Biotic and multi-scale abiotic controls of habitat quality: their effect on coral-reef fishes

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ABSTRACT: The influence of habitat quality on a species' demographics is critical for understanding its ecology and effective conservation. However, quantifying habitat quality is problematic because it may comprise of abiotic components at different spatial scales and also be influenced by biotic processes. This study investigated the relationship between reef-associated Caribbean fishes and habitat quality at 2 spatial scales: (1) multiple characteristics of *Montastraea annularis* coral colonies (<1 m^2) and (2) coral density in a 5 × 5 m plot around each microhabitat. Furthermore, the influence on habitat quality of 2 biotic factors (predation pressure and interactions between competitively superior territorial damselfishes and other species) was considered. A total of 102 *M. annularis* colonies within thirty 25 m^2 plots were surveyed on a Belizean forereef. Generalised linear mixed-effect models demonstrated that both damselfishes and other reef-associated species were correlated with colony-scale habitat quality (more abundant on taller, refuge-rich colonies). Adult reef-associated species were also correlated with larger-scale habitat quality, being more abundant on colonies with high densities of other *Montastraea* colonies within 25 m^2 (probably higher quality home ranges). However, the presence of damselfishes was associated with reduced abundances of other reef-associated species on *M. annularis* colonies, reflecting the importance of both biotic and abiotic controls of habitat quality. On reefs, coral mortality will reduce the density of optimal colonies and potentially increase the proportion occupied by damselfishes. This may lead to smaller populations of inferior competitors as they are increasingly displaced onto sub-optimal microhabitats.

KEY WORDS: Anthropogenic stress · Community ecology · Ecosystem degradation · Fish behaviour · Fish recruitment

INTRODUCTION

Habitat quality is a key variable affecting the distribution, abundance, and demographic rates of species, and a full appreciation of its controls has important implications for conservation (e.g. Franklin et al. 2000, Fleishman et al. 2002). Despite its importance, assessing habitat quality is frequently problematic because it requires an understanding of a range of biotic and abiotic factors that may vary at multiple spatial and temporal scales, and may change during an organism's ontogeny (Mueller et al. 2009). Consequently, there is a growing literature considering habitat quality through a combination of biotic and abiotic factors (e.g. Shima et al. 2008), habitat quality at different scales (e.g. Mueller et al. 2009), and how habitat quality affects different age classes of species (e.g. Bacheler et al. 2009). A greater multi-scale understanding of the controls of habitat quality is vital because the loss of suitable habitat is the great-

est threat to the survival of species worldwide (Barbault & Sastrapradja 1995).

Coral-reef fishes represent an excellent model system for investigating the controls of habitat quality. Reef fishes are diverse, relatively easy to census, and many species are closely associated with benthic communities that provide them with spatially variable resources at a range of scales. For example, coral growth and bioerosion creates small-scale crevices that are critical for most reef-associated fishes (Hixon & Beets 1993), and corals providing such refuges support higher abundances of fishes (Holbrook et al. 2002). These refuges provide foraging, spawning, and nesting sites (Robertson & Sheldon 1979), can help fishes maintain themselves in high-flow environments (Johansen et al. 2008), and sheltering in refuges reduces the high risk of predation on reefs (Hixon 1991). Loss of this scale of complexity, from stressors such as bleaching and hurricanes, has been demonstrated to have dramatic effects on reef-associated species (Jones & Syms 1998, Wilson et al. 2006, Pratchett et al. 2008). However, in addition to coral colony-scale complexity, spatially variable coral recruitment and survival leads to changing densities of colonies across reefs. The influence of this larger-scale complexity on reefs (tens of square metres) is poorly understood, but may affect the hunting efficiency of predators that actively chase prey (Eklöv & Diehl 1994), decrease agonistic encounters between territorial and non-territorial species (Levin et al. 2000), alter settlement patterns (Stier & Osenberg 2010) and provide a wider range of foraging sites within fish home ranges.

Here we quantify habitat quality at both of these 2 nested spatial scales: the smaller microhabitat scale, which occurs within individual coral colonies and includes variables such as colony size and number of crevices, and the larger-scale density of colonies in the surrounding area. Although produced by biotic processes, primarily coral growth, these benthic habitat quality variables are categorised as abiotic as they are functionally different from biotic processes affecting fish abundances, such as predation and competition. We then consider the effects of these multi-scale metrics of abiotic habitat quality on reef-associated Caribbean reef fishes by assuming that high abundances of fishes will be correlated with high-quality habitat traits. Note that this study does not attempt to provide insights into the detailed mechanisms causing the variations in fish abundances, which will be a complex combination of factors such as settlement and post-settlement habitat choices and subsequent survival (e.g. Tolimieri 1998,

Schmitt et al. 1999, White & Warner 2007, Shima et al. 2008). We link habitat quality to adult and juvenile fishes separately because different life-phases within an ecological community may have different habitat requirements (Almany 2004a). By considering different functional aspects of habitat quality, this study provides greater insights into the proximate drivers of fish abundance than the well-established correlations with overall coral cover (e.g. Bell & Galzin 1984) or rugosity at a single scale (e.g. Luckhurst & Luckhurst 1978).

Combining these abiotic assessments of habitat quality with biotic considerations is critical because there may be a significant difference between fundamental habitat quality (habitat quality in the absence of competition) and the realised habitat quality experienced by competing individuals (Johnson 2007), as previously demonstrated for coral-reef fishes (Munday 2001). There are a range of biotic processes occurring within reef fish communities, including larval supply (Doherty & Fowler 1994), predation (Hixon 1991) and competitive interactions (Munday et al. 2001), and many are affected by habitat complexity (Almany 2004a,b, Geange 2010). This study aims to provide new insights into how the combined influences of multi-scale abiotic habitat quality, predation pressure and competition affect reef fish abundances. The competitive interaction considered in this study is the territorial behaviour of damselfishes. Many adult damselfishes pugnaciously defend territories against intruders in order to maintain both food resources and egg masses (Robertson 1996), and the aggressive adults are the superior competitors in a range of asymmetric interactions with other fish species (Foster 1985, Sweatman 1985, Carr et al. 2002). Abiotic habitat quality and predation pressure are likely to affect all reef-associated species, but the competitive dominance of damselfishes may represent an additional biotic control on the abundance of non-damselfishes. Furthermore, the competitive interaction between damselfishes and other species on Caribbean reefs may have increased dramatically since the disease-induced loss of *Acropora cervicornis* that has led to reductions of this primary damselfish habitat and increased damselfish use of other coral species (Precht et al. 2010).

