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REPORT

The effect of coral morphology on shelter selection by coral reef fishes

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Abstract While the loss of structural complexity causes declines in coral reef fish diversity, the processes leading to this decline are largely unexplained. To explore the role of coral morphology in providing shelter for fishes, tabular, branching and massive corals were filmed with video cameras and their usage by large reef fishes compared. Tabular corals were utilised more than the other two morphologies, with at least triple the abundance, biomass and residence times of large fishes. The preference of coral reef fishes for specific structural traits of tabular corals was also examined using artificial structural units. This experimental component showed that large reef fishes preferred opaque rather than translucent canopies. It appears that large fishes cue to tabular corals because of the concealment and/or shade provided. It is suggested that a loss of tabular corals as a result of climate change would have significant ecological impacts for the coral reef fishes that use these structures for shelter.

Keywords Reef fish · Structural complexity · Coral reef · Coral morphology · Shelter · Shade · Climate change

Introduction

As the principal architects of coral reefs, hermatypic corals are bio-constructors (Done et al. 1996) or ecosystem engineers (Jones et al. 1997) that are largely responsible for the structural complexity of coral reefs over fine spatial scales (centimetres to metres). Structural complexity at this scale has critical relevance for reef fishes (Lewis 1997; Syms and Jones 1999, 2000; MacNeil et al. 2009) having been implicated in affecting settlement, competitive interactions, priority effects and predation (Garpe et al. 2006; Grober-Dunsmore et al. 2007; Cabaitan et al. 2008). Differences in habitat usage by fishes over fine scales of complexity suggest that different coral morphologies vary in their functional use to reef fishes (Syms 1995; Wilson et al. 2008a). Although several studies have demonstrated the importance of coral morphology for small, site-attached reef fishes (e.g. Wilson et al. 2008a; Coker et al. 2009; Precht et al. 2010), the importance of coral morphology for large, mobile reef fishes, which are major contributors to the total biomass of reef fish communities (Ackerman and Bellwood 2000), has yet to be determined. It is important to understand whether coral morphology is relevant to large reef fishes given that certain morphologies, such as branching and tabular *Acropora*, are especially threatened by the effects of climate change (Riegl 2002; Hughes et al. 2003; Pratchett et al. 2008; Riegl and Purkis 2009).

If reef fishes show preferences for certain coral morphologies, it is possible to investigate the functional benefits that attract fish to these structures, which is particularly relevant if a given morphology lacks functional replacements on coral reefs. In many studies of structural complexity and reef fish ecology, information about the actual shapes present on the reef is lost through the quantification of habitat by aggregate measures (Jones and Syms 1998; Goatley and

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Bellwood 2011), preventing analysis of the roles of specific morphological features. The majority of studies that have considered the role of habitat structure in reef fish ecology have compared sites with differing degrees of structural complexity. For example, Garpe and Öhman (2003) compared topographic complexity between 11 sites using a ratio of contour length to transect length, often referred to as the ‘chain-and-tape’ method (McCormick 1994). Several of these studies have noted that this approach makes it difficult to separate the relative importance of different functional structures (e.g. Öhman and Rajasuriya 1998; Halford et al. 2004). However, studies that have tested the function of structure using artificial habitats have begun to disentangle specific functional properties of habitat structure (Caley and St John 1996; Cocheret de la Morinière et al. 2004; Verweij et al. 2006). These studies report quick responses of fish to artificial habitat (Lingo and Szedlmayer 2006) and document strong associations between fishes and specific aspects of the structure being examined (Hixon and Beets 1993).

Several studies have noted the importance of hole size relative to body size of reef fishes as a means of predator exclusion (e.g. Hixon and Beets 1993; Almany 2004a). The complex growth of many branching corals may offer potential exclusion zones from larger, predatory fishes and therefore partly explain the preference of the Pomacentridae for branching corals (Wilson et al. 2008a). In contrast, there is evidence that some larger reef fishes associate with tabular corals (Samoilys 1997; Shibuno et al. 2008), perhaps because these structures provide concealment from predation or enhance potential opportunities for ambush predators. Colony size may be relevant to the refuge properties of corals given that this imposes physical limits on the abundance and size of fishes that can be accommodated by these structures. Apart from the immediate visual concealment from above, tabular corals also provide shade, which has been shown to attract settling reef fishes (Hair et al. 1994) and juvenile fishes in mangroves (Cocheret de la Morinière et al. 2004), but to date, no studies have examined the attraction of shade for large reef fishes.

The goals of this study, therefore, are to quantify the use of different coral morphologies for shelter by large reef fishes and to examine the functional basis of shelter selection for the preferred morphology. Specifically, this study (1) examines the relative utility of three coral morphologies (tabular, branching and massive) for reef fishes larger than 10 cm and (2) uses artificial structures to assess whether the mechanism responsible for higher association with tabular corals (the most utilised coral morphology) was the concealment or shade it provided.

