = WB \times 100L^{-3}$; where WB is the gutted body weight (g) and L is the standard length (mm). High K values indicate individuals are heavier for a given length, implying greater physiological condition. Fish weight was measured to the nearest 0.001 g using a HA-series digital balance. Two-way ANOVA was used to compare the Fulton's K between the treatments.

Survival analysis was used to compare the survival curves from the patch reef experiment between the complexity and coral health treatments (Kaplan-Meier survival). The Kaplan-Meier method is a non-parametric estimator of survival that compares survival curves, rather than simply comparing the mean survivorship at the termination of the experiment (Coker et al. 2009). This technique also takes into consideration the survival time of individuals that died during the experiment (uncensored) and those that survived until the trial's end (censored).

Effect of host structure on habitat preferences

To determine whether structural characteristics of habitat would influence the habitat selection of early-stage post-settlement juvenile *Chromis retrofasciata,* the preferences of individual fish for colonies of increasing complexity were tested in the field. Three colonies of *Seriatopora hystrix* of equal size (24 to 27 cm maximum diameter) but varying complexity were laid out on a 3 m deep sandy patch *in situ,* at angles of 60° and 50 cm apart. All 3 colonies were then enclosed within a large barrier net, with a 0.5 cm mesh size, to prevent experimental juveniles fleeing the area and/or the interference of other fish.

Each trial was conducted by placing one juvenile at a time in the centre of the colonies, under a transparent plastic container. This container was weighted down and attached to a surface line and float. The juvenile was allowed a 2 min period in which to settle after placement under the container, and to survey the potential habitats with which it was presented. After this time, an observer at the surface would slowly lift the plastic container, allowing the juvenile access to the colonies. The initial choice was compared to habitats used after a settlement period of at least 6 h (more often overnight) as initial selection may have simply been a flight response. The order of coral complexities was rotated after each trial to avoid any effect of colony location. Proportional differences in occupancy between the complexity levels after the settlement period were compared using a chi-squared homogeneity test.

RESULTS

In situ distributions in relation to habitat characteristics

A total of 154 *Seriatopora hystrix* colonies were surveyed, of which 78 were inhabited by *Chromis retrofasciata* (50%). Group size ranged from 1 to 15 fish per colony with a median of 3 individuals for inhabited colonies (Fig. 2). The mean (±SE) volume of

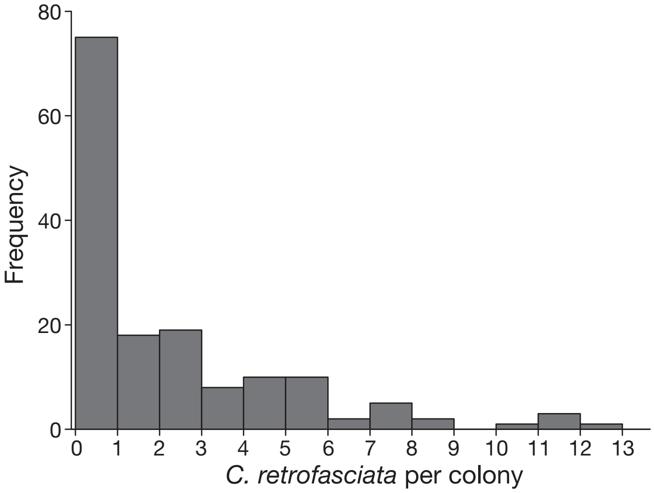

Fig. 2. *Chromis retrofasciata* occupying *Seriatopora hystrix.* Frequency histogram of the number of damselfish per coral colony. N = 154

occupied colonies (1692.9 ± 145.6 cm^3) was significantly larger than unoccupied colonies (1244.6 ± 117.9 cm^3) (ANOVA: $F_{(1,151)} = 7.89$, $p < 0.01$). Occupied colonies also had significantly less branch tips per quadrat (indicative of wider branching or lower complexity) compared to unoccupied colonies (ANOVA: $F_{(1,152)} = 6.59$, $p < 0.02$).