In summary, this study aims to provide novel insights into how the abundances of different components of an ecological community are determined by both biotic and multi-scale abiotic factors that control habitat quality. We tested 3 hypotheses: (1) the abundances of reef-associated fishes are influ-

enced by abiotic habitat quality at both coral colony-scale and the larger-scale metric of density of surrounding corals, (2) biotic factors (competition and predation) significantly affect fish abundances and change fish abundances predicted by patterns of abiotic habitat quality alone, and (3) the most aggressive damselfish species will have the greatest competitive influence on the abundance of other reef-associated species.

MATERIALS AND METHODS

Study site

The study was conducted in March 2009 on a section (<2 km) of the Belize Barrier Reef, just south of Carrie Bow Cay (16° 48.173′ N, 88° 4.928′ W). Using a small section of reef for the entire study minimised the variation in potentially confounding factors such as larval supply and fishing pressure. All surveys were conducted within the species-rich 'Montastraea reef' habitat (forereef habitats visually dominated by Montastraea corals) at a depth of ca. 10 m and <100 m from the escarpment. The dominant Montastraea annularis (sensu stricto) (Ellis & Solander, 1786) represented the microhabitat scale considered, and the density of Montastraea spp. colonies surrounding each focal colony represented the larger scale of complexity. M. annularis is the primary reef-builder in the Caribbean, and colonies are formed by thick columns with living tissue only found on the top of the columns (Weil & Knowlton 1994). These upper surfaces form a series of distinct lobes (ramets) separated by crevices which, along with the chambers among the columns, are used as refuges by fishes (Ebersole 1985). In addition to being one of the most structurally complex corals in the Caribbean (Ebersole 1985), M. annularis colonies support a variety of gorgonians that provide additional fish refuges. Individual M. annularis colonies were separated by areas of reef framework covered by a thin layer of carbonate sand and rubble.

Plot-scale surveys

In order to categorise the larger scale of complexity, 30 plots of 5 × 5 m were haphazardly chosen and delineated by tape measures (subsequently 'plot-scale' complexity). Most of the fishes associated with coral colonies are small, and a plot of 25 m^2 is appropriate for the home ranges of fishes less than ca.

8 cm (Kramer & Chapman 1999). During a period of 10 min within each plot, all piscivorous fishes were identified, counted, and sized to the nearest cm (see Supplement 1 at www.int-res.com/articles/suppl/m437p201_supp.pdf for a list of species). Plot-scale, rather than colony-scale, estimates of piscivory were used because relatively site-attached 'resident' predators have large home ranges (Popple & Hunte 2005) and the even more mobile transient predators also have important effects on prey densities (Hixon & Carr 1997). Biomass data are most appropriate for the consideration of trophic relationships among fish (Bohnsack & Harper 1988). Therefore, the total biomass of piscivorous fishes within each plot was calculated using allometric relationships (Bohnsack & Harper 1988). Large-bodied serranids are not significant predators of juvenile fishes (Stallings 2008), and were excluded from the predation variable included in explanatory models of juvenile reef-associated species. Other taxa that are most appropriately measured at this plot scale (such as roaming herbivores) were not recorded because they are unlikely to have direct effects on reef-associated fishes. Following each fish survey, Montastraea spp. colonies were counted and their heights recorded to assess plot-scale complexity (Fig. 1).

Montastraea annularis colony-scale surveys

Within each 25 m^2 plot, between 1 and 4 Montastraea annularis colonies (total = 102 colonies) were randomly selected and surveyed (Fig. 1). The few colonies in the plots that were obviously cleaning stations were avoided. Firstly, the species and life-phase (determined by colouration or a size of <4 cm for species without distinct colour phases) of all non-piscivorous fishes associated with the colony were recorded (see Supplement 1 for a list of species). These surveys rarely recorded large reef-associated species, such as adult parrotfishes, but the focus on smaller species more intimately linked with individual coral colonies is consistent with the aims of the study. Furthermore, cryptic species such as blennies and gobies were recorded when observed, but destructive techniques are required to comprehensively survey these taxa (Willis 2001). Secondly, the width and depth of every crevice (generally between M. annularis ramets) were measured. The height of the colony was also recorded. Finally, the entire colony, plus a scale bar, was videoed with a high-resolution digital camera (Sanyo Xacti). Subsequently, the digital video of each colony was projected onto a
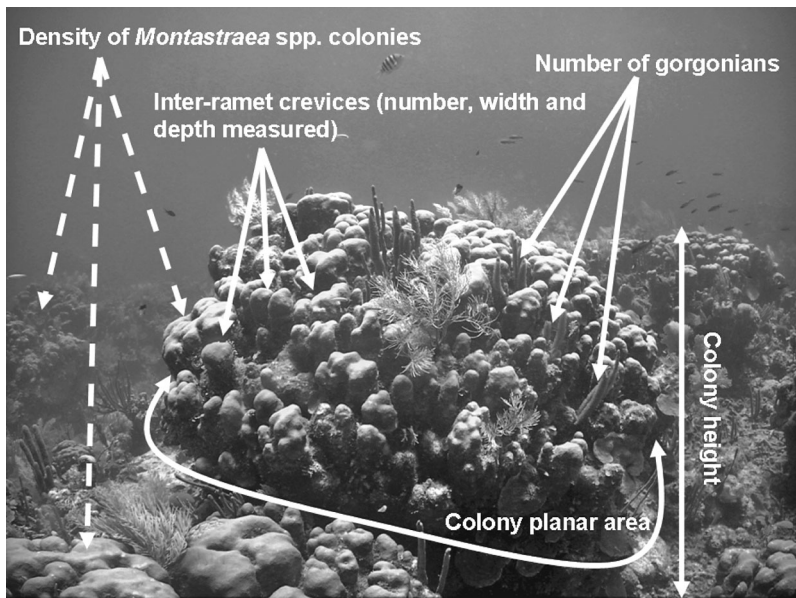
Fig. 1. Colony-scale (solid arrows) and plot-scale (dotted arrows) parameters measured for each *Montastraea annularis* colony surveyed. Plot-scale predator biomass also measured

large monitor for counting the number of gorgonians present. The number of gorgonians was hypothesised to have an important effect on fish abundance because they affect visual fields, and high densities may compromise mating and feeding behaviour (Rilov et al. 2007). The digital video, in combination with bespoke image analysis software (Vidana; freely available from www.ex.ac.uk/msel), was also used to measure colony area.