Materials and methods

This study was conducted during February and March 2011 at Lizard Island, a mid-shelf reef in the northern section of the GBR (14°40′S, 145°28′E). Two studies were conducted. The first was an observational study conducted at 17 separate shallow reef locations bounded by Lizard, South and Palfrey Islands. The second was an experimental study located at two sites approximately 500 m apart in the lagoon at Lizard Island.

Observational study

To record the utilisation of coral colonies by reef fishes, three stationary underwater digital video cameras were placed on tripods approximately 1–2 m from three respective coral morphologies: tabular, branching and massive. This setup minimises observer effects yet permits detailed quantitative observations (Bellwood et al. 2006). Each camera was left to record, undisturbed, for 3 h between 1100 and 1400 hours. Sampling was repeated at a different location each day for 17 days to minimise location-specific effects (three morphologies at each location) so as to ensure results were broadly relevant across a number of locations. This gave 17 replicates per coral morphology.

Upon collection of the cameras, the mean diameter of each focal colony was calculated as the mean of the longest diameter across the upper surface of the coral and that perpendicular to it. Focal colonies were haphazardly selected at each location (mean diameters 40–90 cm), and the minimum distance between focal colonies was at least 5 m. For each coral morphology, every effort was made to select colonies with similar morphological attributes, including minimal colony mortality, and in the case of branching corals, wide branch spacing. Taxonomically, the three coral morphologies were *Acropora hyacinthus* for tabular plates, branching *Acropora* spp. for branching colonies and *Porites* spp. for massive colonies.

The video footage was sub-sampled in 5-min intervals, every 25 min, with 6, 5-min intervals yielding a total of 30 min per colony per location. Species and size of fishes entering the video frame and in close proximity to the focal colony (within 20 cm) were recorded during each 5-min interval.

Experimental study

Artificial structural units (ASUs) were constructed to test the potential role of shade or concealment by tabular corals in shaping sheltering behaviour of reef fishes. The base of a plastic storage container was bolted to one end of PVC pipe (10 cm in diameter and 20 cm in length), which was filled with sand and closed at both ends using plastic caps, forming the control ASU (Fig. 1a). A plastic lid (70 cm long and 40 cm wide) was similarly fixed to the top of the PVC pipe and either left see-through or spray-painted entirely black forming two alternate ‘canopy’ ASUs

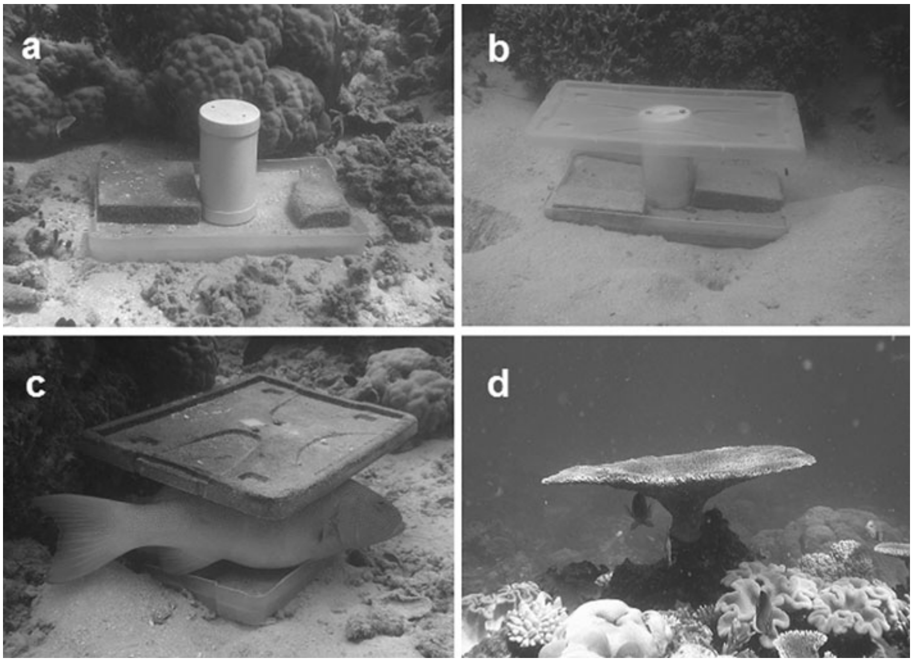

Fig. 1 **a** Control artificial structural unit. **b** Clear artificial structural unit. **c** Black artificial structural unit with *Plectropomus leopardus* beneath. **d** Tabular coral with *Sargocentron spiniferum* beneath

(Fig. 1b, c). ASUs were placed on the sand immediately adjacent to the reef and weighted down with concrete tiles. Each ASU was 25 cm high, 70 cm long and 40 cm wide, with a gap of 20 cm between base and lid (a pilot study suggested that a 20-cm gap was preferred over 10 and 30 cm).