Variations in the group size of *Chromis retrofasciata* among occupied *Seriatopora hystrix* colonies were explained (ANOVA: $F_{(3,74)} = 4.35$, $p < 0.001$) based on differences in colony size ($\beta = 0.00054$, $p = 0.029$) and depth ($\beta = 0.158$, $p < 0.01$). During model optimisation, colony height and colony size, as well as branch spacing and complexity were found to co-vary. The variable that explained the least variability, in each of these pairs of variables, was excluded during the stepwise model formulation as they did not explain significantly more variation when both were included in the model. The covariation observed between branch spacing and complexity confirms the validity of the quadrat technique, indicating that as the number of branch tips per quadrat decreased, the branch spacing increased. The explanatory variables in the final model were not seen to co-vary. Overall, this model could only account for 11.5% of the variation in the number of *C. retrofasciata* per colony of *S. hystrix*. The partial mortality and structural complexity of coral colonies had no apparent influence on *C. retrofasciata* group size ($p > 0.05$). However, the maximum number of *C. retrofasciata* per colony was greatest for colonies of an intermediate size (Fig. 3). The 'envelope' containing the observed values shows that both small and large colonies are unable to support high numbers of *C. retrofasciata*. Similarly, *C. retrofasciata* abundance was maximised on colonies with the lowest partial mortality (Fig. 4). None of the predictive variables measured were able to account for the observed *C. retrofasciata* size distributions.

Throughout the surveys, no correlations were detected between *Seriatopora hystrix* size, complexity or percent live tissue or between the abundance of *Chromis retrofasciata* and *C. retrofasciata* mean size (Table 1).

Experimental evaluation of the effects of coral structure and health on fish survival and condition

The experimental manipulation showed that survivorship was significantly higher on live corals, compared to dead corals (Cox's *F*-test: $F_{(34,80)} = 2.539$, $p < 0.001$). Initial declines were observed on

Table 1. *Chromis retrofasciata* occupying *Seriatopora hystrix.* Results of linear regression analyses between the different characteristics of *S. hystrix* colonies and between the number and mean size of inhabiting *C. retrofasciata*

Dependent variable	Independent variable	β	R^2	*t*	p
Colony complexity	Colony size	–0.081	0.006	–1.000	0.319
Percent live coral	Colony size	–0.147	0.022	–1.826	0.070
Colony complexity	Percent live coral	0.005	<0.001	–0.057	0.954
C. retrofasciata size	No. *C. retrofasciata*	0.048	0.002	0.658	0.511

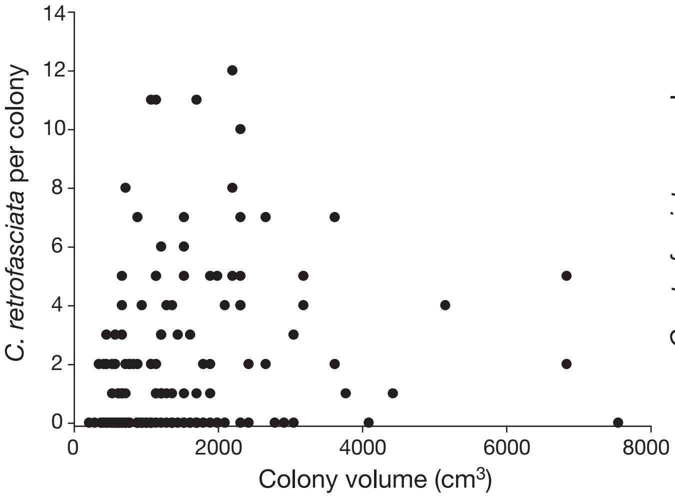

Fig. 3. *Chromis retrofasciata* occupying *Seriatopora hystrix.* Relationship between coral colony volume and the number of resident damselfish. N = 154