Data analysis

Generalised linear models were used to examine the relationship between all the abiotic and biotic variables and the abundance of fishes. Firstly, models were constructed for damselfishes. Few juvenile damselfishes were recorded, so models focused on the effect of habitat quality variables on the abundance of adults of each species. Four species of adult damselfishes were seen during the study: *Stegastes adustus* and *S. diencaeus* (which were considered together because of the difficulties of distinguishing them reliably underwater), *S. partitus*, *S. planifrons* and *Microspathodon chrysurus*. Multiple adults of each species were rarely found on a single coral (4 out of 102, maximum number of adults on a single colony was 3). Therefore, it was appropriate to transform the abundances of each damselfish species into presence/absence per *Montastraea annularis* colony, and use

binomial error structures and the logit link function. A total of 16 explanatory variables and selected interactions were used to explain the presence/absence of each species (see Table 2, all colony-scale parameters except 'number of *Montastraea* colonies' and 'biomass of predators' which are measured at the plot scale). Other damselfish species were included in the models because confamilial interactions are well-established, and the presence of adult damselfishes was used as an explanatory variable as this life phase is the most aggressively territorial (Robertson 1996). The abundances of other reef-associated species on the same coral were not included because damselfishes are the superior competitor for space and are unlikely to be influenced by their presence. *Montastraea* colonies >50 cm were used as the explanatory variable to ensure the plot-scale metric of complexity represented functionally important corals. The interaction between plot-scale complexity and predator biomass was included to establish whether plot-scale complexity may be important because it affects the hunting efficiency of predators. Explanatory variables were log or square-root transformed where necessary to improve normality.

Since sampling of *Montastraea annularis* colonies was nested within plots, a random variable representing plot number was included within the analyses. Therefore, generalised linear mixed-effects models were performed using the lme4 package (Bates & Maechler 2009. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-31. http://CRAN.R-project.org/package=lme4) in R (R Development Core Team 2008). Models were fitted using the procedure outlined by Crawley (2007). Briefly, a maximal model was fitted including all factors and interactions. Least significant terms were then removed in turn, starting with the highest-order interactions. After each term was removed, models were compared to ensure that term removal did not lead to a significant increase in deviance. Terms were removed until the model contained only significant terms or removal of any non-significant terms caused a significant increase in deviance (minimal adequate model).

Generalised linear mixed-effects models were also used to examine the correlation between explanatory

variables and the abundance of other adult and juvenile reef-associated species (i.e. non-piscivores, non-damselfishes; subsequently 'reef-associated species'). Too few intermediate-phase fish were recorded to allow meaningful analysis of this life stage (see Table 1). Response variables were count data and, therefore, Poisson error structures and the log link function were used with the mixed-effects models. Investigations into the distribution of the count data demonstrated that the variables were not overdispersed and Poisson error structures were appropriate (see Supplement 2 at www.int-res.com/articles/suppl/m437p201_supp.pdf). The explanatory variables were as for damselfish models, but with the addition of the interaction between the number of *Montastraea* spp. colonies >50 cm in height within the plot and the number of adult damselfishes. This interaction aimed to seek evidence that plot-scale complexity may be important because it reduces the number of agonistic interactions.

The generalised linear models provide an understanding of the effects of plot-scale and colony-scale variables on the different fish taxa, but are not well suited to address additional questions such as whether particular colony types facilitated the co-occurrence of the competitively superior adult territorial damselfishes (*Stegastes adustus*, *S. planifrons* and *S. diencaeus*; Robertson 1996) and other reef-associated species or whether colonies with only damselfishes or only reef-associated species are significantly different. Therefore, multivariate statistics were used to establish which characteristics (colony height and area, number of gorgonians on each colony, and the number, median width, and median depth of crevices) of *Montastraea annularis* colonies appeared to influence their habitat quality for different components of the fish community. For the analyses, the data were split into colonies supporting (1) no reef-associated fishes or adult territorial damselfishes, (2) reef-associated species only, (3) adult territorial damselfishes only, and (4) territorial damselfishes and reef-associated species. The normalised characteristics of colonies supporting these different fish taxa were analysed using analysis of similarities (ANOSIM) (Clarke 1993). ANOSIM returns a statistic R, which is a measure of separation among groups where 0 indicates complete mixing and 1 represents full clustering in which all samples within groups are more similar to one another than to any sample in another group. The discriminating characteristics between groups of colonies identified by ANOSIM as being significantly different were determined using similarity percentage (SIMPER) analysis (Clarke 1993).

RESULTS

Colony and plot-scale properties

Plots had a mean of 10.4 (SE = 1.2) *Montastraea* spp. colonies >50 cm. Mean biomass of all predatory fishes was 304.5 g 25 m^{-2} (SE = 106.2 g 25 m^{-2}), and mean biomass of predatory fishes excluding large-bodied serranids was 246.6 g 25 m^{-2} (SE = 101.7 g 25 m^{-2}) (see Supplement 1 for biomasses of each species). Mean colony height was 0.83 m (SE = 0.03 m), mean area was 3508 cm^2 (SE = 273 cm^2), and each colony had a mean of 15.4 crevices (SE = 1.4). When all crevices were pooled, median crevice width was 4 cm and median depth was 11 cm. Each colony supported a mean of 8.2 (SE = 0.4) gorgonians.