At both sites, five replicates of each of the three ASUs were placed in a haphazard sequence at least 2.5 m apart and allowed an acclimation period of 9 days (a pilot study found an asymptote in usage by fishes after approximately 7 days). Natural tabular corals (Fig. 1d) were also identified at both sites and included in surveys as a fourth ‘treatment’. Five tabular corals were selected at site 1, but only two tabular corals were present at site 2. The planar surface area of these tabular corals was 0.24 ± 0.03 m^2, which is similar to the surface area of the ASUs: 0.28 m^2. All four study types control, clear, black ASUs and tabular corals are hereafter referred to collectively as ‘treatments’. Light levels under black ASUs were comparable to light levels under tabular corals. Light levels under clear ASUs offered minimal shading, being markedly higher than under black ASUs and tabular corals. Algal growth on the ASUs was removed daily to prevent additional shading or biological effects being introduced.

Data collection took place between 0800 and 1600 hours on day 10. Each treatment was examined on snorkel, recording the species and size of all fish associating with an individual treatment. Association was defined as fishes wholly or partially within the physical space created by the treatment. A full census of all treatments on one site was defined as a spot check. Eight spot checks were performed at each site, and the time between spot checks was at least 30 min. Values were averaged over the day for each individual ASU or tabular coral, which were then used as replicates in the analyses.

Statistical analyses

Observational study

Linear regressions were used to test for significant trends in abundance, biomass and residence times of fishes in response to colony size. As colony size influenced abundance of fishes, all three variables were standardised by colony area. Area (m^2) was calculated as πr^2 with the average radius for each colony estimated from replicate ($n = 2$) radial measurements taken by projecting the colony downward on to a two-dimensional surface. Variation in abundance, biomass and residence time between different coral morphologies was analysed for large fishes (>10 cm) using three, one-way analyses of variance (ANOVA). Data were $\log_{10}(x + 1)$-transformed to meet assumptions of heteroscedasticity (Levene, $P \geq 0.672$ for all three variables) and normality (Shapiro–Wilk, $P \geq 0.141$ for all three variables). With each ANOVA, a Tukey’s HSD post hoc test was conducted to assess the source of differences for significant effects. Length estimates of fishes were converted to biomass using published length–weight relationships for each species following Bellwood et al. (2006).

Changes in community composition of families between coral morphologies were investigated using non-metric multidimensional scaling (MDS) based on a Bray–Curtis similarity matrix with 51 colonies in total (three coral morphologies, 17 locations). An MDS was selected as it made no a priori assumptions about group membership. A one-way pairwise analysis of similarity (ANOSIM) was also conducted to determine the significance of any observed differences between the three morphologies (Clarke and Warwick 1994).

Experimental study

Analysis of the experimental study was performed on data from the last day as this gave the longest acclimation period (9 days), reflecting the most natural interaction of fishes with ASUs. To compare relative occupancy rates between treatments, a percentage score was calculated for each treatment from the proportion of ASUs (10 replicates) or tabular corals (seven replicates) at both sites occupied by one or more fishes. This score was averaged over 8 spot checks to generate a mean daily occupancy value per replicate for each treatment. This analysis was performed for small fishes (<10 cm) and again for large fishes (>10 cm). Variation in the abundance, biomass and occupancy rates of fishes was examined separately using fully factorial, three-way ANOVA with site as a random factor and size class (large vs. small fishes) and treatment as fixed factors. As site produced no significant effects, the model was reduced to exclude site and rerun (results from the three-way ANOVA are included in electronic supplementary material). Type III sums of squares were used to adjust for missing tabular coral replicates on site 2 (Quinn and Keough 2002) (five replicates, three ASUs, two sites = 30 ASUs and seven tabular corals). Abundance and biomass data were $\log_{10}(x + 1)$-transformed, and occupancy rate data were arcsine-transformed to improve assumptions of heteroscedasticity ($P \geq 0.111$ for both variables) and normality (Shapiro–Wilk, $P \geq 0.034$ for all variables).

Changes in community composition between treatments were investigated using an MDS of the mean abundance of fishes grouped by family: 30 ASUs (10 control ASUs, 10 clear ASUs and 10 black ASUs) and seven tabular corals. The analysis was based on a Bray–Curtis similarity matrix of $\log_{10}(x + 1)$-transformed data. Differences between the four treatments were also analysed using an ANOSIM as for the observational study.

Results

Observational study

A total of 746 large individuals (>10 cm) from 11 families (Acanthuridae, Haemulidae, Holocentridae, Kyphosidae, Labridae (wrasses and parrotfishes), Lethrinidae, Lutjanidae, Nemipteridae, Pomacanthidae, Serranidae and Siganidae) were observed during video analysis. Of those 746 individuals, 92, 200 and 454 were associated with massive, branching and tabular corals, respectively. The abundance of large fishes (>10 cm) was significantly and positively related to colony size of tabular and branching corals (Table 1). Massive corals, however, showed no significant relationship between colony size and fish abundance. Mean biomass and residence times of fishes were not significantly related to coral size for any of the three morphologies (Table 1).