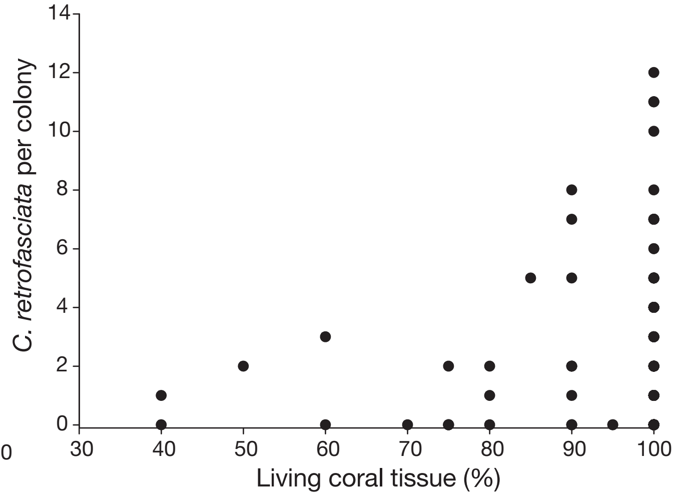

Fig. 4. *Chromis retrofasciata* occupying *Seriatopora hystrix.* Relationship between the percent living tissue per coral colony and the number of resident damselfish. N = 154

both live and dead colonies. However, the rate of decline remained higher on dead corals (Fig. 5a). At the end of the 30 d trial, 67 and 86% survival were observed on the dead and live treatments, respectively.

The structural complexity of coral habitat was also shown to influence survival (survival analysis: χ^2 = 10.22, df = 2, $p < 0.01$). While losses were observed for each of the complexity categories, the lowest survival was recorded with the high complexity corals (tightest branching structure), followed by the low then medium complexities due to differential rates of decline (Fig. 5b). Here, 65% survival was recorded with the high complexity corals compared to 79 and 85% with the low and medium complexity categories, respectively.

No statistical interaction was observed between the 2 orthogonal treatments (coral health and complexity), indicating that the magnitude of the effect of one factor is not dependent on the other. Overall, survivorship was highest on live corals with medium complexity (95%) and lowest on dead corals with high complexity (55%).

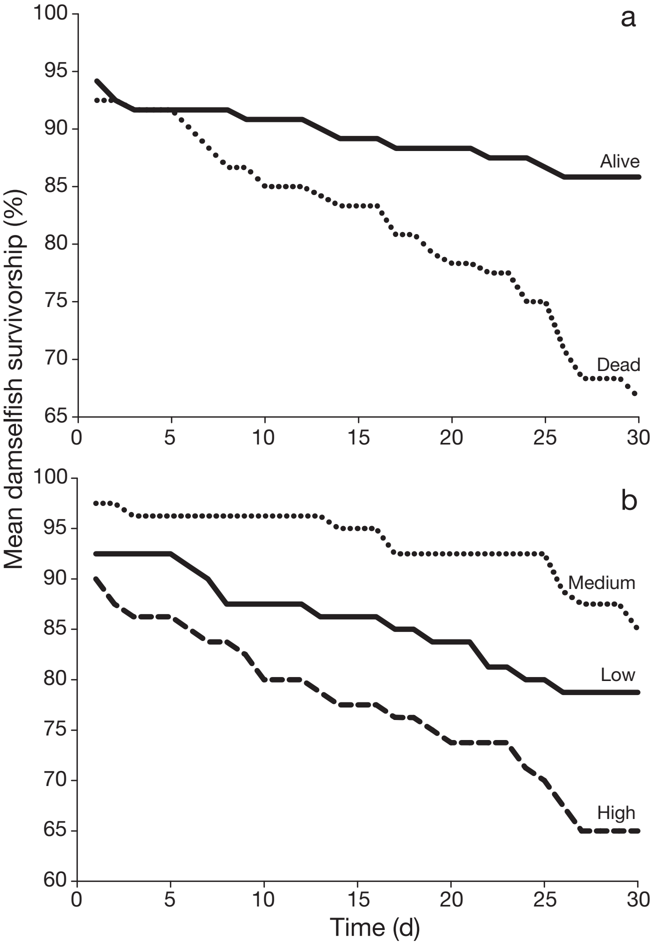

Fig. 5. *Chromis retrofasciata* occupying *Seriatopora hystrix.* Mean survivorship of the 8 stocked juvenile damselfish between (a) the live and dead treatments (n = 15 for each treatment) and (b) the 3 complexity treatments (n = 10 for each treatment); high, medium and low. Mean total SE = 7.2%

