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The Role of Tabular Structure in the Ecology of Large Reef Fishes

Thesis submitted by

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Statement on the contribution of others

This thesis includes some collaborative work with my supervisor, Professor David Bellwood (James Cook University). While undertaking this collaboration, I was responsible for the project concept and design, data collection, analyses and interpretation, as well as the final synthesis of results into a form suitable for publication. Professor Bellwood provided intellectual guidance, equipment, editorial assistance and financial support.

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“The bottom was absolutely hidden by a continuous series of corals, sponges, actinae and other marine productions, of magnificent dimensions, varied forms, and brilliant colours. In and out among them moved numbers of blue and red and yellow fishes, spotted and banded and striped in the most striking manner. ... It was a sight to gaze at for hours, and no description can do justice to its surpassing beauty and interest”

Alfred Russell Wallace, “The Malay Archipelago”, 1869

Abstract

The ecology of an organism is defined by its relationship with the environment. In many ecosystems, the structural complexity (physical, three-dimensional structure) of the environment is a major facet that determines the nature of this relationship. For example, on coral reefs, structural complexity provides reef associated fishes with numerous functions including, access to food, shelter, and recruitment habitat.

The vulnerability of coral reefs to degradation and loss of structure, particularly in the face of climate change, adds impetus to understand the relationship between structural complexity and coral reef fishes. This is especially important given that numerous studies have documented positive relationships between the structural complexity of coral reefs and the abundance and diversity of associated coral reef fishes. However, few studies have been able to identify the specific functional properties of structural complexity that drive these associations. This thesis, therefore, endeavoured to examine the functional importance of a particular morphological structure on coral reefs – tabular structure – and to assess its relevance to a diverse assemblage of large reef fishes, which had been previously identified to strongly associate with this structure on coral reefs.

Although previous studies had hypothesised that declines in the abundance and diversity of large reef fishes might be seen following the loss of tabular structures, no studies had experimentally demonstrate this relationship. The first data chapter (Chapter 2), therefore, examined this outcome by experimentally excluding access of large reef fishes to the understory of tabular structures. The exclusion of large reef fishes from tabular structures using mesh wire had a significant effect on the distribution of large reef fishes, even though these structures only constituted a small fraction (4%) of the benthic cover. Reduction in the

availability of tabular structures at this spatial scale (200 m^2) shifted activity spaces of large reef fishes away from these localities. Importantly, the observed movement of large reef fishes is likely to occur at reef wide scales during disturbance events. Indeed, if large reef fishes abandon areas of impacted reefs, there is a strong possibility that this may severely impact ecosystem function in those areas.

In the second data chapter (Chapter 3), video analysis of fishes sheltering under tabular structures at midday and at sunset was used to test two alternate hypotheses to explain sheltering behaviour: avoidance of predation or avoidance of solar irradiance. Patterns of shelter use offered minimal evidence in support of the predation avoidance hypothesis, with usage of tabular structures being low during the sunset period when predators of large reef fishes were likely to be most active. However, tabular structure usage reached a peak during the middle of the day when incident solar irradiance would reach its zenith. As such, the data suggest that large reef fishes are primarily sheltering beneath tabular structure to protect themselves from harmful UV irradiance, which can be extreme in shallow, oligotrophic waters. Furthermore, given the significant costs of producing UV-blocking mycosporine-like amino acids, fishes may achieve considerable energetic savings by sheltering beneath tabular structure.

Intense use of tabular structures by large reef fishes suggests that these structures may already be a limited resource on some coral reefs. The third data chapter (Chapter 4), therefore, used video analysis to record competition for access to tabular structures by large reef fishes. Examination of 26 tabular structures revealed an exceptionally high mean biomass of sheltering large reef fishes (4.71 kg m^{-2}), which is one or two orders of magnitude greater than typical coral reef biomass estimates between (0.031 to 0.1 kg m^{-2}). There was also strong interactions among the 30 species of large reef fishes observed using tabular structures for shelter, which resulted in displacement and exclusion of losing individuals.

This behaviour generated a dominance hierarchy for access to tabular structures, with several species of functionally-important large reef fishes being located in the lower ranks of the hierarchy. This raises cause for concern, given the likelihood of a future reduction in the availability of tabular structures, which may mean that these species are excluded from these shelter by more dominant species.

The fourth data chapter (Chapter 5), evaluated the role of multiple environmental factors in driving sheltering behaviour by large reef fishes under tabular structure. Patterns of tabular structure usage by large reef fishes were documented through video analysis and compared to six environmental variables that were collected *in situ* and from weather stations at the study sites. Two environmental factors emerged as key drivers of sheltering behaviour in large reef fishes: increased visibility (decreasing turbidity) and increasing wind speed (increasing wave energy). Turbidity correlates negatively with in-water irradiance and, therefore, as water clarity improves large reef fishes are more likely to seek out shelter to avoid UV irradiance, as observed in Chapter 3. Increasing wave energy places energetic costs on swimming or station holding in fishes. Fishes therefore seek refuge from water movement. Tabular structures likely reduce water momentum by creating drag and also reduce turbulence by preventing mixing of surface flow with understory flow, providing station-holding large reef fishes with a potential refuge from energetic swimming. Chapter 5, therefore, provides further evidence that tabular structures are important energetic refuges for large reef fishes, offering shade from down-welling UV-irradiance and respite from wave energy.

Overall, the sheltering behaviour of large reef fishes beneath tabular corals appears to be driven by the energetic savings that these structures can provide for fishes. Both in the form of providing shade from harmful UV-irradiance and in offering respite from wave energy. Movement from of reef localities where tabular structure are unavailable suggests that multiple species of large reef fishes place a high priority on the energetic savings that these structures provide. This observation is further supported by the strong competitive interactions that were observed to occur for access to tabular structures. If, as predicted, the availability of tabular structures on coral reefs declines in the future, there may be associated losses of large reef fishes and an accompanying loss in ecosystem functionality. The importance of tabular structures, demonstrated herein, highlights the need for conservation planning to preserve these key structures, or for consideration of alternative structural restoration where this is no longer possible.

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Chapter 1: General Introduction

The physical, three-dimensional structure of an ecosystem may be defined as its structural complexity (Graham and Nash 2013). In many ecosystems, this structural complexity can be provided by living organisms, such as trees, kelp and corals, which act as ecosystem engineers or bio-constructors (Jones et al. 1994; Done et al. 1996). Other, non-living structural elements of the environment, such as holes, also provide structural complexity, and together they create a range of microhabitats that are implicated in increased abundance and diversity of associated organisms (MacArthur and MacArthur 1961; Graham and Nash 2013). This relationship has been demonstrated in a range of ecosystems, including kelp beds (Holbrook et al. 1990), forests (Schiegg 2000), mangroves (Cocheret de la Morinière et al. 2004), and coral reefs (Wilson et al. 2008).

The importance of structural complexity has recently come to the fore with global degradation of habitats occurring at an unprecedented scale (Kleypas et al. 2001; Pandolfi et al. 2003; Alongi 2008; Reyer et al. 2013). Corals reefs are among the most susceptible environments to climate change and associated stresses (Walther et al. 2002), having suffered extensive disturbance and degradation in recent decades (Gardner et al. 2003; De'ath et al. 2012), leading to an overall flattening of reef structural complexity (Lindahl et al. 2001; Alvarez-Filip et al. 2009). This is primarily because the principle architects of coral reefs, hermatypic corals (Done et al. 1996), are especially vulnerable to increasing environmental stresses (Hoegh-Guldberg et al. 2007; Pratchett et al. 2008).

The structural complexity of coral reefs is a key element in the multi-faceted relationship between coral reefs and associated fishes, and has been the focus of intensive study (see reviews in Wilson et al. 2006; Pratchett et al. 2008; Graham and Nash 2013). Aside from being relatively permanent shelter locations, coral structures are thought to improve access to food (Clarke 1992), regulate predation rates (Almany 2004) and mitigate environmental stresses (Johansen et al. 2007). These processes may account for the role of structural complexity as the primary correlate with reef fish assemblage structure across a range of spatial scales (Holbrook et al. 2002b; Purkis et al. 2008; MacNeil et al. 2009; Vergés et al. 2011). The majority of studies have found a positive relationship between structural complexity and the diversity and/or abundance of reef-associated fishes (Harborne et al. 2012; Graham and Nash 2013). However, despite numerous studies demonstrating that reef complexity is an important predictor of reef fish assemblages, a comprehensive understanding of the importance of specific components of structure is still lacking.

In many studies of structural complexity and reef fish assemblages, 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 Bellwood 2011), preventing analysis of the roles of specific morphological features. For example, one common technique measures reef rugosity as a ratio of contour length to transect length. Several studies have noted that this approach makes it difficult to separate the relative importance of different structures (e.g. Öhman and Rayasuriya 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, and document strong associations between fishes and distinct structures. For instance, Hixon and Beets (1993) showed that the number and size of holes on a reef had a positive relationship with fish abudance and diversity. While a study by Cocheret de la Morinière and others (2004) showed that the shade provide by mangroves was an important feature for juvenile reef fishes). Another technique used to measure structural complexity is the visual estimate, which allows a more rapid assessment of the habitat at broader spatial scales (Harborne et al. 2012). However, these techniques are typically semiquantitative, such as the 6-point scale of Polunin and Roberts (1993). Like smaller-scale protocols, these techniques intentionally summarise complexity at a survey site and in so doing amalgamate structural characteristics, thereby limiting more detail analyses of the relative effects of structure on reef fish assemblages (Harborne et al. 2012).