Tabular corals were used by significantly greater numbers of large fishes (>10 cm) (ANOVA, $F_{2,48} = 21.95$, $P < 0.001$, Fig. 2a), with higher mean biomass (ANOVA, $F_{2,48} = 7.56$, $P < 0.01$, Fig. 2b) and longer mean residence times (ANOVA, $F_{2,48} = 12.64$, $P < 0.001$, Fig. 2c) than branching or massive morphologies (for both morphologies: Tukey's HSD, $P < 0.001$ for abundance, $P < 0.05$ for biomass and $P < 0.01$ for residence time). The data suggest that branching corals may be used more than massive corals, but post hoc analysis did not find statistically significant differences between these two morphologies for abundance, biomass or residence time (Tukey's HSD, $P = 0.302$, $P = 0.604$, $P = 0.285$, respectively) (Fig. 2).

Reef fish assemblages differed across the three coral morphologies (ANOSIM, global $R = 0.235$, $P < 0.001$). The primary axis of the MDS supported the separation of tabular corals from branching (ANOSIM, $R = 0.249$, $P < 0.001$) and massive (ANOSIM, $R = 0.348$, $P < 0.001$) corals, showing an association of 11 families with tabular corals (Fig. 3). In contrast, branching and massive corals occupied similar ordination space and were not found to differ significantly (ANOSIM, $R = 0.01$, $P = 0.259$), being characterised by a single family, the Nemipteridae (Fig. 3).

Experimental study

A total of 691 individuals from nine families (Apogonidae, Blenniidae, Gobiidae, Haemulidae, Labridae (wrasses), Lutjanidae, Mullidae, Pomacentridae and Serranidae) were recorded during the eight spot checks across both sites on the final day. Of those 691 individuals, 164 were large fishes (23.7%), with 67, 90, 3 and 4 occupying tabular corals, black ASUs, clear ASUs and control ASUs, respectively. Of the 527 small fishes (76.3%), 58, 141, 183 and 145 occupied

Table 1 Variation in the abundance, biomass and residence time of fishes among different sizes of three coral morphologies

Coral morphology	Abundance		Biomass		Residence time	
	R^2	P	R^2	P	R^2	P
Tabular	0.259	**0.018**	0.003	0.835	0.004	0.800
Branching	0.341	**0.011**	0.023	0.587	0.081	0.268
Massive	0.159	0.177	0.028	0.584	0.101	0.215

Significant values given in bold

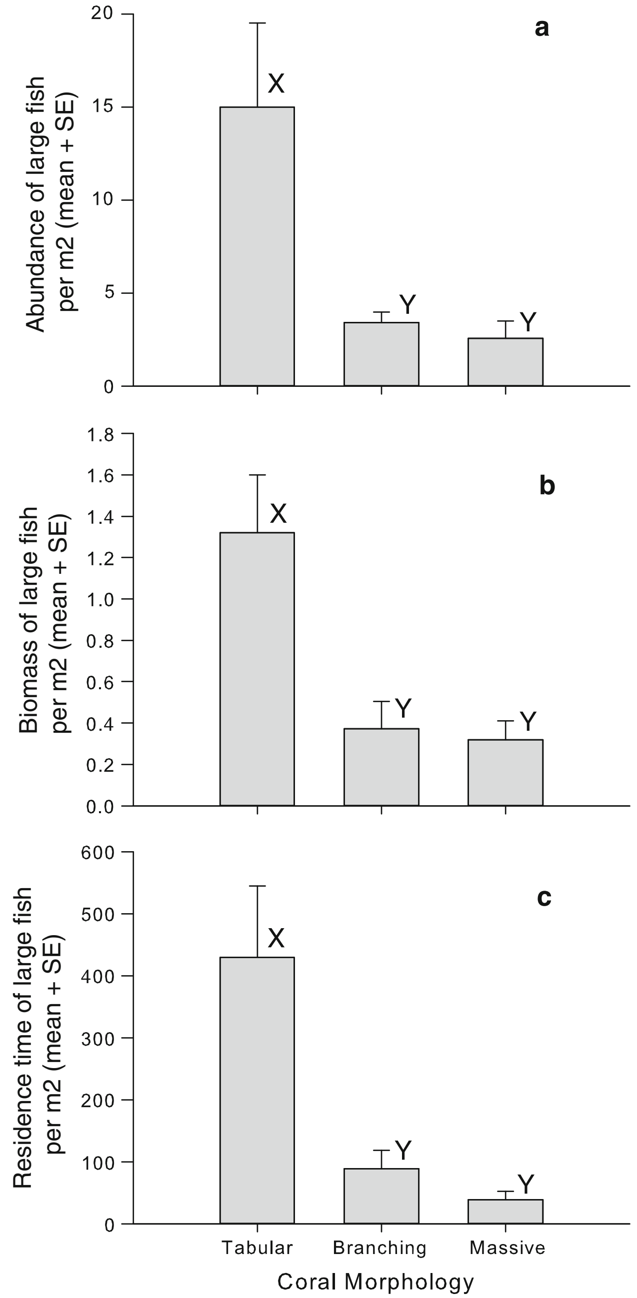

Fig. 2 Abundance (**a**), biomass (**b**) and residence time (**c**) (mean + SE) of large fishes (>10 cm) during 30-min census periods per colony ($n = 17$). *Bars* marked with the *same letters* indicate no significant difference (based on Tukey's HSD test). Response variables are standardised by colony area

tabular corals, black ASUs, clear ASUs and control ASUs, respectively.