Colony area was strongly positively correlated with colony height and the number of crevices and gorgonians on the colony (Pearson product-moment correlation coefficients, r > 0.50, p < 0.001). Such collinearities can lead to unstable parameter estimates during multiple regression (Crawley 2007). Therefore, colony area was excluded from the generalised linear mixed-effects models. All other variables had only modest, weak or non-significant correlations (Pearson product-moment correlation coefficient, r < 0.41) with the exception of colony height and the number of crevices on the colony (Pearson product-moment correlation coefficient, r = 0.65, p < 0.001).

The 102 *Montastraea annularis* colonies supported a total of 214 fish, with a majority (57.5%) being reef-associated species (Table 1). The most abundant reef-associated species were *Canthigaster rostrata* (34 fish recorded), *Thalassoma bifasciatum* (27), *Sparisoma aurofrenatum* (15), *Chromis cyanea* (12) and *Halichoeres garnoti* (10) (see Supplement 1 for abundances of each species).

Models of habitat quality and biotic interactions

The abundances of *Stegastes adustus/diencaeus* and *S. planifrons* on *Montastraea annularis* colonies were negatively correlated with each other, but the abundance of *Microspathodon chrysurus* was not a significant term in either model (Table 2, Supplement 2). The presence or absence of *S. partitus* on a colony was negatively related to the abundance of *S. planifrons*, and the reciprocal relationship was also included in the final model for *S. planifrons*. None of the *Stegastes* species had a significant effect on the presence or absence of the large-bodied *M. chrysu-*

rus on colonies. *S. planifrons* was most frequently seen on taller colonies, and *S. adustus/diencaeus* and *S. planifrons* were more abundant on colonies with a large number of crevices. *M. chrysurus* and *S. planifrons* were more frequent on colonies with narrower crevices, and there was a significant interaction of

this parameter with the number of crevices for *M. chrysurus* and with crevice depth for *S. planifrons.*

Reef-associated species were more abundant on tall colonies, and adult abundance increased with increasing numbers of gorgonians (Table 3, Fig. 2a,d, Supplement 2). Adult reef-associated species were significantly correlated with crevice number (Fig. 2b), median width and depth (being associated with more numerous wider and deeper crevices), and the interactions among these parameters, while juveniles were correlated with the interaction between crevice number and median width. Furthermore, adult reef-associated species were positively correlated with the number of *Montastraea* spp. colonies >50 cm in the plot (Fig. 2c) and the biomass of predators, but negatively correlated with the interaction term between these 2 plot-scale variables. The use of high-quality colonies only appeared to occur in the absence of damselfishes. The abundance of adult and juvenile reef-associated species was significantly negatively correlated with the abundance of *Stegastes planifrons*, and adult reef-associated species were

Table 1. Abundance (total number of fish and percentage of *Montastraea annularis* colonies occupied) of each damselfish species and other reef-associated fishes considered in this study. 102 *M. annularis* colonies surveyed

Fish species/group	Life phase	No. of fish	% of colonies occupied (no. of colonies)	
Microspathodon chrysurus	Juvenile	0	0.00	(0)
	Intermediate/Adult	10	7.84	(8)
Stegastes adustus/ diencaeus	Juvenile	0	0.00	(0)
	Adult	18	16.67	(17)
Stegastes leucostictus	Juvenile	9	8.82	(9)
	Adult	0	0.00	(0)
Stegastes partitus	Juvenile	4	3.92	(4)
	Adult	28	23.53	(24)
Stegastes planifrons	Juvenile	2	1.96	(2)
	Adult	20	16.67	(17)
Other reef-associated species	Juvenile	65	37.25	(38)
	Intermediate	4	3.92	(4)
	Adult	54	27.45	(28)
Total		214	78.43	(80)

Table 2. Minimal adequate generalised linear mixed-effects models for the presence/absence of adult damselfishes on *Montastraea annularis* colonies. Values are model coefficients with p-values in parentheses. ×: interaction term. −: term not included in model. ns: non-significant term (p > 0.05). Removal of non-significant terms led to a significant increase in model deviance

Model term	Response variable			
	Stegastes adustus/ diencaeus	*Stegastes partitus*	*Stegastes planifrons*	*Microspathodon chrysurus*
Intercept	−4.57 (<0.001)	−1.66 (<0.001)	−17.73 (0.007)	−2.11 (0.376)
Abundance of adult *Stegastes adustus/diencaeus*	−	ns	ns	ns
Abundance of adult *Stegastes partitus*	ns	−	−19.18 (0.996)	ns
Abundance of adult *Stegastes planifrons*	−2.20 (0.066)	−17.15 (0.994)	−	ns
Abundance of adult *Microspathodon chrysurus*	ns	ns	ns	−
Number of gorgonians	ns	ns	ns	ns
Colony height	ns	ns	6.07 (0.043)	ns
Number of crevices (NoC)	1.14 (0.021)	ns	2.61 (0.029)	ns
Median crevice width (MCW)	ns	ns	−10.84 (0.076)	−4.42 (0.045)
Median crevice depth (MCD)	ns	ns	ns	ns
NoC × MCW	ns	ns	ns	1.41 (0.004)
NoC × MCD	ns	ns	ns	ns
MCW × MCD	ns	ns	4.73 (0.024)	ns
NoC × MCW × MCD	ns	ns	ns	ns
Number of *Montastraea* colonies (NoMC)	ns	ns	ns	ns
Biomass of predators (BoP)	ns	ns	ns	ns
NoMC × BoP	ns	0.08 (0.018)	ns	ns

also negatively correlated with the abundance of *S. adustus/diencaeus*. Juvenile reef-associated species were positively associated with the presence of *Micro-spathodon chrysurus*.