Nonetheless, one major factor that has arisen in the literature examining the relationship between structures and fishes is the importance of fish body size (Hixon and Beets 1993; Harborne et al. 2011; Karkarey et al. 2014; Pratchett et al. 2014). There are a number of studies documenting the importance of different coral morphologies for small, site-attached reef fishes, which typically utilise complex microhabitat for settlement and shelter (Jones et al. 2004; Wilson et al. 2008; Precht et al. 2010; Bonin 2012). However, evidence for the importance of specific reef structures for large, mobile reef fishes is scarce, although for several decades several species have been anecdotally reported to shelter under canopy structures (Hobson 1974; Helfman 1986; Zeller 1997).

Large reef fishes are not only major contributors to the total biomass of reef fish communities (Ackerman and Bellwood 2000), they also perform a number of important functional roles on coral reefs, including herbivory, predation and transport of nutrients and sediment (Hixon and Carr 1997; Bellwood et al. 2003). Studies that have looked at the response of large size classes of reef fishes to declining structural complexity found mixed responses of these fishes but were unable to account for these changes beyond a general attribution to the loss of prey items (Graham et al. 2007; Noble et al. 2013). Given the functional importance of multiple species of large reef fishes there is, however, a strong incentive to examine whether specific structural elements of the reef are important in their ecology.

Evidence that large reef fishes associate with tabular corals (Samoilys 1997; Shibuno et al. 2012) was reinforced in a study by Kerry and Bellwood (2012), which examined usage of three different coral morphologies by large reef fishes. They found that tabular corals were utilised by a significantly higher abundance and diversity of large reef fishes for significantly longer periods than either branching or massive corals. Tabular corals are especially threatened by the effects of climate change and direct anthropogenic stresses on reefs, including bleaching (Marshall and Baird 2000), crown-of-thorns outbreaks (Baird et al. 2003), ocean acidification (Fabricius et al. 2011), and storms (Madin et al. 2014). As such there is an urgency to understand the importance of this structural feature of coral reefs for large reef fishes. Lirman (1999) and Kerry and Bellwood (2012), respectively found that *Acropora palmata* (arborescent table) and *Acropora hyacinthus* (tabular) were used as a diurnal refuge by a high diversity of large reef fishes, whether the structure was living or dead. Therefore, the present thesis examined both living and non-living tabular structure, the latter including both dead tabular corals and carbonate reef overhangs. Reef overhangs were included because they may endure for substantially longer periods than dead tabular corals (Pratchett et al. 2008), and as a result, may provide important alternate tabular structure on coral reefs.

The aim of this thesis, therefore, is to provide a comprehensive assessment of the role of tabular structure in the ecology of large reef fishes. The four key objectives of the thesis are addressed in separate data chapters, each of which relates to a publication derived from the present work (Appendix D).

Although previous studies have hypothesised that declines in the abundance and diversity of large reef fishes might be seen following the loss of tabular structures, no studies have experimentally tested this hypothesis. In **Chapter 2** this question is addressed by experimentally excluding access of large reef fishes to the understory of tabular corals. Furthermore, this chapter provides data on the propensity of large reef fishes to colonise novel tabular structure, and examines the potential higher order effects of changes in tabular structure as they relate to smaller reef fishes.

Chapter 3 investigates the mechanistic basis of tabular structure use and tests two alternate hypotheses: avoidance of predation or avoidance of solar irradiance. To test the hypothesis, tabular structure usage was examined at midday and sunset. It is hypothesised that if large reef fishes are using tabular structure primarily for avoiding solar irradiance, sheltering activity should be significantly higher during the period when irradiance is highest, i.e., midday. Alternatively, if large reef fishes are using tabular structure primarily for avoiding visually active diurnal predation, then increased sheltering activity should be observed during sunset when this threat peaks.

Intense use of tabular structures by large reef fishes suggests that these structures may be a limited resource on some coral reefs. **Chapter 4** assesses whether sheltering large reef fishes compete for access to these structures, and identifies a dominance hierarchy in shelter use. These findings are interpreted in the context of declines in the availability of tabular structures on reefs, considering whether certain functionally important reef fishes may suffer from reduced shelter options given their position with the dominance hierarchy.

Finally, **Chapter 5** evaluates the role of multiple environmental factors in driving sheltering behaviour by large reef fishes under tabular structure. In doing so, this final data chapter provides an important overview of how and why tabular structure benefits such a broad diversity of large reef fishes. This thesis ends with a concluding discussion which examines the nature of the relationship between structure and fishes, particularly in the context of habitat degradation.

Chapter 2: Do tabular corals constitute keystone structures for fishes on coral reefs?

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2.1 Introduction

A keystone structure is defined as a distinct structure that has a disproportionate effect on its ecosystem relative to its abundance, providing shelter or 'services' crucial for other species (cf. Tews et al. 2004; Manning et al. 2006). This description differs from 'foundation species' or 'ecosystem engineers' because the ecosystem services provided by keystone structures relate primarily to their structural properties. For example, deadwood stacks in mixed beechspruce forests in Switzerland were shown to be critical in maintaining insect diversity (Schiegg 2000), while in Botany Bay, Australia, pits in rocky intertidal shores regulate the density and richness of gastropods (Beck 2000). Identification of such keystone structures can provide significant insight into the relationship between the availability of a distinct structure and the abundance and diversity of entire species groups in a given environment (Tews et al. 2004). For example, large trees provide nesting, shelter and connectivity for up to 30 % of vertebrate species in some ecosystems and have been shown to have a positive effect on bird diversity as they become larger in size (Cockle et al. 2011; Stagoll et al. 2012).

On coral reefs, loss of scleractinian (hard) corals and the concomitant erosion of structural complexity (e.g. Alvarez- Filip et al. 2009) have been implicated in declines in the abundance and diversity of reef fishes (e.g. Graham et al. 2006; Paddack et al. 2009; Wilson et al. 2010). At present, however, the identification of associations between fishes and distinct structural components of coral reefs is mostly limited to individual species of smaller reef fishes (e.g. Munday et al. 1997; Wilson et al. 2008; Bonin 2012). As a result, few, if any, distinct structural components of coral reefs might be classified as keystone structures, although the availability and size of holes or interior cavities, may act as an important means of predator exclusion (Holbrook et al. 2002a; Lingo and Szedlmayer 2006). In the Caribbean, Lirman (1999) found that *Acropora palmata* was heavily used as a diurnal refuge by a wide community of reef fishes, whether the structure was living or dead. More recently, a study on the Great Barrier Reef demonstrated the preference of multiple families of large reef fishes for the tabular-shaped coral *Acropora hyacinthus* compared to two other distinct coral morphologies and also showed that large reef fishes had an affinity for this structure whether it was living or dead (Kerry and Bellwood 2012). Although neither study experimentally tested the impact of the loss of these structures on reef fish community composition, both hypothesised that declines in abundance and diversity might be seen following such a disturbance event. The present study seeks to assess this hypothesis and scale up the previous studies to specifically test the hypothesis that changes in the availability of these structures on coral reefs will impact reef fish communities.

Large reef fishes are not only major contributors to the total biomass of reef fish communities (Ackerman and Bellwood 2000), but perform a number of important functional roles on reefs including herbivory, predation and transportation of nutrients and sediment (e.g. Hixon and Carr 1997; Bellwood et al. 2003). As such, it is important to investigate the level of dependence large reef fishes places upon the structure provided by tabular corals. A clear dependence on tabular structure by multiple families of large reef fishes may provide evidence that tabular corals act as a keystone structure on coral reefs as tabular corals typically comprise only a small fraction of overall reef habitat. Moreover, if tabular corals do constitute keystone structures on coral reefs the impact of their loss should be observable in higher order effects on smaller reef fishes resulting from shifts in competitive and predatory equilibria (e.g. Lemoine and Valentine 2012). The aim of this study, therefore, was to determine whether the availability of tabular structure shapes communities of coral reef fishes across a broad area of reef habitat, moving beyond previous studies that looked at fish usage of individual coral colonies. Specifically, this was assessed by excluding access of large reef fishes to the understory of tabular structures and by adding replicate tabular structure to reef areas previously devoid of large tabular corals. If tabular corals are keystone structures on coral reefs, then changes in the availability of understory habitats should markedly affect local communities of large reef fishes.

2.2 Materials and methods

This study was conducted on reefs surrounding Lizard Island (14°409S; 145°279E) during the austral summer months 2012–2013. Lizard Island is a continental island on the northern Great Barrier Reef (GBR), 35 km off the eastern coast of Australia. Three large patch reefs (0.5–0.9 km^2) located on the western side (back reef) of the island were selected as sites for this study (see Fig. A1). These sites are separated by a minimum of 0.5 km and have flat profiles that typically lack well-defined reef edges with overhangs. A pilot study was conducted to survey all three reefs and found comparable benthic and fish communities.