There was a significant interaction between size class and treatment on abundance of fishes (ANOVA, $F_{3,66} = 3.61$, $P < 0.05$, Fig. 4a). For large fishes (>10 cm), mean abundance was greater on tabular corals and black ASUs than other treatments, whereas for small fishes, no difference in abundance was detected between treatments (Fig. 4a).

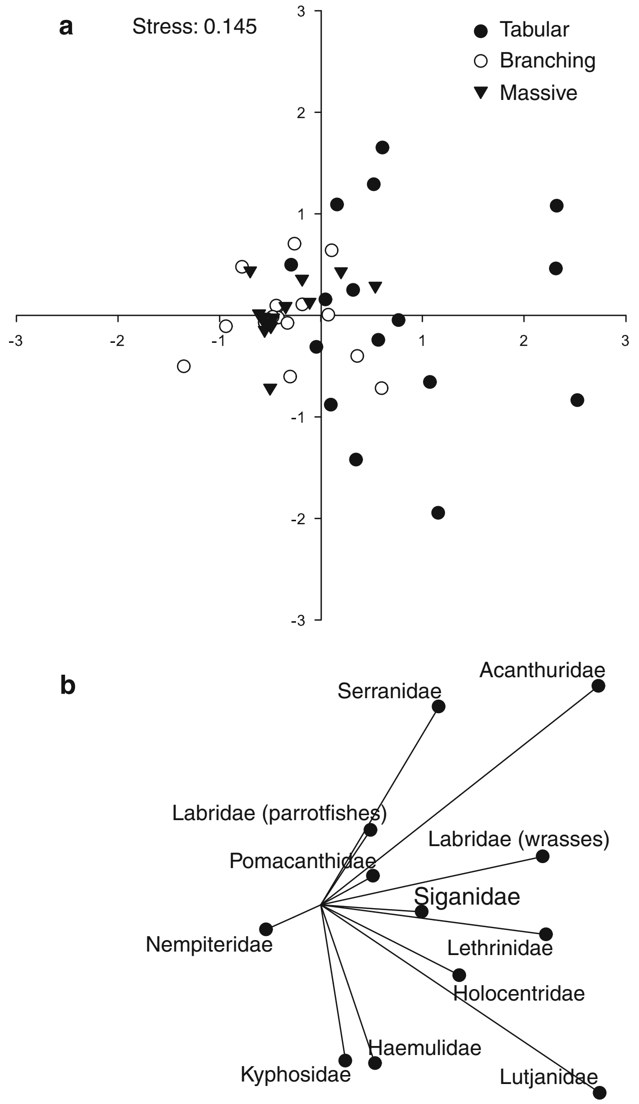

Fig. 3 Non-metric multidimensional scaling analysis showing the relationships between families of large reef fishes across three different coral morphologies (tabular, branching and massive) at Lizard Island, Great Barrier Reef. **a** Ordination plot showing the relationship between 17 colonies of each of the three different morphologies. **b** Species loadings showing the relative contribution of each family to the observed differences in usage of the three different morphologies

There was also a significant interaction between size class and treatment on biomass of fishes (ANOVA, $F_{3,66} = 3.65$, $P < 0.05$, Fig. 4b). For large fishes, mean biomass was greater on tabular corals and black ASUs than the other treatments, whereas for small fishes, no difference in biomass was detected between treatments (Fig. 4b). As with abundance and biomass, there was a significant interaction between size class and treatment on occupancy rates of fishes (ANOVA, $F_{3,66} = 15.46$, $P < 0.001$, Fig. 4c). Mean occupancy rates of large fishes were much higher on tabular corals and black ASUs (occupied more than 40% of the time, Fig. 4c), when compared with clear and control ASUs (occupied less than 5% of the time, Fig. 4c). In contrast, occupancy rates of small fishes were much higher on clear ASUs and controls (occupied more than 90% of the time, Fig. 4c), when compared with tabular corals and black ASUs (occupied less than 60% of the time, Fig. 4c). Occupancy rates across each of the four treatments were consistently higher for small fishes (<10 cm) than large fishes across each treatment, although only marginally so on both tabular corals and black ASUs (Fig. 4c).