Numerous piscivorous fishes were observed within the study area, including trevallies (Carangidae), juvenile snappers (Lutjanidae), lizardfishes (Synodontidae) and flounders (Bothidae) that are known to prey upon juvenile damselfish (Holbrook & Schmitt 2002). A predation event was also observed during a daily census, whereby a cryptic lizardfish captured a juvenile *Chromis retrofasciata* that strayed slightly from its patch.

The size distributions of remaining recruits differed between the patch complexity levels. On highly complex coral heads, where branch spacing was reduced, the mean (±SE) standard length of remaining recruits was 17.32 ± 0.2 mm, compared to 18.93 ± 0.4 mm and 18.30 ± 0.2 mm for the medium and low complexities, respectively. As such, the remaining recruits on the highly complex coral heads were significantly smaller than the other 2 complexity categories, which were considered homogenous (ANOVA: $F_{(1,24)} = 9.31$, $p < 0.002$, Tukey's HSD).

A comparison of the physiological condition of the surviving recruits at the end of the experiment indicated that there was little effect of the treatments on condition. There was also no significant difference in Fulton's K between the health ($F_{(1,24)} = 1.08$, $p > 0.3$) and complexity ($F_{(1,24)} = 1.99$, $p > 0.1$) factors or their interaction ($F_{(2,24)} = 3.105$, $p > 0.05$).

Effect of coral branching structure on habitat selection

The 3 habitat complexity categories had a statistically significant effect on patterns of habitat selection by *Chromis retrofasciata* juveniles (chi-squared homogeneity: χ^2 = 6.62, df = 2, $p < 0.05$). Initial selection tended to favour the low complexity category (Fig. 6). However, after the settlement period the medium and low complexity corals were utilised in even proportions. If the medium complexity colony was initially selected, no later movement was detected after the settlement period. Two of the 7 juveniles choosing low complexity corals moved into the medium complexity corals, while the single juvenile that initially chose a high complexity coral was later observed in the medium complexity coral. The highly complex category was never inhabited after the settlement period (Fig. 6).

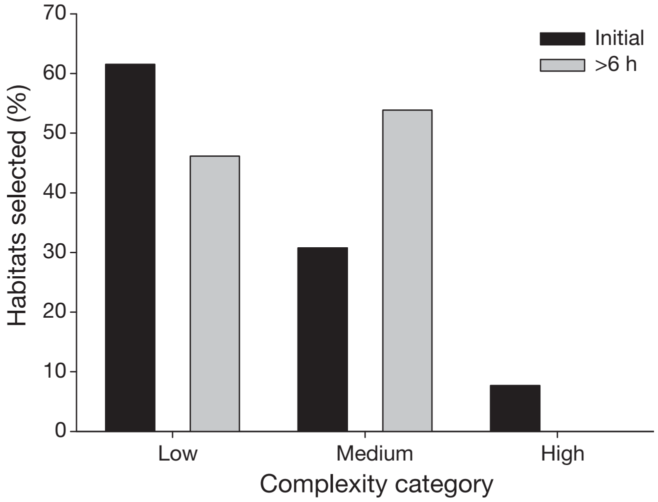

Fig. 6. *Chromis retrofasciata* occupying *Seriatopora hystrix*. Proportions of the habitats selected by *C. retrofasciata* recruits of differing complexity. Initial choice is compared to habitats utilised after a settlement period of at least 6 h. n = 13