Availability of tabular structure

Tabular structure is defined herein as any reef structure forming a horizontal canopy that provides a shaded overhang greater than 20 cm in height (e.g. Fig. 2.1a). The pilot study showed that most of the tabular structure on shallow back reefs at Lizard Island consisted of living or dead colonies of *Acropora hyacinthus* and *A. cytherea*. Four 50 x 4 m fixed belt transects (200 m^2 area) were laid at each site, marked every 5 m with small sub-surface floats (2 cm radius) and a surface buoy (10 cm radius) at the start of each transect to assist location. The depth of transects was never greater than 3 m and the minimum distance between transects at each site was 80 m. At each site, the four transects were laid on the reef flat, three with large tabular corals (mean diameter > 0.2 m) and one without large tabular corals. These transects covered between 1 and 2 % of the total surface area of each patch reef. Tabular structure on each transect was measured on SCUBA and included all tabular structures falling wholly or partially within the transect belt. Available tabular structure was measured as area (m^2) calculated as πr2 with the average radius for each structure estimated from two measurements across the planar surface (maximum diameter and the diameter perpendicular to the first measurement). Tabular structures with a planar surface area less than 0.125 m^2 (mean diameter ≤ 0.2 m) were not included in analyses because these structures were considered too small to support the minimum length of focal fishes (0.2 m TL). All tabular structures surveyed were either living or dead tabular acroporids. The mean number of tabular corals on transects with tabular corals was 8.89 ± 0.33, which equates to a mean planar surface area of 7.07 ± 0.55 m^2 per transect or 3.53% of total transect area (see Table A1). The canopy height of tabular structures above the reef substratum was consistent across sites (0.43 ± 0.01 m).

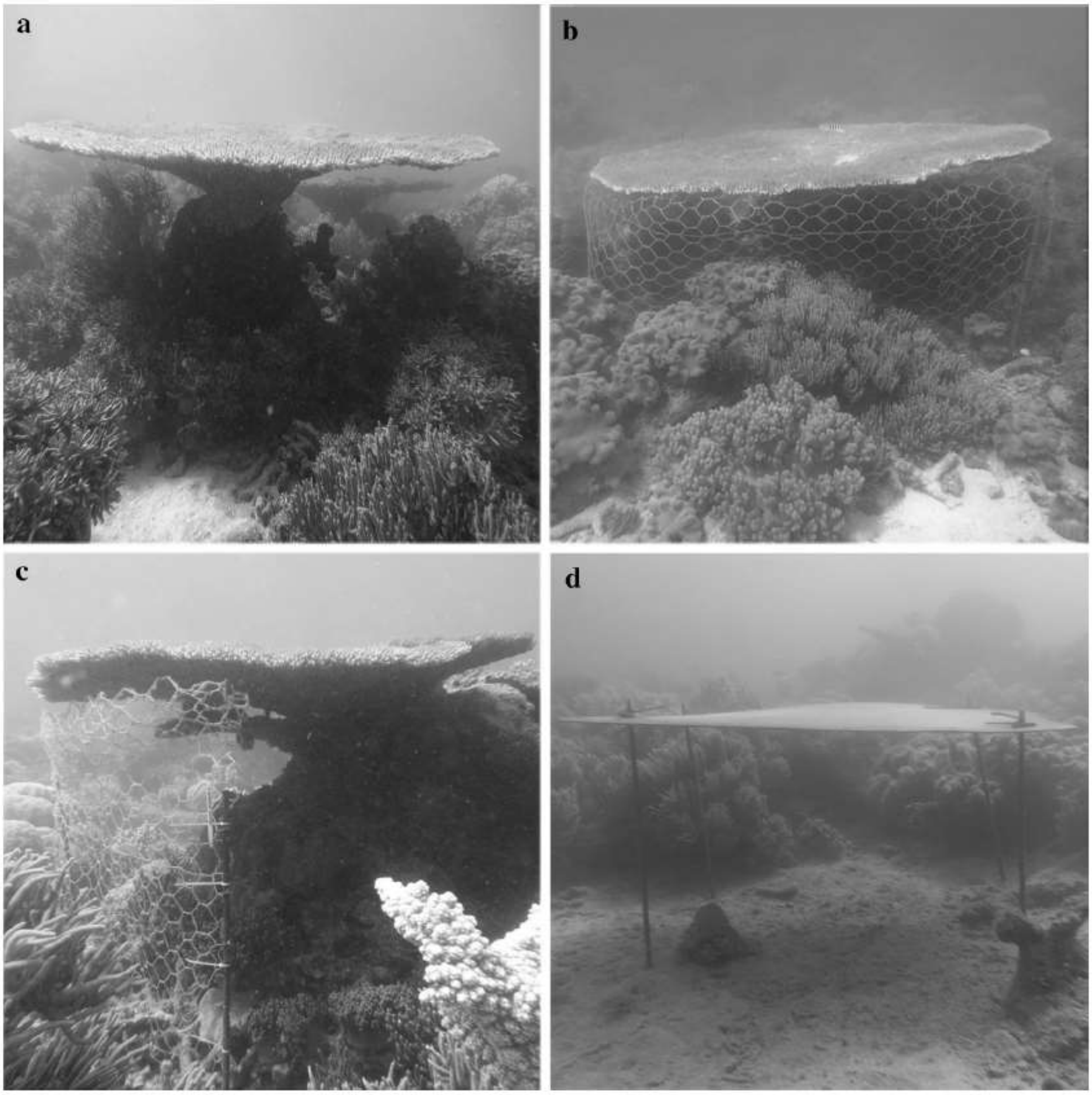

Figure 2.1 (a) *Acropora hyacinthus*, located on a control transect, (b) Caging-control, a mesh wire cage is applied to half the circumference of the tabular coral to simulate the caging effect but permitting access to the structure by large reef fishes, (c) Exclusion, the entire underneath of the tabular coral is excluded for large reef fishes and (d) Addition, a tabular structure *in situ*.

Assemblages of reef fishes

Reef fishes were surveyed between 0900 and 1500 h by two snorkelers swimming slowly side by side along the transect median. One snorkeler recorded species and size (to nearest 5 cm) of all large reef fishes (>20 cm total length) that either passed through or remained within the belt transect. The size of focal species and underwater visibility allowed observations to be made at least 4 m ahead of the snorkeler, to maximise chances of recording fish presence prior to any snorkeler-induced response of large reef fishes (Welsh & Bellwood 2012). In-water observations on snorkel are preferable to SCUBA because the latter can induce substantial diver effects on the behaviour and recorded densities of fishes (Dickens et al. 2011; Welsh & Bellwood 2012). The second snorkeler recorded the number of reef fishes less than 10 cm total length using the same technique as the first snorkeler, recording species from four abundant families: Acanthuridae, Chaetodontidae, Labridae and Pomacentridae. The presence of small-bodied fishes from these four common families (Depczynski et al. 2007) was recorded to monitor any higher order effects that might result from changes in communities of large reef fishes. Fish censuses were repeated for six consecutive days, starting at a different site each day to minimise the effect of temporal factors (e.g. time of day, tide). Because consecutive days of data collection do not represent statistically independent data, values were averaged over the six day survey period for each transect, which were then used as replicates in the analyses. Identical six day survey periods were repeated after the experimental manipulation of tabular structure had been in place for one week, and two months, respectively.

Experimental manipulation of tabular structure

Experimental manipulation of the availability of tabular structure was undertaken to assess its effect on the densities of large reef fishes over 200 m^2 reef areas. Four different treatments were assigned to the four respective fixed belt transects at each site: control, caging-control, exclusion and addition (Fig. 2.1). In the control transects (Fig. 2.1a) no structures were added or excluded.

On exclusion transects the four tabular corals with the largest surface area were excluded (Fig. 2.1b) using steel rods (12 mm diameter x 1000 mm) hammered into the substratum adjacent to the coral, 5 cm from the perimeter of the planar surface. Chicken-mesh wire fencing (50 mm hole width) was then attached to the steel rods using cable ties and drawn around the circumference of the coral creating a barrier for large reef fishes. The lower edge of the wire mesh was moulded around benthic features and the upper edge was neatly tucked under the coral, ensuring the wire did not come into contact with any live coral. Exclusion of the four tabular corals with the largest surface area reduced total available understorey 'shelter area' of tabular structure on exclusion transects by approximately 75 - 80% or 6 - 8 m^2 (see Table A1). The exclusion of surface area slightly overestimates the exclusion of actual available shelter area because of the attachment point (stalk) on living and dead tabular corals (cf. Stimson 1985).

The caging-control treatment (Fig. 2.1c) followed the same design as the exclusion treatment except that mesh wire was only drawn around one half of the circumference of the tabular structure, allowing large reef fishes continued access to the underside of the structure.

In order to add artificial tabular structure to the transect (Fig. 2.1d), four steel rods (12 mm diameter x 1000 mm) were driven into the substratum in a rectangular arrangement such that each rod extended 500 mm above the substratum and was inserted into one corresponding corner of a 1200 x 800 x 2 mm black corflute sheet (rigid polypropylene plastic). The sheet was secured using a combination of plastic washers and cable ties, with the sheet resting 0.45 m above the substratum, creating a shaded canopy. This height correlates closely with recorded heights of tabular corals at these sites (0.43 ± 0.01 m). Four of these tabular structures were added haphazardly along the addition transect at each site to approximate the area included in the caging-controls four exclusions and caging-controls on the other transects. These additions increased the shelter area provided by tabular structure by approximately 4 m^2 on each addition transect (2% of total transect area) (see Table A1).

Statistical analyses

Changes in community composition between treatments and survey periods were investigated using non-metric multi-dimensional scaling (nMDS) based on a Bray-Curtis similarity matrix of $\log_{10}(x + 1)$ transformed data. This analysis was based on the mean abundance of large reef fishes grouped by family per 200 m^2 transect (n = 36, four treatments x three time periods x three reefs). MDS was selected as it made no *a priori* assumptions about group membership and is relatively insensitive to zero values. A one-way pairwise analysis of similarity (ANOSIM) was conducted to determine the significance of any differences between combinations of treatment and time period following grouping by cluster analysis.