The differences between small and large fishes were also reflected in the family associations. Reef fish assemblages differed across the four treatments (ANOSIM, global $R = 0.314$, $P < 0.001$). The primary axis of the MDS shows the separation of tabular corals and black ASUs from clear and control ASUs (Fig. 5). Larger reef fishes used both tabular corals and black ASUs, which were characterised by the Haemulidae and Lutjanidae, along with lower counts of the Serranidae and Mullidae. Smaller reef fishes used control and clear ASUs, which were characterised by the Pomacentridae, Gobiidae and Blenniidae (although Apogonidae associated mainly with black ASUs; Fig. 5). The ANOSIM identified differences in reef fish assemblages between every pairing of treatments except for tabular corals and black ASUs, which showed no significant difference (Table 2).

Discussion

Tabular corals were used significantly more by large reef fishes than branching or massive corals, with more than triple the abundance, biomass and resident times of large fishes compared to the other morphologies. The association of all but one of 11 families of large reef fishes with tabular corals underlines the importance of this result and provides quantitative evidence in support of previous studies that point to a relationship between fishes and tabular corals (Samoilys 1997; Shibuno et al. 2008). Our data suggest that it is not just coral cover or rugosity that is important, but the species composition of corals or specific structural attributes that shape habitat usage by large reef fishes.

There are clear structural differences between the three morphologies studied herein. Given their canopy, it is intuitive that tabular corals should outperform both branching and massive corals in providing concealment or shade for large reef fishes. Branching corals provide highly complex microhabitat, which is often utilised by smaller reef fishes for shelter (Beukers and Jones 1997; Munday and Jones 1998; Wilson et al. 2008a). It is interesting to note that although the branching corals observed in this study had branch spacing wide enough to accommodate large fishes, they were still avoided. Perhaps manoeuvrability and rapid escapes are restricted within the maze of a branching coral, compared to the simple, more open refuge of tabular corals (cf. Caley and St John 1996; Bennett et al. 2010). Jones et al. (2004), however, found approximately 65% of fishes recruited to live coral, including branching coral, suggesting that this morphology may be critically important at earlier ontogenetic stages of fishes than those considered here. The data presented here suggest that the roles of corals may differ markedly with fish size and ontogeny. Tabular corals may be more important to large fishes, while branching corals support smaller species and the early ontogenetic stages of larger species.

Massive corals represent the simplest morphology considered here and offer few obvious structural benefits for large reef fishes, although there is some evidence that they provide microhabitat complexity that can be utilised by smaller reef fishes (Precht et al. 2010). Large massives may, however, provide similar functional characteristics as tabular corals once their undercut edges create overhangs, producing a similar canopy effect to that offered by tabular corals. There is also anecdotal evidence that large piscivorous fishes may exploit shifting current flows around large massives when hunting (GR Russ, personal communication), although this remains to be quantified.

Colony size of tabular corals had a positive effect on the abundance of large reef fishes but showed no clear relationship with biomass or residence times, suggesting that larger colonies can accommodate greater numbers of fishes but are otherwise no more useful to large fishes than moderately sized colonies (>40 cm mean diameter). The families recorded using tabular corals in the observational study are predominantly roving fishes. It may be that these fishes utilise refuge stations such as tabular corals to reduce predation risk when resting in between feeding and other activities (cf. Munday and Jones 1998).

The experimental study suggests that large fishes were attracted to tabular corals because of the concealment they provide. Small reef fishes were associated with all three ASU treatments, but large reef fishes showed a clear preference for black ASUs and tabular corals, which both offered substantial levels of shade during the daytime, as well as physically hiding the fish from above. It is not possible here to separate the relative contribution of shade, from the attribute of being physically hidden, but the consequence of either mechanism is much the same; the fish is relatively concealed. This sheltering behaviour has a number of potential explanations, which may relate to specific species' ecology. In this study, some large fishes were observed moving under black ASUs on the approach of a snorkeler (cf. Hixon and Beets 1993), presumably to conceal the fish from a potential predator, and because a fish in shade is better able to see approaching threats (Helfman 1981). It is equally possible that ambush