Table 3. Minimal adequate generalised linear mixed-effects models for the abundances of adult and juvenile reef-associated species on *Montastraea annularis* colonies. Values are model coefficients with p-values in parentheses. ns: non-significant term (p > 0.05)

Model term	Response variable	
	Adult	Juvenile
Intercept	−36.76 (0.016)	−3.38 (<0.001)
No. of adult *Stegastes adustus/diencaeus*	−0.99 (0.013)	ns
No. of adult *Stegastes partitus*	ns	ns
No. of adult *Stegastes planifrons*	−1.36 (<0.001)	−0.94 (0.003)
No. of adult *Microspathodon chrysurus*	ns	0.59 (<0.001)
No. of gorgonians	1.23 (0.016)	ns
Colony height	1.51 (0.010)	1.20 (0.011)
No. of crevices (NoC)	20.15 (0.006)	ns
Median crevice width (MCW)	17.40 (0.035)	ns
Median crevice depth (MCD)	12.10 (0.043)	ns
NoC × MCW	−13.14 (0.002)	0.42 (<0.001)
NoC × MCD	−7.69 (0.007)	ns
MCW × MCD	−7.18 (0.031)	ns
NoC × MCW × MCD	5.11 (0.003)	ns
No. of *Montastraea* colonies (NoMC)	0.99 (0.009)	ns
NoMC × No. of adult damselfishes	ns	ns
Biomass of predators (BoP)	0.71 (0.009)	ns
BoP × NoMC	−0.35 (0.001)	ns

Multivariate analyses of habitat quality

ANOSIM demonstrated that there was significant variation (Global R = 0.266, p = 0.001) among colonies supporting no juvenile reef-associated fishes or adult territorial damselfishes (46 *Montastraea annularis* colonies), only juvenile reefassociated species (23), only adult territorial damselfishes (18), or both territorial damselfishes and juvenile reef-associated species (15). Similarly, there was significant variation (Global R = 0.275, p = 0.001) among colonies supporting no adult reef-associated fishes or adult territorial damselfishes (49 *Montastraea annularis* colonies), only adult reef-associated species (20), only adult territorial damselfishes (25), or both territorial damselfishes and adult reef-associated species (8). Pairwise comparisons among groups of colonies were qualitatively similar for both juvenile and adult reef-associated species: all pairs were significantly different (p ≤ 0.028) with the exception of the comparisons between colonies supporting only reef-associated fishes and
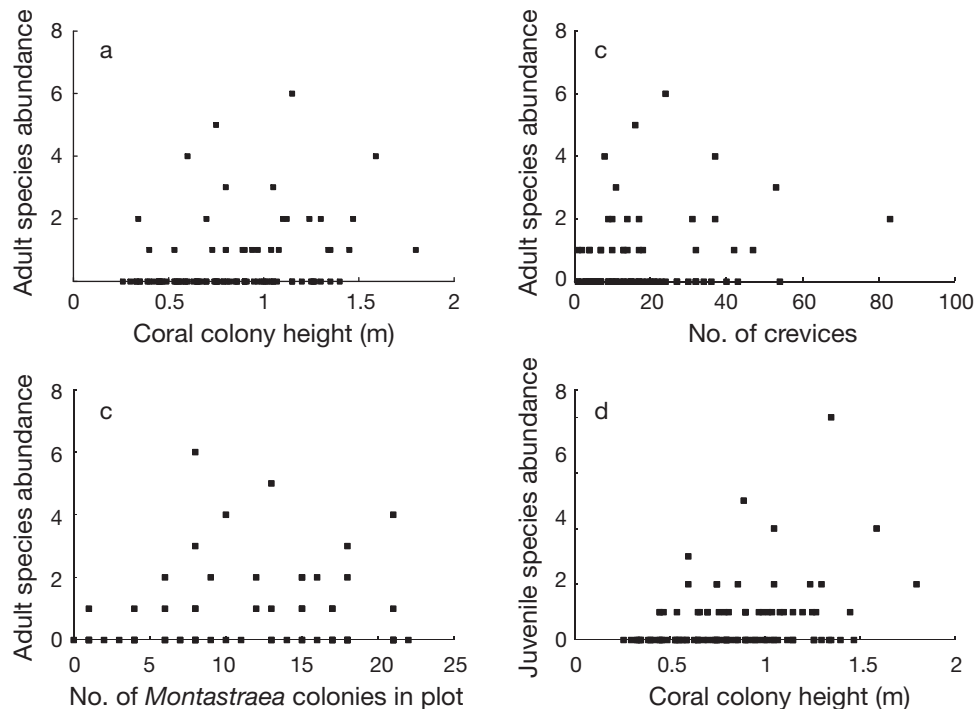

Fig. 2. Scatter plots of selected relationships between habitat complexity variables and the abundance of (a–c) adult and (d) juvenile reef-associated fish species (non-damselfishes, non-piscivores). n = 102 colonies

those supporting only territorial damselfishes, and between colonies supporting only territorial damselfishes and those supporting both territorial damselfishes and reef-associated species (Tables 4 & 5). SIMPER analyses revealed that, in general, colonies supporting no fishes were shorter and smaller, had fewer, wider, shallower crevices, and fewer gorgonians than colonies supporting territorial damselfishes and reef-associated species (Tables 4 & 5). Colonies supporting only reef-associated species were significantly shorter, had a smaller area, and contained fewer crevices than those supporting both damselfishes and reef-associated species. Cooccurrence of territorial damselfishes and reef-associated species was facilitated by colonies that were larger and more crevice rich than those supporting only reef-associated species.

DISCUSSION

Evaluating how individuals of a species respond to varying habitat quality is complex because of scale-dependent responses and the combined influence of biotic and abiotic factors (Mueller et al. 2009). This study supports the growing recognition that both biotic variables and scale-dependent effects must be considered when assessing habitat quality, which traditionally assesses only abiotic variables and is measured at a single scale. We demonstrated that the nested microhabitat and plot-scale variables both appear to significantly influence habitat quality for reef-associated fishes, but the effects varied among components of the fish community and plot-scale coral density was only correlated with the abundance of adult fishes. The importance of assessing habitat quality at multiple scales has been recognised in a variety of ecosystems including woodland birds (Mueller et al. 2009), fog desert lichens (Lalley et al. 2006), and pond newts (Denoël &

Table 4. SIMPER analysis for comparisons among characteristics of *Montastraea annularis* colonies supporting different categories of damselfishes and juvenile reef-associated fishes. Top right cells in the table show significances of pairwise comparisons. Columns indicate which characteristics were larger within significant pairwise comparisons (e.g. only crevice depth larger on colonies supporting 'No juvenile reef-associated fishes or adult territorial damselfishes' in comparison to those supporting 'Juvenile reef-associated fishes only'). Figures in parentheses indicate percentage contribution to the pairwise difference: percentage contribution = average squared distance/average dissimilarity between colonies supporting the different fish groups. ns: not significant (p > 0.05)