For each treatment, variation in the mean abundance of grouped families of large reef fishes were analysed using a one-way ANOVA with survey period as a fixed factor, groupings were based on the mean response of individual families of large reef fishes to both exclusion and addition of structure. With each ANOVA, a Tukey's HSD post hoc test was conducted to assess the source of differences for significant effects. The same analyses were carried out for individual families of small reef fishes. Prior to analyses, data were $\log_{10}(x + 1)$ transformed to meet assumptions of heteroscedasticity and normality.

Relative change in the abundance of each family of large reef fishes recorded in this study was calculated from the difference between mean abundance in the pre-treatment survey and mean abundance in the two month treatment survey, divided by the maximum mean abundance of those survey periods. To obtain a mean relative percentage change for each large reef fish family these values were averaged over the three sites and converted to a percentage. Statistical comparisons of abundances of individual large reef fish families between pre-treatment and two month post-treatment surveys were conducted with two-tailed student's *t*-tests, using Bonferroni correction to adjust for multiple comparisons (n = 3).

2.3 Results

Shifting community composition

A total of 1,838 large reef fishes from nine families (Acanthuridae, Haemulidae, Holocentridae, Kyphosidae, Labridae (parrotfishes and wrasses separately), Lethrinidae, Lutjanidae, Pomacanthidae and Serranidae) were counted during 54 observations (see Table A3). Of those individuals, 640, 495 and 703 were recorded in pre-treatment, one week treatment and two month treatment survey periods, respectively.

The loss of access to tabular corals on exclusion transects resulted in a marked shift from a relatively abundant and diverse community of large reef fishes to a reduced subset of the original (Fig. 2.2). This shift is seen on the x-axis of Figure 2 where pre-exclusion transects (quadrant 3; lower-left) are characterised by a relative abundance of large reef fishes from multiple families with strong loadings, but exclusion transects after one week and two months (quadrants 1 and 4; right-side) are characterised by only one family (Acanthuridae) with a weak loading. The change in community composition therefore occurred within the first week after corals were excluded and remained after two months treatment (Fig. 2.2). On exclusion transects, the ANOSIM identified a significant difference between the pre-treatment assemblages of large reef fishes and both treatment assemblages (Table 2.1). On addition transects, no clear shift in large reef fish assemblages was evident one week after the application of tabular structure, with transects continuing to be characterised by a low number and diversity of large reef fishes (Fig. 2.2). However, two months after the application of tabular structure the community of large reef fishes was more abundant and diverse (Fig. 2.2). The ANOSIM identified this as a significant change (Table 2.1), highlighting the delay in occupation of addition transects by large reef fishes. Interestingly, the ANOSIM found no difference between the pre-treatment assemblage of large reef fishes on exclusion sites and the two month treatment assemblage of large reef fishes on addition sites (Table 2.1). In comparison to the exclusion and addition treatments, the control and caging-control treatments did not exhibit significant differences in abundance between the pre-treatment and treatment assemblages of large reef fishes (see Fig. A2 and Table A2).

Table 2.1 Results of analysis of similarities (ANOSIM: Primer-e) based on Bray-Curtis similarities of $\log_{10}(x + 1)$- transformed abundance data comparing large reef fish assemblages between addition and exclusion treatments at three sites, over three survey periods. Global $R = 0.352$, $P < 0.01$

Treatment (Period)	Addition (1-2)	Addition (3)	Exclusion (1)	Exclusion (2-3)
Addition (1-2)		0.036*	0.012*	0.022*
Addition (3)	0.036*		0.1	0.012*
Exclusion (1)	0.012*	0.1		0.024*
Exclusion (2-3)	0.022*	0.012*	0.024*	

Survey periods are grouped in line with cluster analysis and consist of survey period pre-treatment (1), survey period one week treatment (2) and survey period two months treatment (3). Significant values are marked with an asterisk.

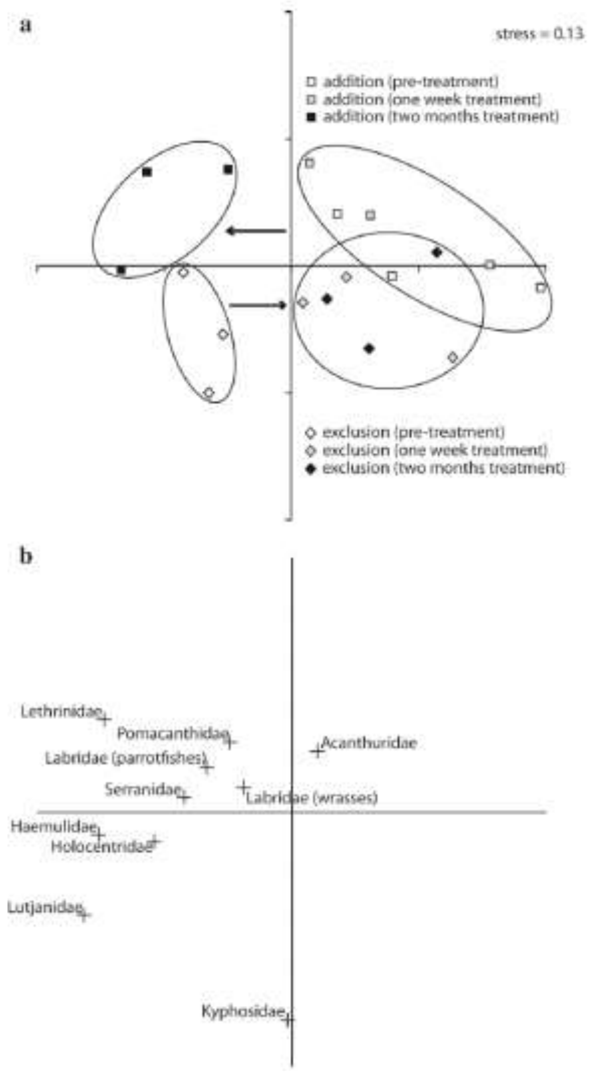

Figure 2.2 Non-metric multi-dimensional scaling analysis showing the relationships between families of large reef fishes across two different structure treatments at Lizard Island, GBR. (a) Ordination plot showing the relationship between three different sites and three different time periods for each treatment. Arrows highlight the transition from pre-treatment and one week treatment communities to two months treatment community on addition transects, and transition from pre-treatment community to one week and two month treatment communities on exclusion transects. Circles indicate groupings used in analysis of similarities. Control and caging-control transects are not shown here (see Fig. A2). (b) Families loadings showing the relative contribution of each family to the observed differences in usage of the two different treatments.

Large reef fish family responses

Three distinct groupings of reef fish families were identified based on their response to the exclusion or addition of tabular structure: obligate structure users, facultative structure users and non-structure users. Obligate structure users displayed a combined mean change in abundance greater than 50% across addition and exclusion transects, and included the Lethrinidae, Haemulidae, Lutjanidae and Holocentridae (Fig. 2.3). Facultative structure users displayed a 10 – 50% mean change in abundance, and included the Labridae (parrotfishes and wrasses), Serranidae and Acanthuridae. These families showed a positive change in abundance to an increase in tabular structure but appeared unresponsive to the loss of tabular structure (Fig. 2.3). The Pomacanthidae and Kyphosidae displayed a mean change in abundance of less than 10% and were therefore categorised as non-structure users (Fig. 2.3).

The mean abundance of obligate structure users changed significantly on exclusion transects across the three survey periods (ANOVA, $F_{2,6} = 14.06$, $P < 0.01$), with pre-treatment abundance being significantly higher than both one week treatment (Tukey's HSD $P < 0.05$) and two month treatment (Tukey's HSD $P < 0.01$) abundances. One week treatment and two month treatment abundances were not found to differ significantly (Tukey's HSD $P = 0.482$). The mean abundance of obligate structure users on addition transects was not found to change significantly across the three survey periods (ANOVA, $F_{2,6} = 3.62$, $P = 0.093$), although there was a non-significant trend that may suggest differences between the time periods. The mean abundance of obligate structure users was not found to change significantly on control and caging-control transects across the three survey periods (ANOVA, $F_{2,6} = 0.18$, $P = 0.837$) and (ANOVA, $F_{2,6} = 0.415$, $P = 0.678$), respectively.

The mean abundance of facultative structure users was not found to change significantly on exclusion, control and caging-control transects across the three survey periods (ANOVA, $F_{2,6} = 2.11$, $P = 0.202$), (ANOVA, $F_{2,6} = 0.91$, $P = 0.453$) and (ANOVA, $F_{2,6} = 1.93$, $P = 0.225$), respectively. On addition transects, however, mean abundance of facultative structure users did change significantly across the three survey periods (ANOVA, $F_{2,6} = 9.47$, $P < 0.05$), although a significant difference only occurred between pre-treatment and two month treatment (Tukey's HSD $P < 0.05$).

Mean abundance of non-structure users was not found to vary significantly on any of the four treatments across the three survey periods; exclusion (ANOVA, $F_{2,6} = 2.77$, $P = 0.141$), addition (ANOVA, $F_{2,6} = 0.02$, $P = 0.976$), control (ANOVA, $F_{2,6} = 0.382$, $P = 0.698$) and caging-control (ANOVA, $F_{2,6} = 2.20$, $P = 0.192$).