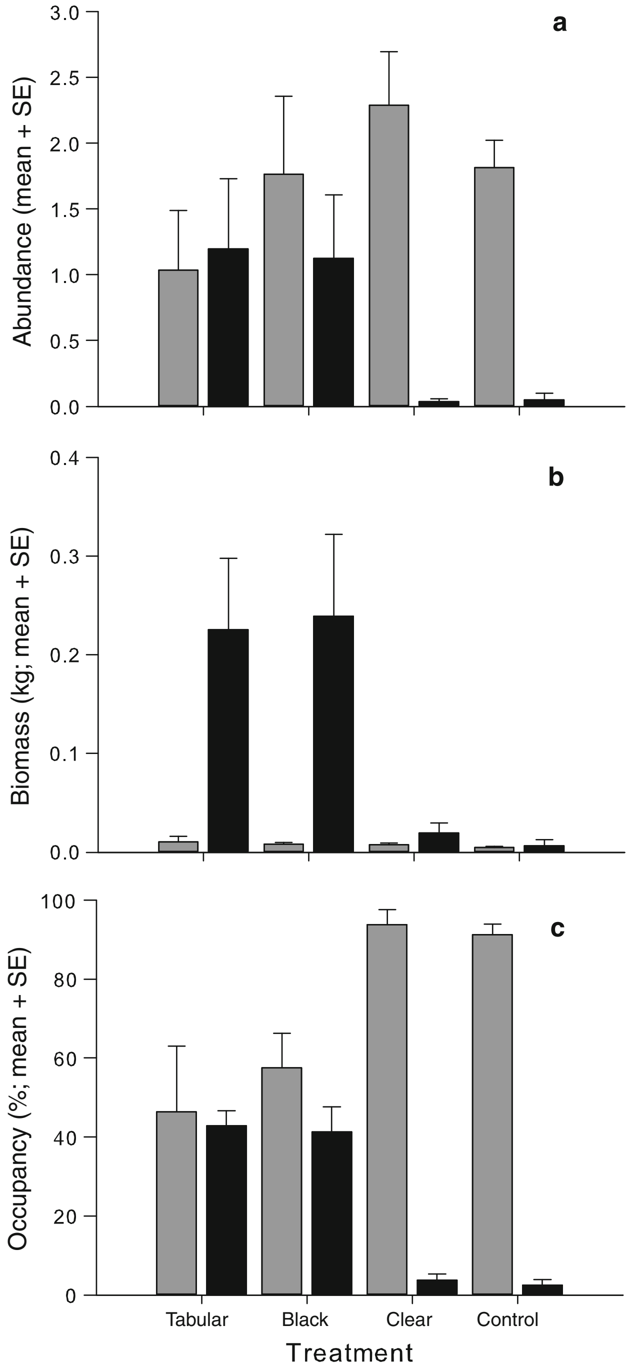

Fig. 4 Mean abundance (**a**), biomass (**b**) and per cent occupancy (**c**) for each of the four treatments (tabular corals, black ASUs, clear ASUs and control ASUs) per spot check ($N = 8$) for large fishes (>10 cm) (*black bars*) and small fishes (<10 cm) (*grey bars*). Per cent occupancy is how often a single ASU or tabular coral was occupied by one or more fishes. Although untransformed data are shown, all statistical tests were performed on transformed data (see "Methods")

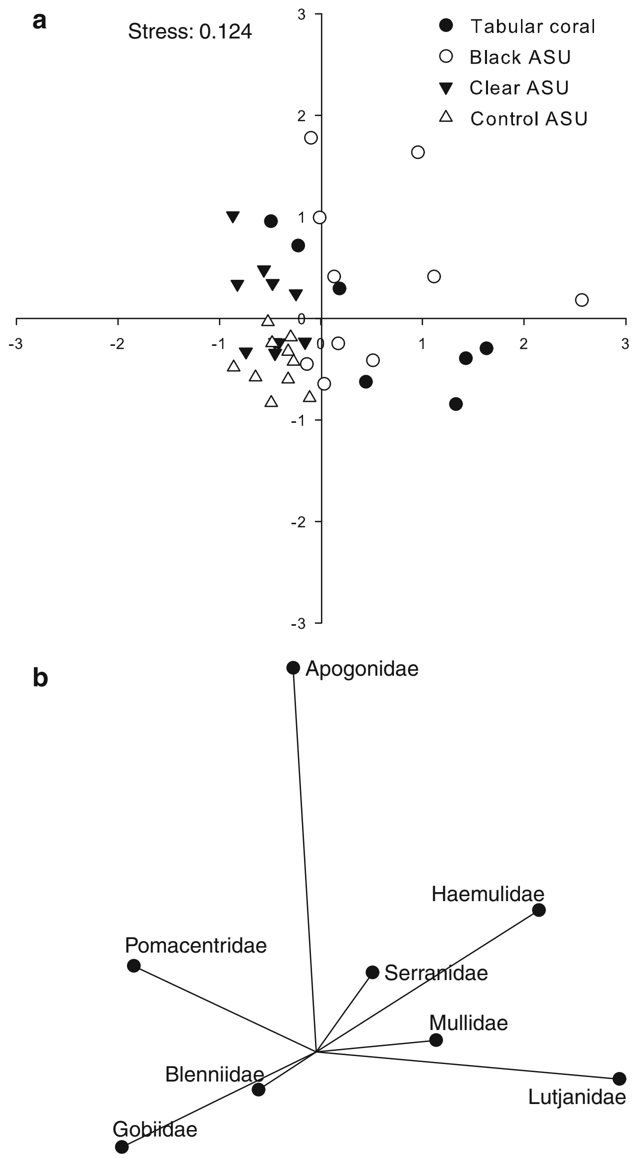

Fig. 5 Non-metric multidimensional scaling analysis showing the relationships between families of reef fishes across four treatments (tabular corals, black ASUs, clear ASUs and control ASUs) at Loomis Reef, Lizard Island, Great Barrier Reef. **a** Ordination plot showing the relationship between treatments. **b** Species loadings showing the relative contribution of each family to the observed differences in usage of the four different treatments

predators might benefit from this concealment when hunting prey, as has been previously suggested for *Plectropomus leopardus* (Samoilys 1997). In this case, the same principles apply but in reverse, so the ambush predator is both better able to see oncoming prey (Helfman 1981) and at the same time less easy to detect (Mazur and Beauchamp 2003).