DISCUSSION

This study confirmed that a range of different habitat characteristics can influence the ecology and behaviour of a reef fish closely associated with the coral substratum. Variation in colony size, partial mortality and branch spacing of a single coral species (*Seriatopora hystrix*) all contributed in some way to explaining variation in group size, juvenile survival and habitat selection in the damselfish *Chromis retrofasciata*. Observational studies showed that group size was greatest on corals with an intermediate size and that occupied colonies were consistently larger and had wider branch spacing than unoccupied colonies. Coral partial mortality was also observed to influence group size, with 100% healthy corals supporting the largest groups. The experimental manipulation of coral health and branch spacing clearly showed that the survivorship of juvenile *C. retrofasciata* is influenced by the branch spacing and health of coral habitat. Here the lowest survival was observed in dead corals and those with the closest branch spacing and that the effects were additive when these factors were combined. The importance of branch spacing was also illustrated by the habitat choice experiment, which showed that juvenile *C. retrofasciata* actively avoid corals with the closest branch spacing.

The group size of *Chromis retrofasciata* was strongly influenced by the size of coral hosts, with the largest group size detected on intermediate-sized corals. Group size has been seen to correlate with patch size for a number of other coral-dwelling damselfishes (Sale 1972, Fricke 1980, Schmitt & Holbrook 1999, Holbrook et al. 2000). The interior portion of a coral colony provides inhabitants with the most protection from predation (Holbrook & Schmitt 2002), raising the carrying capacities of larger colonies (Jeffries & Lawton 1984, Thompson et al. 2007). The observed decline in group size on larger colonies in the present study may be due to either sampling limitations (as there were few large colonies) or other ecological processes; larger patches may sustain potential predators or competitors that could reduce *C. retrofasciata* abundance (Belmaker et al. 2009, Schmitt et al. 2009). Other potentially limiting factors (larval supply, colony depth etc.) may have obscured the observed relationship between patch size and *C. retrofasciata* abundance; however, results suggest that smaller colonies are less preferable as they were uninhabited more frequently.

There is increasing evidence that suggests the health of coral habitat may be important for the survivorship and health of coral-dwelling fishes (Jones et al. 2004, Wilson et al. 2008, Coker et al. 2009, Feary et al. 2009, McCormick 2009, McCormick et al. 2010, Bonin et al. 2012). In the present study, both observational and experimental components indicated the maximum number of *Chromis retrofasciata* per colony was influenced by the amount of living coral tissue. Colonies with higher partial mortality were unable to support the larger groups seen in healthy colonies. The small group sizes seen in corals with higher partial mortality may be primarily due to differential predation. Partial colony mortality has been shown to have little influence on the settlement decisions of closely related damselfishes, and damselfish are unlikely to relocate to alternate habitats once settled (Feary et al. 2007a). Recent behavioural studies of damselfish occupying corals of degraded health have shown that these colonies attract increased mortality rates. Dominant individuals can force subordinate conspecifics out of degraded colonies (McCormick 2009), and prey species may be more conspicuous against a backdrop of degraded coral (Coker et al. 2009), both of which increase susceptibility to predation. It may be that, in the search for shelter, settling fish will not discriminate between habitats based on partial mortality (Feary 2007, Feary et al. 2007a); however, these corals ultimately have lower total carrying capacities. This response may simply be due to a detectable degradation in habitat quality as its integrity is beginning to fail (i.e. via later erosion of structure). If this was the case, it could be predicted that a similar response would be observed for *C. retrofasciata* inhabiting other forms of degraded habitat including branching sponges and is something that requires further investigation.

Variations in the branching structure of *Seriatopora hystrix* colonies were shown to influence the distributions of resident *Chromis retrofasciata*. Observations indicated that occupied colonies had wider branch spacing than those without resident *C. retrofasciata*. Shelter sizes in colonies with narrow branch spacing may have been too small to allow easy access for *C. retrofasciata* and subsequently provided little effective shelter (Hixon & Beets 1993). Holbrook & Schmitt (2002) showed that juvenile damselfish were 5 times more likely to be eaten by small predators that were closer to their own body size than larger ones, and subsequently chose shelter sites that exclude access to slightly larger predators (Shulman 1984, Hixon & Beets 1993, Caley & St. John 1996). In the survival experiment of this study, colonies with intermediate branch spacing could house the highest number of individuals. These colonies may accommodate an overlap of fish that are either too large to occupy small shelter sites or small individuals that receive little shelter from refuges much larger than their own body size (Hixon & Beets 1993, Almany 2004a).