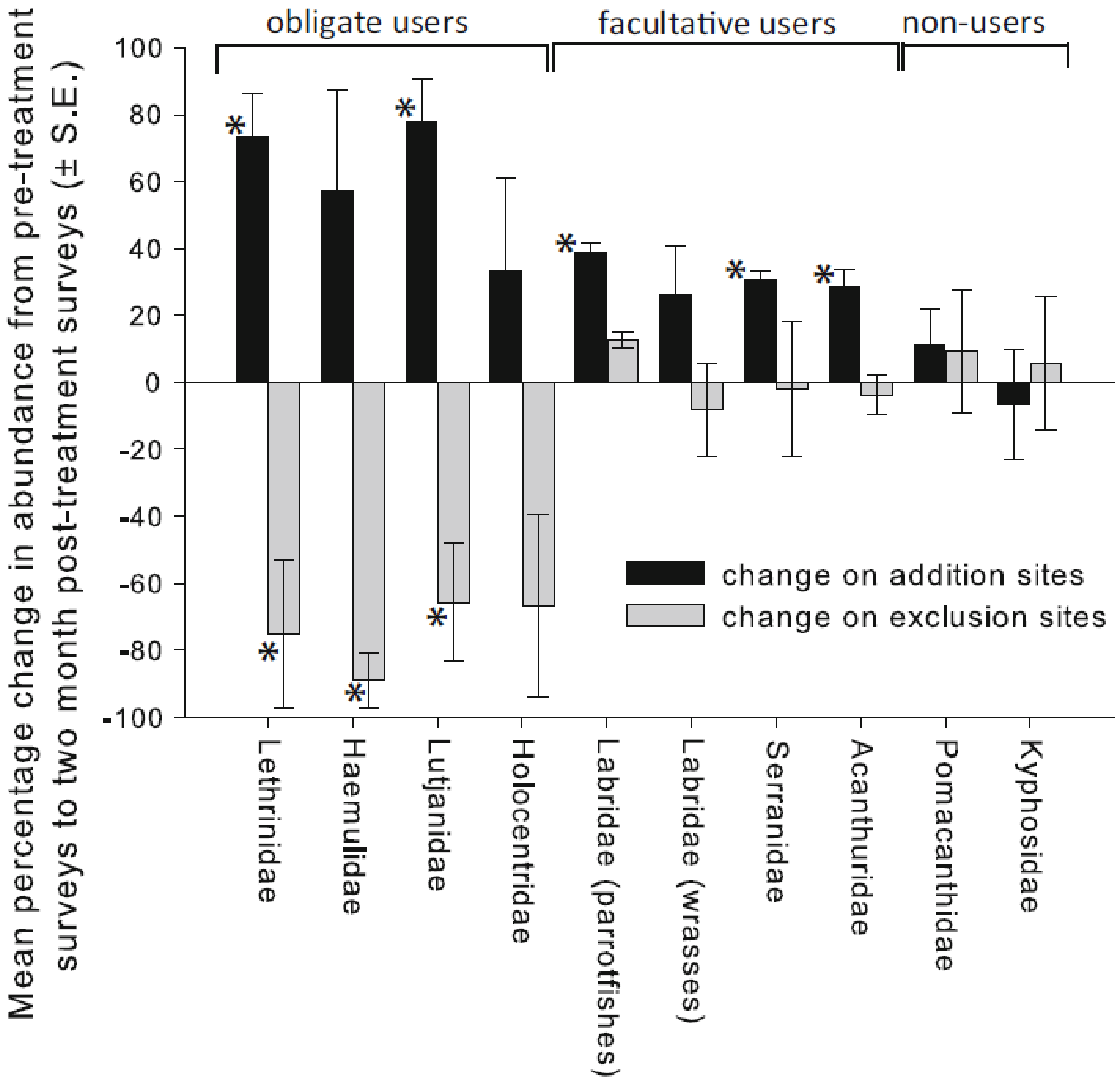

Figure 2.3 Absolute percentage change in mean abundance of large reef fishes by family on exclusion and addition transects from pre-treatment survey periods to two-month post-treatment survey periods. Change is marked (*) if shown to be significant based on two-tailed student's *t*-test with Bonferroni correction. Families are grouped into one of three structure-usage categories based on their mean response to the exclusion and addition of tabular structure.

Small reef fish family responses

The mean abundance of Acanthuridae changed significantly on addition and exclusion transects across the three survey periods (ANOVA, $F_{2,6} = 9.32$, $P < 0.05$) and (ANOVA, $F_{2,6} = 6.72$, $P < 0.05$), respectively. For addition transects, two month treatment abundance was found to be significantly lower than one week treatment abundance (Tukey's HSD $P < 0.05$), and for exclusion transects, two month treatment was significantly lower than both pre-treatment and one week treatment abundances (Tukey's HSD $P < 0.05$). Mean abundance of Acanthuridae was not found to change significantly across control and caging-control treatments.

The mean abundance of Labridae was found to vary significantly on addition transects across the three survey periods (ANOVA, $F_{2,6} = 8.20$, $P < 0.05$), with two month treatment abundances found to be significantly higher than pre-treatment abundances (Tukey's HSD $P < 0.05$). The mean abundance of Labridae was not found to change significantly on exclusion, control and caging-control transects across the three survey periods.

The mean abundance of Pomacentridae was found to vary significantly on addition transects across the three survey periods (ANOVA, $F_{2,6} = 8.35$, $P < 0.05$), with two month treatment abundances found to be significantly lower than pre-treatment and one week treatment abundances (Tukey's HSD $P < 0.05$). The mean abundance of Pomacentridae was not found to change significantly on exclusion, control and caging-control transects across the three survey periods. The mean abundance of Chaetodontidae was not found to vary significantly on any of the four treatments across the three survey periods.

2.4 Discussion

The present study found that changes in the availability of shelter area provided by large tabular structures on shallow coral reefs can have significant effects on the distribution of large reef fish communities, even when these structures only constitute a small fraction of the overall habitat (<4% benthic cover). Given this disproportionate effect of tabular structures on local communities of large reef fishes it is suggested that tabular corals may constitute keystone structures on coral reefs where access to alternate shelter sites or deeper reef environments is limited.

The disproportionate effect of tabular structures

The data herein suggest that the exclusion of four tabular corals from a 200 m^2 area of reef (reducing access to approximately 3.4% of the transect surface area) is sufficient to substantially reduce the daytime presence of multiple families of large reef fishes from the transect areas. The findings support the idea that large reef fishes utilise these structures as 'stepping stones' or 'refuge stations' across a reef (Samoilys 1997; Appeldoorn et al. 2009).

The home range utilisation patterns of an individual fish may vary greatly depending upon its activity, such as, resting, foraging or spawning (Pittman and McAlpine 2003). The 'activity spaces' of large reef fishes that shelter (rest) during the daytime are typically smaller than at night when they forage (Nanami & Yamada 2009; Hitt et al. 2011). Even so, it is likely that activity spaces of large reef fishes at rest during the daytime exceeded the areas covered by transects in this study (Nanami & Yamada 2009; Hitt et al. 2011). The observed transect-level effects may, therefore, have wider implications. Obligate structure users may have narrowed their 'resting' activity space or somewhat shifted their activity spaces to compensate for lost shelter options (Pittman and McAlpine 2003; Grüss et al. 2011). Although changes in the availability of tabular structure at this spatial scale may appear to have relatively benign consequences for large reef fishes, they may lead to usage of sub-optimal activity spaces, and may increase competition for key shelter sites (Almany 2004). The strength of the localised response suggests that the loss of tabular structures at a reef-wide scale, might lead to the displacement of several large reef fish families from the reef, which may severely impact ecosystem function at that locality (Bellwood et al. 2003).

It should be noted that alternate shelter options at other reef locations may be greater, for example, when large reef fish are able to retreat to deeper waters or utilise other tabular structures such as overhanging ledges, which were limited at the study sites. Importantly, however, the exclusion effect simulated in the present study may occur at reef-wide scales during natural disturbance events because tabular corals become more susceptible to dislodgement from strong wave energy as they increase in planar area (Madin and Connolly 2006). Tabular corals (*Acropora*) are also one of the most susceptible growth forms to coral bleaching (Marshall and Baird 2000), ocean acidification (Fabricius et al. 2011), and crown-of-thorns outbreaks (Baird et al. 2013).

In the contrasting scenario, where tabular structure was added to a 200 m^2 area with relatively low tabular structure tabular structure (modifying approximately 2% of total surface area), assemblages of large reef fishes became comparable with assemblages on pre-treatment exclusion transects after no more than two months. In reality, the colonisation and growth of tabular corals to sizes simulated here (1 m mean diameter) would take at least 10 years based on planar growth rates of 10 cm per year (Stimson 1985), suggesting suitable alternative habitat may be limited in typical coral reef environments after a major physical disturbance, such as a cyclone. This situation might compare with the terrestrial environment where efforts to recover declines in native bird species by planting new vegetation are anticipated to undergo future bottlenecks because of the time taken for trees to reach sufficient sizes (Mac Nally 2008). Indeed, the present study suggests that large reef fishes are able to adjust their activity spaces relatively quickly (within a few months) to take advantage of new habitat features. It is possible that inclusion of novel locations into one type activity space (e.g. resting) may be facilitated by a wider home range of another activity space (e.g. foraging) (Pittman and McAlpine 2003). Ultimately, however, the establishment of tabular corals at new reef sites might open up these localities to increased species richness, abundance and ecosystem function.