Larger reef fishes are less likely to be subjects of ambush predation, are more at risk from roving apex predators and are also more likely to be ambush predators (Almany 2004b), hence the attraction of concealment and shade. In contrast, smaller fishes cued mainly to ASUs that did not visually obstruct their view. Perhaps this is because smaller bodied species are more likely to be subjects of ambush

Table 2 Results of analysis of similarities (ANOSIM: Primer-e) based on Bray–Curtis similarities of $\log_{10}(x + 1)$-transformed abundance data comparing reef fish assemblages across tabular corals and three ASUs at two sites

	R statistic	*P*
Global test		
Sample statistic (global *R*)	0.314	**0.001**
Pairwise tests		
Tabular, black ASU	0.072	0.225
Tabular, clear ASU	0.526	**0.001**
Tabular, control ASU	0.688	**0.001**
Black ASU, clear ASU	0.251	**0.001**
Black ASU, control ASU	0.311	**0.001**
Clear ASU, control ASU	0.149	**0.027**

Significant values given in bold

predation (Almany 2004b) and benefit from being able to see in every direction, thereby reducing opportunities for ambush predators. It is also possible that smaller reef fishes did not generally associate with shaded treatments because they were displaced by larger fishes (Shulman 1985).

Sheltering behaviour may also be driven by an attraction to shade (concealment from the Sun) (Cocheret de la Morinière et al. 2004). Many tropical reef fishes are reported to have substantial quantities of UVA- and UVB-absorbing compounds in their epithelial mucus (Zamzow and Losey 2002), which may represent a significant energetic cost to these fishes. Shade-seeking behaviour may therefore double not only as a means to reducing predation risk but also in conserving energy by reducing the need to produce mucus to prevent harmful ultraviolet exposure (Kelly and Bothwell 2002).

Black ASUs and tabular corals were functionally equivalent within 10 days of placement, supporting fish communities that were not significantly different, and had comparable occupancy rates for large reef fishes. This suggests that the relatively short field duration of the black ASUs was sufficient to make comparisons with the tabular corals. This further suggests that the functional attributes of tabular corals are relatively easily replicated, quickly evaluated and rapidly utilised by reef fishes. This may have been helped by the fact that ASUs were optimised in terms of height as a result of a pilot study. A 20-cm gap between base and canopy was selected to maximise ASU use by fishes. The similarity with natural tabular corals in usage rates and community composition suggests that this height provided a reasonable proxy for ‘natural’ tabular corals, which could then be compared across treatments.

Tabular corals are one of the most susceptible growth forms to coral bleaching (Marshall and Baird 2000), storms (Madin and Connolly 2006) and ocean acidification (Fabricius et al. 2011), all of which are expected to increase in the future as a result of climate change (Hoegh-Guldberg et al. 2007). This presents a clear threat to the long-term availability of structural complexity on coral reefs; however, Samoilys (1997) observed the movement of *P. leopardus* between tabular corals, overhangs, tunnels and reef edges. This suggests that other reef geomorphological features that provide concealment are already used by large fishes, and that fishes may cue to both perennial geomorphological features of the reef such as overhangs and more ephemeral elements such as tabular corals (cf. Arias-Gonzalez et al. 2006). This highlights the need for a better understanding of the movement and habitat association of mobile reef fishes (e.g. Welsh and Bellwood 2011).

Even though alternative shelter might be available on the reef, the loss of tabular corals still represents a reduction in shelter options for large coral reef fish. It is noteworthy that alternate stable states on reefs do not offer useful alternatives, with soft corals (Syms and Jones 2001), macroalgae (Hoey and Bellwood 2011) and other structures (Norström et al. 2009), providing limited useful shelter for large fishes. If climate change leads to further collapse of complex reef structures, then the abundance of reef fishes that use these structures may be severely comprised. It is currently unclear how important structural complexity is for large reef fishes with studies showing varying responses of fishes in different trophic groups to reef collapse (Graham et al. 2007; Wilson et al. 2008b). The mechanistic bases for these changes are as yet undetermined, but the present study suggests a strong preference of large reef fishes for sheltering options on the reef. It may be that such concealment is an important aspect of the ecology of some large reef fishes.

The present study has demonstrated that large reef fishes cue strongly to tabular corals for shelter rather than branching and massive morphologies, and that this probably reflects the concealment and/or shade that these structures offer. There may be multiple reasons for the attraction depending on specific species’ ecology, including refuge from predation, shelter from sunlight and concealment for ambush predation. If tabular corals are lost as a result of climate change or other anthropogenic impacts, then reefs will offer large fishes less options for shade and concealment, which may have serious consequences for large coral reef fishes that are themselves important for reef resilience.

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