Colonies supporting:	No juvenile reef-associated fishes or adult territorial damselfishes (n = 46)	Juvenile reef-associated fishes only (n = 23)	Adult territorial damselfishes only (n = 18)	Both juvenile reef-associated fishes and adult territorial damselfishes (n = 15)
No juvenile reef-associated fishes or adult territorial damselfishes		R = 0.194; p = 0.001 Crevice width (25.1) Number of gorgonians (16.7) Height (16.2) Area (15.3) Number of crevices (11.8)	R = 0.284; p = 0.001 Height (22.0) Number of crevices (20.1) Crevice depth (20.0) Number of gorgonians (13.3) Crevice width (12.3) Area (12.3)	R = 0.558; p = 0.001 Area (23.0) Number of crevices (20.8) Height (19.1) Number of gorgonians (17.0) Crevice depth (15.0)
Juvenile reef-associated fishes only	Crevice depth (14.8)		ns	R = 0.116; p = 0.024 Area (24.0) Number of crevices (18.8) Number of gorgonians (16.5) Height (13.7) Crevice depth (9.2)
Adult territorial damselfishes only	–	–		ns
Both juvenile reef-associated fishes and adult territorial damselfishes	Crevice width (5.1)	Crevice width (17.8)	–	

Table 5. SIMPER analysis for comparisons among characteristics of *Montastraea annularis* colonies supporting different categories of damselfishes and adult reef-associated fishes. Top right cells in the table show significances of pairwise comparisons. Columns indicate which characteristics were larger within significant pairwise comparisons (e.g. only crevice width larger on colonies supporting 'No adult reef-associated fishes or adult territorial damselfishes' in comparison to those supporting 'Adult reef-associated fishes only'). Figures in parentheses indicate percentage contribution to the pairwise difference: percentage contribution = average squared distance/average dissimilarity between colonies supporting the different fish groups. ns: not significant (p > 0.05)

Colonies supporting:	No adult reef-associated fishes or adult territorial damselfishes (n = 49)	Adult reef-associated fishes only (n = 20)	Adult territorial damselfishes only (n = 25)	Both adult reef-associated fishes and adult territorial damselfishes (n = 8)
No adult reef-associated fishes or adult territorial damselfishes		R = 0.203; p = 0.003 Crevice depth (22.5) Height (16.7) Number of gorgonians (16.7) Area (15.0) Number of crevices (11.7)	R = 0.263; p = 0.001 Area (19.2) Number of gorgonians (18.3) Height (17.9) Number of crevices (15.7) Crevice depth (12.1)	R = 0.717; p = 0.001 Number of crevices (26.8) Height (22.8) Area (15.8) Crevice depth (15.7) Number of gorgonians (9.0)
Adult reef-associated fishes only	Crevice width (17.5)		ns	R = 0.226; p = 0.028 Number of crevices (28.8) Crevice depth (20.3) Area (17.1) Height (17.0) Number of gorgonians (8.6) Crevice width (8.3)
Adult territorial damselfishes only	Crevice width (16.8)	–		ns
Both adult reef-associated fishes and adult territorial damselfishes	–	Crevice width (17.8)	–	

Lehmann 2006). However, most studies of reef fishes consider only a single habitat scale along with larger (often landscape) scales. For example, some parameters of reef-fish assemblages are correlated with both small-scale reef complexity and landscape-scale (ca. 3 ha) habitat quality variables (Grober-Dunsmore et al. 2008). Similarly, in temperate blenny assemblages, communities vary at large geographical scales (up to 100 km) and also depending on finer scale biophysical habitat features such as depth and shelter availability (Syms 1995). Our finding that intra-habitat quality itself can also affect fish abundances at different spatial scales highlights the complexity of establishing the relationship between organisms and their habitat requirements.

Despite the growing recognition of the importance of both abiotic and biotic controls of habitat quality, an analysis of 173 ornithological studies demonstrated that only 6% considered how constraints such as predation or competition affected habitat quality (Johnson 2007). Our study adds to the literature on abiotic and biotic controls of habitat quality in reef fishes by demonstrating how both the competitive effects of territorial damselfishes and abiotic habitat quality are correlated with the abundance of reef-associated species. Other examples of abiotic and biotic controls of habitat quality in reef fishes include the work of Shima et al. (2008), who artificially added *Pocillopora* coral colonies to improve habitat quality for the wrasse *Thalassoma hardwicke*, but these additional corals also attracted greater numbers of predators that increased wrasse mortality rates. Quantifying the habitat requirements of different life stages of reef-fish species by assessing the effects of a range of biotic and abiotic variables at multiple spatio-temporal scales represents a challenging research agenda requiring manipulative experiments, but is critical for many conservation and restoration ini-

tiatives. This research should address the effects of habitat quality on both abundance and key demographic parameters to ensure that there is no decoupling between density and reproductive success, as has been reported in some bird studies (Van Horne 1983).

Microhabitat-scale habitat quality

All the groups of fishes associated with *Montastraea annularis* colonies were distributed nonrandomly, presumably because of a combination of settlement preferences, differential post-settlement mortality, and inter-colony movement. Specifically, both damselfishes and reef-associated species were more abundant on large, complex colonies. Height and number of crevices were particularly important metrics, as 4 models of fish abundances or presence/absences were significantly positively correlated with one or both of them. These variables are correlated with each other because large colonies tend to have a greater number of ramets and hence a greater number of crevices among these ramets. However, the 2 variables did occur singly within models, indicating that they have some independent explanatory power. Colony height, irrespective of complexity, may be important for at least 4 reasons. Firstly, there is some evidence that tall colonies provide fishes with a better view of approaching predators (Nemeth 1998). Secondly, taller colonies offer a better chance for fishes to observe mates and maximise the effectiveness of courtship displays (Rilov et al. 2007). Thirdly, planktivorous food is more abundant higher in the water column, and can affect the distribution of planktivores (Clarke 1992). Finally, settlement may simply scale with colony size and, if post-settlement mortality is density independent, larger colonies will subsequently support more fishes.