Divergent responses to manipulation of tabular structure

Graham et al. (2007) looked at the response of multiple size classes of reef fishes, including large reef fishes (> 20 cm total length), following a severe bleaching event and subsequent structural declines in the Seychelles. Their data showed a varying response to a reduction in structural complexity both within and between different trophic groups of large reef fishes, although piscivores showed a general decline in abundance, which has been attributed to the loss of their prey (Graham et al. 2007). A more recent study in Saba Marine Park, Netherland Antilles, also observed a mixed response of large reef fishes to the loss of coral cover, again with a general decline in carnivores (Noble et al. 2013). It is unlikely, however, that these responses relate solely to declines in prey items because several families of carnivorous large reef fishes move off the reef to feed (Nanami and Yamada 2009; Hitt et al. 2011). The results of the present study may help to explain these variable results as it appears the responses of large reef fishes to the loss of tabular structure differs at the family level, with three identifiable groups: obligate, facultative and non-structure users.

The obligate structure users in this study (Lethrinidae, Lutjanidae, Haemulidae and Holocentridae) showed strong responses to the addition and exclusion of tabular structure. These families of reef fish are predominantly crepuscular or nocturnal, typically sheltering during the day and moving to sand flats or seagrass beds to feed at night (e.g. Craig et al. 2007; Clark et al. 2009; Nanami and Yamada 2009; Farmer and Ault 2011). Given that these fishes are at rest during the day it is likely that they benefit from the shelter provided by tabular structure. This can conceal them from predators, improve detection of approaching threats, and create a physical barrier that will increase the chances of escape (Helfman 1981; Caley and St John 1996; Mazur and Beauchamp 2003; Almany 2004). Tabular structures also provide shaded microclimates on coral reefs (Baird and Hughes 2000), and may be occupied by obligate structure users to avoid harmful ultraviolet (UV) radiation in shallow reef environments (Sweet et al. 2012), thereby reducing the substantial energetic costs involved in producing UV-absorbing compounds (Zamzow and Losey 2002). Tabular structures may therefore decrease in value to sheltering fishes outside of the principle diel period of UV radiation in which this study was conducted (0900 – 1500 hrs). Moreover, greater intensity of UV radiation may increase the attraction of large reef fishes to tabular corals during the austral summer months (the period examined) when the sun reaches its zenith in the Southern Hemisphere (Wozniak and Dera 2007). The crepuscular or nocturnal behaviour of obligate structure users (Clark et al. 2009; Nanami and Yamada 2009; Farmer and Ault 2011) suggests that reef locations with large tabular corals may be occupied by fewer numbers or different species of reef fishes at night.

Facultative structure users (Acanthuridae, Labridae (parrotfishes and wrasses) and Serranidae) displayed a positive response to the addition of tabular structure but minimal response to the exclusion of tabular corals. In this study, these large reef fishes were occasionally observed retreating under tabular structures when a snorkeler approached, suggesting that this group of fishes recognises the value of tabular structure in threat avoidance, even though lack of available tabular structure may not supersede the importance of accessing feeding grounds. For example, the behaviour of an abundant member of the Serranidae, *Plectropomus leopardus*, may provide support for this theory. This diurnally-active, generalist piscivore, has been documented sheltering under tabular structures (e.g. Zeller 1997; Kerry and Bellwood 2012) but was categorised as a facultative structure user in the present study. Perhaps the minimal change in the abundance of the Serranidae on exclusion transects can be explained by their attachment to up-current (‘run on’) reef locations as hunting grounds (Zeller 2002). The modest response of the Serranidae to exclusion transects in the present study may suggest that affinity with these hunting grounds takes preference over the availability of shelter. This also assumes that, in general, facultative structure users are prepared to invest more energy in UV-absorbing compounds (Zamzow 2004), to maintain access to key feeding locations during the diurnal period, when the majority of these families are active (e.g. Pittman & McAlpine 2001; Grüss et al. 2011). Conversely, the increased presence of facultative structure users on addition transects may be opportunistic, allowing fishes to utilise tabular structure as it becomes available within already established activity spaces, thereby reducing energetic costs and predation risk.

Higher order effects on small reef fishes

Three of the four families of small reef fishes observed in this study showed significant changes in abundance on addition transects. Although these responses may be a direct consequence of changes in the availability of tabular structure, it is also possible that they reflect a response to increasing numbers of large reef fishes at addition sites. Pomacentridae are a major component of small reef fishes on coral reefs (Ackerman and Bellwood 2000) and considered to be a major prey item for larger reef fishes (e.g. Beukers-Stewart and Jones 2004). Their decline on addition sites, in contrast to increases in predatory large reef fishes (e.g. *Lutjanus carponotatus*, *Lutjanus bohar*, *Plectropomus leopardus*) may suggest a trophic cascade in response to changing availability of shelter area provided by tabular structure on coral reefs. Small-bodied Acanthuridae also declined on addition sites, in contrast to increases in the abundance of large-bodied Acanthuridae. While the effect of predation cannot be discounted in this case it is also possible that larger Acanthuridae moving into the area drove out smaller individuals, especially as this family contains a number of highly aggressive species (Choat and Bellwood 1985). While it is difficult to account for the increase in small Labridae on addition transects this may reflect the strong association of certain small species of Labridae with larger reef fish, such as *Labroides dimidiatus* or the opportunistic *Thalassoma lunare* (Connell 1998). The failure to detect any significant change in Chaetodontidae on addition transects may be attributed to relatively low predation rates on these species, owing to their multiple predator defences (e.g. Neudecker 1989). As this family contains many corallivores (Cole et al. 2008) it is also possible that numbers of Chaetodontidae did not increase because no new coral food sources became available on addition transects. Over a longer time period increased success following recruitment pulses may also have shown increasing abundance of small reef fishes on exclusion transects, where numbers of large predators had declined.

Keystone structures may be present in virtually all ecosystems, but their identification remains relatively scarce and largely restricted to terrestrial and shoreline environments. In this study, experimental manipulation of specific structures has revealed substantial changes in local communities that can help to explain broader patterns in disturbed or recovering ecosystems. Given the disproportionate effect manipulation of shelter provided by tabular structures had on reef fish communities in this study, it is suggested that tabular corals may constitute keystone structures on shallow coral reefs. As the only common carbonate depositing species to adopt a ‘canopy’ growth form in shallow coral reef environments, tabular corals may provide reef fishes with a number of unique, structure-specific functions.

Chapter 3: The functional role of tabular structures for large reef fishes: avoiding predators or solar irradiance?

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3.1 Introduction

Most fishes that inhabit coral reefs are among the more recently evolved teleosts, having diversified and adapted to take advantage of the rich complexity offered by modern scleractinian coral reefs (Hobson 1974; Cowman et al. 2009). The structure provided by coral reefs is thought to be a key element of the multi-faceted relationship between reef fishes and coral reefs, and has been the focus of intensive study (see reviews in Wilson et al. 2006; Pratchett et al. 2008; Graham and Nash 2013). One major factor determining the relationship between structures and fishes is the body size of the latter (Hixon and Beets 1993; Harborne et al. 2011; Karkarey et al. 2014; Pratchett et al. 2014), thus emphasising the need to investigate the utility of reef structures for specific size classes of reef fishes.

For several decades, large reef fishes (Total Length (TL) > 20 cm) have been anecdotally reported sheltering under canopy structures (e.g., Hobson 1974; Helfman 1986; Zeller 1997). More recently, the availability of tabular structures has been shown to be important in moderating the activity spaces (area of an activity, e.g., foraging) of large reef fishes during the day (Kerry and Bellwood 2014). To date, however, no studies have demonstrated the reason for this sheltering behaviour, although three potential reasons for diurnal sheltering behaviour are: avoidance of solar irradiance, avoidance of predators, and concealment for ambush predation (Almany 2004; Sweet et al. 2012). Of these, the latter hypothesis can only apply to a subset of the shelter-using large reef fishes as many of these fishes are nocturnal invertivores (cf. Kerry and Bellwood 2012). The present study, therefore, will seek to weigh the relative importance of solar irradiance avoidance or predator avoidance in the sheltering behaviour of large reef fishes.

Coral reef habitats are generally characterised by high light intensities and relatively oligotrophic waters (Falkowski et al. 1990). On clear days, irradiance (the flux of light energy on an area) is highest in shallow waters (< 5 m) for visible (400 – 700 nm), UV-A (320 – 400 nm), and UV-B (280 -320 nm) spectra (Falkowski et al. 1990; Loew and McFarland 1990). UV-photoexposure can be extreme under such conditions (Losey et al. 1999).

UV-B irradiation appears to be the key factor in damage to fishes and can cause severe necrosis, surface edemas, and secondary fungal infections in the epidermis (Blazer et al. 1997; Zamzow et al. 2013). Some fishes secrete photoprotective substances in their epithelial mucous, which primarily act to block incident UV-B irradiation (Zamzow and Losey 2002; Eckes et al. 2008). These mycosporine-like amino acids (MAAs) are thought to be energetically costly to sequester, in limited supply, or both (Zamzow and Losey 2002). Therefore, during sedentary diurnal periods, fishes would benefit from avoiding downwelling irradiance in the shallow, clear waters that typify and sustain coral reefs.