The observed differences in total length of *Chromis retrofasciata* between colonies with different branch spacing further supports the idea that shelter size may influence the body size of associates. The mean body length of remaining recruits from the survival experiment was seen to be lowest in colonies with narrower branch spacing. This may have been due to either size selective mortality or differential growth between colonies. There is some indication that coral branch space may influence growth rates of coral-dwelling fishes, where smaller maximum size is attained in corals with tighter branch spacing (Munday 2001). Moreover, larger individuals may not be able to shelter within the small sites offered by the highly complex corals (Kane et al. 2009). Observed ontogenetic habitat shifts in reef fishes between separate coral species with different structures are frequently attributed to this need for differentially sized shelter as fish grow (Holbrook et al. 2000, Wilson et al. 2008, Belmaker et al. 2009). Unfortunately it is not possible to assign causation in this case, as length measurements were not attained prior to the commencement of the experiment.

Increased habitat complexity is often predicted to be beneficial for reef fishes as it can reduce encounter rates between predators and prey and modify predators' search and capture capabilities (Jones 1988, Beukers & Jones 1998, Almany 2004b). However, numerous lines of evidence in the present study indicated colonies of *Seriatopora hystrix* with the narrowest branch spacing (high complexity) were not preferable habitat for *Chromis retrofasciata.* Juvenile *C. retrofasciata* were seen to actively avoid highly complex colonies, preferring those with larger shelter sites. Reef fish have long been known to actively select settlement sites (Sale et al. 1984, Victor 1986, Danilowicz 1996, Lecchini et al. 2007), and this choice may have fitness consequences that are realised at an early stage. Juveniles are most vulnerable shortly after settlement and high initial mortality is common (Holbrook & Schmitt 2002, Almany & Webster 2006). Even if juveniles successfully recruit to colonies with narrow branch spaces, larger shelter sites will be required as they grow. Any habitat shifts come with increased exposure to predation, and it may be that larger shelter sites are sought in order to maximise body size attainment before relocation is required (Munday & Jones 1998).

This study has shown that the structure and health of coral habitat can influence the population dynamics and demographics of a coral-dwelling fish. Effects were seen for these 2 habitat characteristics in isolation and in combination with one another. Experimental survival was shown to be highest in live corals with medium branch spacing and lowest in dead colonies with the tightest branch spacing. Similarly, the survey data indicated that closer branch spacing and increasing partial mortality resulted in smaller maximum group sizes. This provides further evidence for the growing recognition that the health of coral habitat influences the wider reef fish community (Jones et al. 2004, Feary 2007, Munday et al. 2008, Wilson et al. 2008, Coker et al. 2009) and that sustained declines in both coral cover and coral health will have important ramifications for coral-dependent organisms such as *Chromis retrofasciata.* Furthermore, the fact that weaker effects were seen in colonies with wider branch spacing indicates that the complexity of *Seriatopora hystrix* may rarely be low enough under natural conditions to reduce the shelter offered to this species (hence the preferential association). The documented erosion of habitat complexity following live coral tissue loss, however, may reduce complexity enough to limit the shelter colonies of *S. hystrix* can provide. These findings indicate that fish species will be influenced by disturbances that affect not only the amount of live coral of preferred species, but also the patch size and structural characteristics.

Overall, this study indicates that potential carrying capacities or the availability of suitable habitat may not always depend on the abundance of a coral species. Heterogeneity in habitat quality needs to be considered in conjunction with habitat quantity in order to better understand ecological processes and species distributions. Future studies need to investigate what actually constitutes habitat quality, for individual species or species groups, by controlling for the effects of different habitat characteristics. These studies would allow for more accurate predictions of how habitat-dependent animals may respond to habitat disturbances.

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