The positive correlations of fish abundance to the number of crevices are likely to be driven by the need for predator avoidance (Hixon & Beets 1993), but will also reflect the use of crevices as spawning, nesting and foraging sites (Robertson & Sheldon 1979). As highlighted previously (e.g. Nemeth 1998), simply having more crevices available was not always the only important factor determining fish abundance and the particular characteristics of the crevices were also important, e.g. adult *Stegastes planifrons* and *Microspathodon chrysurus* were more abundant when crevices were narrower. These patterns may reflect fishes seeking refuges that match their body shape and size and exclude preda-

tors (Hixon & Beets 1993, Nemeth 1998, Almany 2004a,b). Finally, the abundance of adult reef-associated species was positively correlated with the number of gorgonians on *Montastraea annularis* colonies. Gorgonians can inhibit the ability of territorial fishes to see predators, find mates and feed (Rilov et al. 2007), but their effect on non-territorial species is poorly understood and they may provide additional refuges.

Plot-scale habitat quality

The increased abundance of adult reef-associated fishes on colonies in habitat areas with high densities of other colonies has not been documented previously, but reinforces the need to consider habitat complexity at multiple scales. It seems likely that as fish home ranges increase with body size (Kramer & Chapman 1999), plots with more coral colonies are likely to provide greater opportunities for foraging, mating and predator refuges as fishes move about the reef. Corals surrounded by other corals may also receive more fish recruits and experience reduced density-dependent mortality than more isolated corals (Stier & Osenberg 2010). Furthermore, fishes may have fewer agonistic interactions with damselfishes in more complex habitats (Levin et al. 2000), but the interaction term in our models was not significant. Finally, the significant interaction term between the density of *Montastraea* spp. colonies and the biomass of predators provides some support for evidence from other ecosystems that more complex habitats can affect the hunting ability of predators (Eklöv & Diehl 1994). The lack of a correlation between abundances of juvenile reef-associated species or the presence or absence of adult damselfishes on a *M. annularis* colony and plot-scale coral density is presumably because these individuals forage or maintain a territory on a single colony, and whether this colony is isolated or not is of limited importance compared to access to refuges.

Influence of biotic factors on habitat quality

While reef-associated species are more abundant on large, complex *Montastraea annularis* colonies, their use of these corals was significantly negatively correlated with the presence of adult damselfishes, perhaps driven by damselfish influences on settlement rates (e.g. Sweatman 1985) and post-settlement mortality (e.g. Carr et al. 2002). As hypothesised,

abundances of juvenile and adult reef-associated species were negatively correlated to the abundance of the highly aggressive *Stegastes planifrons*, and adults appeared to avoid the similarly aggressive *S. adustus/diencaeus*. Both damselfishes and reef-associated species did occur together, but generally only on very tall and large colonies with a large number of deep, narrow crevices and gorgonians. In contrast, reef-associated species were not correlated with the abundance of the less aggressive *S. partitus* and *Microspathodon chrysurus*. Juveniles were positively correlated with the abundance of *M. chrysurus*. *M. chrysurus* is less territorial than *S. planifrons* and *S. adustus/diencaeus* (Robertson 1984), and the association between this species and reef-associated juveniles could be caused by similar microhabitat preferences or some benefits to juvenile fishes of living in *M. chrysurus* territories (e.g. reduced predation pressure). Among damselfishes, the negative correlation between abundances of *S. planifrons* and *S. adustus/diencaeus* may reflect each species displacing the other on a given colony, or 1 dominant species consistently out-competing the other. There is some evidence that *S. planifrons* is a superior competitor to other damselfishes on complex *M. annularis* colonies (Ebersole 1985). Colonies of *M. annularis* are not the primary microhabitat of *S. partitus* (Nemeth 1998), but when they did occur on colonies they appeared to avoid territories of the more aggressive *S. planifrons*. As expected, the number of large-bodied *M. chrysurus* was not negatively correlated with any of the *Stegastes* species; *M. chrysurus* often has territories that overlap with those of *Stegastes* species (Robertson 1984).

Predation pressure did not explicitly appear to have a major negative influence on the abundances of either damselfishes or reef-associated species. Most piscivores hunt widely across reefs (Hixon & Carr 1997, Popple & Hunte 2005), and there is unlikely to have been much variation in predation pressure across the study site. However, many of the characteristics of optimal microhabitats, particularly the abundance of crevice refuges, reflect the importance of predator avoidance. A larger-scale study would be required to test the effects of varying predation pressure, and also examine the potential interaction between predation and competition from damselfishes. Agonistic interactions with adult damselfishes can lead to predation rates on recruits being density-dependent because of displacement from refuges and, therefore, alter the population dynamics of the prey species (Carr et al. 2002). The effect of varying habitat quality on this interaction between

biotic factors is equivocal (Almany 2004a,b). However, Almany (2004a, 2004b) artificially added *Agaricia tenuifolia* to patch reefs in order to alter refuge availability. Variations in refuge availability on forereef *Montastraea annularis* colonies may be functionally more important to the interaction among territorial damselfishes, prey fishes and piscivores.

Effect of the interaction between competition and decreasing habitat quality on reef fishes

The data from this study allow us to conclude with a hypothesis on how the clear asymmetric competitive interaction between damselfishes and other reef-associated species may influence their relative abundances on reefs where habitat quality is declining. Damselfishes and other reef-associated species have very similar microhabitat requirements: large, complex *Montastraea annularis* colonies. It appears that damselfishes and other reef-associated species can co-occupy the largest coral colonies, but reef-associated species frequently have to inhabit sub-optimal colonies or optimal colonies without damselfishes (Fig. 3a). Other coral species might not be regarded as optimal microhabitat because they do not provide the equivalent numbers of refuges (Ebersole 1985). Mortality rates of *M. annularis* are high in the Caribbean (Edmunds & Elahi 2007), and subsequent bioerosion, macro-algal overgrowth and hurricanes will reduce the number of optimal coral colonies on a reef. If the number of optimal *M. annularis* colonies occupied by damselfishes remains constant, but the total number of those colonies decreases, damselfishes will occupy a larger proportion of them and the reduction of populations of other fishes seems highly likely (Fig. 3b). This process may have already occurred to some degree because of the loss of coral cover from Caribbean reefs (Gardner et al. 2003), and will be exacerbated by the switch of damselfishes to *M. annularis* microhabitats following the decline of *Acropora cervicornis* on forereefs (Precht et al. 2010). Furthermore, the ubiquity of asymmetrical competitive interactions in ecological communities (Connell 1983, Schoener 1983) may mean that this could be a generic mechanism causing reduced populations of inferior competitors across a range of threatened ecosystems.