In contrast to the above hypothesis, the diurnal sheltering behaviour of nocturnal fishes, followed by a predictable migration to feeding grounds after sunset, has been suggested to relate to predation pressure (Hobson 1972; Helfman 1986; McFarland et al. 1999). Sharks, the most likely predators of large reef fishes, increase in activity from late afternoon into twilight (McKibben and Nelson 1986; Gruber et al. 1988; Whitney et al. 2007; Vianna et al. 2013). This correlates with the peak efficiency in the visual senses of sharks

(Cohen 1990; McFarland 1990), which enhances their scotopic vision by contrasting darker prey against a lighter background. Although the scotopic pigments of other marine fishes have also typically evolved to match twilight conditions (McFarland 1990; Marshall 2000), predators may retain the upper hand by better utilising the remaining photopic light at sunset as they typically possess larger cones, which may sacrifice high acuity but increase light capture per receptor cell (Munz and McFarland 1973). While in full daylight this would offer little advantage, during sunset, when photopic light is fading, it would enhance the contrast of potential prey against their surroundings (Munz and McFarland 1973). Diurnal and nocturnal fishes, on the other hand, cannot sacrifice the high visual acuity typically needed for foraging and are at a relative visual disadvantage during sunset (Munz and McFarland 1973).

Structurally complex environments can help fishes to avoid predation (Almany 2004). This may account for the role of structurally complex habitats as the primary correlate with reef fish assemblage structure at various spatial scales (MacNeil et al. 2009; Verges et al. 2011). The size of holes on an artificial reef was found to be an important factor in predator exclusion (Hixon and Beets 1993). While large tabular structures such as *Acropora hyacinthus* may not exclude access by large predators such as reef sharks (Randall et al. 1997; Wetherbee et al. 1997; Kerry and Bellwood 2014), they may deter more high speed predators such as jacks. Regardless of the predator, sheltering under tabular structures can help to visually conceal resting fishes and may reduce the encounter rate of predators with their prey, rather than reducing actual vulnerability to predation (Shulman 1985). Although this sheltering behaviour may help to avoid diurnal mobile predators such as jacks and reef sharks, it is likely these open structures will have no effect for nocturnal, olfactory predators such as the large moray eel, *Gymnothorax javanicus*, which sneak through crevices in the reef and corner their prey in holes (Bshary et al. 2006). Two alternative hypotheses are therefore proposed. If large reef fishes (TL > 20 cm) are using tabular structure primarily for solar irradiance avoidance, sheltering activity should be significantly higher during the period when irradiance is highest, i.e., midday (Falkowski et al. 1990), compared with sunset. On the other hand it is hypothesised that if large reef fishes are using tabular structure primarily for avoiding visually active diurnal predation, increased sheltering activity should be observed during sunset when compared to midday.

3.2 Materials and methods

This study was conducted during November and December 2013 at Lizard Island, a mid-shelf reef in the northern section of the GBR (14°40’S 145°28’E). The use of tabular structures was quantified using underwater video observations at 21 shallow reef locations bounded by Lizard, South, and Palfrey Islands. The 21 locations were located in 2-5 m of water and adjacent locations were separated by a minimum of 250 m.

Experimental setup

To test if the use of tabular structures was higher during midday or sunset, at each location a single, large tabular structure was recorded from 1100 - 1400 h and from 1630 – 1930 h on separate days using two GoPro Hero 3 Silver video cameras (Battery BacPac; 16GB microSD Card; 720p; 25fps; Indicator Light <off>) in underwater housings attached with cable ties to a small dive weight. The two video cameras were deployed on snorkel and positioned so that the front and profile of the tabular structure could be seen during analysis. Tabular structures are herein defined as either living or dead tabular corals (*A. hyacinthus* and *Acropora cytherea*, n = 17, mean planar surface area = 3.97 m^2 ± 0.48 SE) or carbonate reef overhangs (n = 4, mean planar surface area = 4.26 m^2 ± 0.67 SE) that provide a shaded canopy greater than 20 cm in height above the substratum. Filming was only carried out at one location on any given day, equating to 42 d of filming over a two-month period in the austral summer. During the course of the study, sea conditions were typically calm with clear skies and moderate to low turbidity.

To observe usage throughout the diurnal period, one large tabular coral was also filmed on five separate days in late December 2013 from 1730 - 1930 h using a series of GoPro 3 video cameras. Measurements of photosynthetically active radiation (PAR; measure of solar radiation in visual light spectrum) covering this period were obtained from a LI-COR 192 light metre (LI-COR, Nebraska, USA) located above the water and within the study zone at Seabird Islet (source: Australian Institute of Marine Science).

Video analysis

To account for the variation in the transition of the sun over the course of the two-month study, video footage taken during the midday period was analysed for one hour from the time at which the sun was highest in the sky at Lizard Island (solar noon; NOAA 2014). For sunset footage, analysis was conducted for one hour up until civil twilight (defined as the point at which the geometric centre of the sun is 6° below the horizon; NOAA 2014). This correlated closely with the point at which loss of light prevented further accurate video analysis. Throughout the study window, this meant that start times for midday analyses varied from 1203 - 1215 h and start times for sunset analyses varied from 1745 - 1815 h. In each case, therefore, analysis took place on footage from video cameras that had been in place for at least one hour of ‘soak’ time.

Analysis was carried out by sampling the video footage every 3 min. For each sample the video footage was examined for 30 s, which allowed sufficient time to determine which fishes were underneath the tabular structure at that time period, i.e., whether they were simply passing through the structure or intentionally sheltering beneath it. A fish was considered to be sheltering if it spent more than 10 s under the structure and was either static or not moving in one clear direction. Ten seconds was set as a conservative cut-off because fishes tended to pass either rapidly through the structure within several seconds or remain underneath the structure for periods much longer than 10 s. The length of a sheltering period was therefore calculated as (3:00 min) x (n – 1) + (10 s), where ‘n’ is the number of contiguous sampling periods in which the individual was sheltering. The mean residence time of an individual fish was calculated by taking an average of each contiguous sheltering period. For analysis, mean residence time for a structure was calculated as an average of the residence times of all fishes sheltering under that structure during the 1-h observation period. The majority of large reef fishes that occupied a structure over multiple sample periods were easily identified as unique individuals based on their species, size, and distinct markings (such as scarring or fin damage). Where this was not clear it was necessary to go through the full hour of video footage to verify the identity of an individual. The species, length, and position under the structure of each large fish (> 20 cm TL) were recorded for each sample period.

Abundance of fishes under a structure was the total number of unique individuals sheltering during that observation period. Species richness was the total number of unique species sheltering during that observation period. Length estimates were facilitated by placing a graduated rule in front of the structure at the start of filming. Length estimates of fishes were converted to biomass using published length-weight relationships. Mean length and mean biomass of fishes under a structure were respectively calculated as an average of the length and biomass of all individuals sheltering during that observation period. Position was recorded as one of three categories, based on their predominant behaviour: ‘under lip’, 'throughout', or 'deep'. ‘Under lip’ referred to fishes that were positioned directly under the outer edge of the tabular structure, ‘throughout’ to fishes that showed no attachment to any particular area under the tabular structure, and ‘deep’ to fishes that positioned themselves towards the centre of the understorey of the tabular structure. Fishes occupying ‘under lip’ and ‘deep’ positions were almost always oriented so that they faced outward from the centre of the coral, and fishes tended to consistently adopt one of the three positions. The position of each fish was assigned based on which position was most frequently assumed by the individual.

Statistical analyses

Changes in assemblages of large reef fishes under tabular structures between midday and sunset were visualised using non-metric multi-dimensional scaling (nMDS) based on a Bray-Curtis similarity matrix of $\log_{10}(x + 1)$ transformed data. This analysis was based on the mean abundance of fishes per tabular structure, per time period (n = 42, 21 tabular structures x 2 time periods). Fishes were either treated as individual species, or grouped if rarely encountered, into higher orders (species: *Acanthurus dussumieri*, *Balistoides viridescens*, *Cheilinus undulatus*, *Diagramma pictum*, *Lutjanus carponotatus*, *Lutjanus gibbus*, *Lutjanus russelli*, *Sargocentron spiniferum*, and groups: *Naso* spp., *Plectorhincus* spp., *Plectropomus* spp., *Pomacanthus* spp., large groupers (ex. *Plectropomus* spp.), large snappers (ex. *Lutjanus carponotatus*, *Lutjanus gibbus*, *Lutjanus russelli*), parrotfishes (see Table B1). A one-way permutational multivariate analysis of variance (PERMANOVA) was used to investigate any difference in assemblages of large reef fishes between midday and sunset time periods. Ten thousand permutations were undertaken using PERMANOVA with site as a random factor.

Variation in the total abundance, species richness, mean length, mean biomass, and mean residence time of large reef fishes sheltering under tabular structure between midday and sunset was analysed using two-tailed, paired t-tests to account for midday and sunset observations on each structure (n = 21 tabular structures). All data were $\log_{10}(x + 1)$ transformed prior to analyses and met assumptions of normality and homoscedasticity (see Table B2). Differences in the position of fishes between midday and sunset were compared using multiple two-tailed Fisher's exact test (Under Lip vs Throughout, Under Lip vs Deep, Throughout vs Deep). Given the three pairwise comparisons the P-value was Bonferroni corrected to be significant at $P < 0.05/3$ or $P < 0.017$ (cf. Gardner and MacDonald 2000). The filming of a single tabular coral across 5 d was only used to indicate a possible pattern for fish behaviour throughout the day, and no statistical analyses were applied to these data.