As the quality and number of large *Montastraea annularis* colonies on forereefs decrease, populations of both damselfishes and reef-associated species will be affected. Therefore, the question of the relative rates of change of densities of damselfishes and reef-
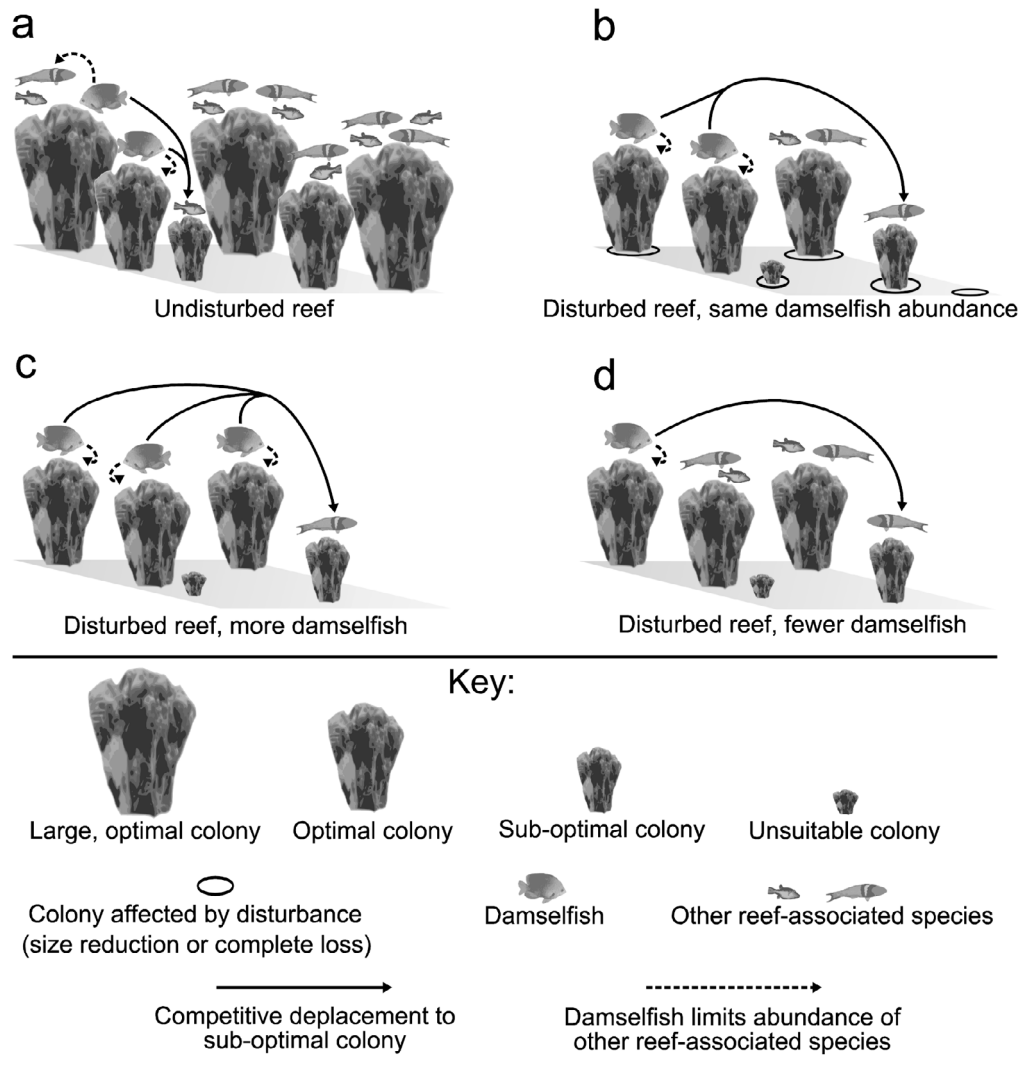
Fig. 3. Stylised representation of the potential effects of decreasing habitat quality (fewer, smaller, less complex *Montastraea annularis* colonies) and a superior competitor (damselfish) on inferior competitors (other reef-associated species). (a) Other reef-associated species are restricted to co-occupying the largest colonies with damselfishes, optimal colonies without damselfishes, or sub-optimal colonies (which support lower densities of fishes); (b) habitat quality declines (e.g. hurricanes, bleaching-induced coral mortality), but damselfish density remains the same as the first panel and reduces the density of other reef-associated species (less optimal habitat available); (c) habitat quality declines but damselfish densities increase (e.g. removal of predators), further reducing densities of other reef-associated species, and (d) habitat quality declines but damselfish densities decrease (e.g. reduced recruitment rates), allowing relatively high densities of other reef-associated species

associated species as optimal microhabitat availability decreases is critical. Only if decreases in damselfish densities are faster than those in other species will reef-associated species have access to a relatively larger number of optimal microhabitats (Fig. 3c,d). Damselfish densities on reefs may be habitat limited (Precht et al. 2010) but appear to be below carrying capacity (Robertson et al. 1981), and this is consistent with damselfishes not occupying all the optimal colonies in our study (ca. 35% of colonies >1 m tall). In addition to space, damselfish densities are likely to be limited by larval supply (Doherty & Fowler 1994)

and predation (Almany & Webster 2006), and there is little evidence that the interaction among these processes and decreasing microhabitat quality is reducing damselfish densities more quickly than other reef-associated species. Indeed, the loss of large piscivores to fishing may actually be increasing the densities of some damselfishes (Ceccarelli et al. 2006). Thus a better understanding of how pre- and post-settlement processes control reef fish population dynamics will be vital to assess the importance of asymmetric competition in affecting reef-fish communities following the loss of coral cover.

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