3.3 Results

Fish assemblages

There was a significant difference between assemblage structures of large reef fishes at midday and at sunset (Figs.1 and 2; PERMANOVA, $F = 8.888$, $P < 0.001$). This clear separation between midday and sunset was driven by greater usage of tabular structures by Lutjanidae and Haemulidae at midday and *Naso* spp. and *Balistoides viridescens* at sunset (Fig. 3.2). Paired t-tests supported the nMDS with mean total abundance and species richness being significantly higher at midday than at sunset (Table 3.1). The mean length of time a fish spent under tabular structure (residence time) was also significantly greater at midday than at sunset (Table 3.1). However, the mean length and mean biomass of large reef fishes using tabular structures was not found to differ significantly between time periods (Table 3.1).

Observation of the diurnal sheltering behaviour of large reef fishes under a single tabular coral over 5 d suggested that the greater abundance at midday may reflect a noon-time peak in usage of tabular structures (Fig. 3.3). This peak in the abundance of large reef fishes remained until approximately 3 pm, after which there was a sustained departure of fishes from under the structure (Fig. 3.3). Several species of large reef fishes that had ceased sheltering under structure remained visible in the locality up until the loss of light at approximately 7:00 pm (Fig. 3.1b).

Table 3.1 Variation in the total abundance, species richness, mean length, mean biomass and mean residence time of large reef fishes sheltering under tabular structures between midday and sunset

	Midday	Sunset	T_{20}	P
Total abundance ± S.E.	13.6 ± 3.1	5.3 ± 0.8	2.961	**0.0077**
Species richness ± S.E.	6.90 ± 0.71	4.67 ± 0.66	2.891	**0.0091**
Mean length (cm) ± S.E.	43.9 ± 1.2	41.9 ± 1.8	1.023	0.3185
Mean biomass (kg) ± S.E.	2.02 ± 0.18	1.83 ± 0.22	0.799	0.4337
Mean residence time (hh:ss) ± S.E.	28:06 ± 5:55	07:47 ± 2:19	5.652	**<0.0001**

Significant values given in bold. Untransformed data are shown, all statistical tests performed on transformed data

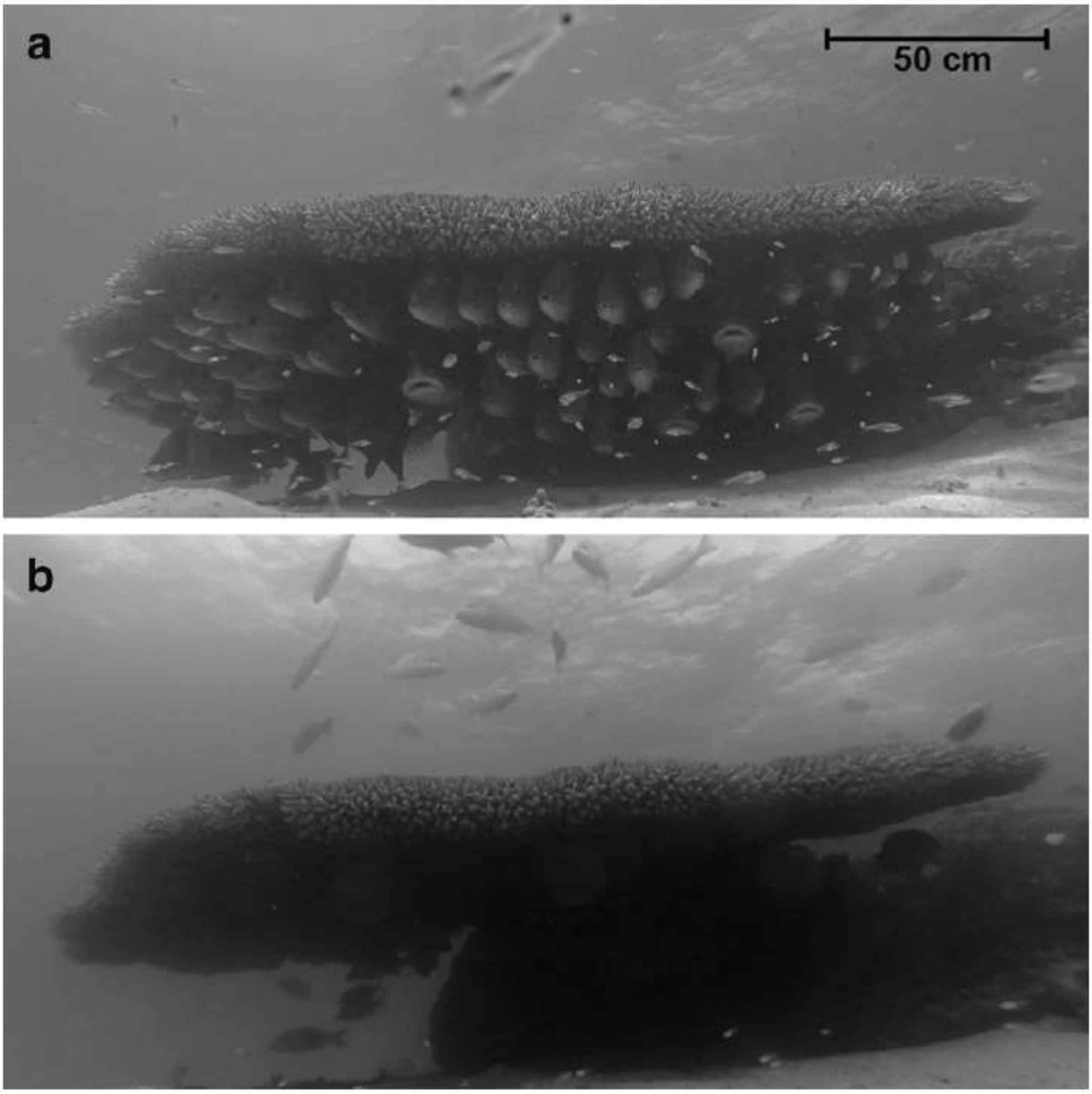

Figure 3.1 (a) Snapshot of large tabular structure with multiple large reef fishes sheltering; taken at 12:56 pm on 28th December 2013. (b) Snapshot of same large tabular coral with significantly fewer sheltering fishes, with others visible in the water column; taken at 18:40 pm on 28th December 2013.

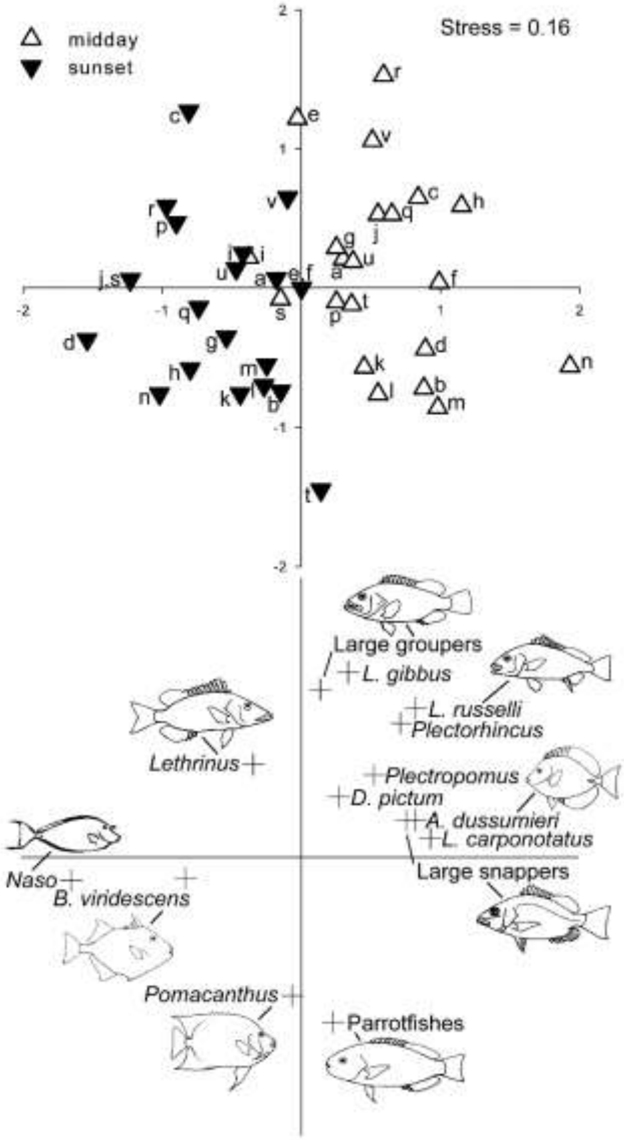

Figure 3.2 Non-metric multi-dimensional scaling analysis showing differences in assemblage structures of large reef fishes sheltering under tabular structures at Lizard Island, GBR, across two time periods: solar noon and sunset. (a) Ordination plot showing the relationship between 21 tabular structures at the two time periods. Pairs of letters denote the same site at midday (white triangles) and at sunset (black triangles), respectively (b) Taxonomic loadings showing the relative contribution of species and other groups to the observed differences between the two time periods.

Position under structure

Between midday and sunset there was a significant difference in the proportion of fishes sheltering under the lip versus fishes that did not shelter in any one particular location (under lip vs. throughout, $P < 0.0001$, two-tailed Fisher's exact test). This difference was driven by an increase in the number of fishes that did not hold to any particular position at sunset (Table 3.2). No significant difference was found in the proportion of fishes sheltering under the lip versus deep, or throughout versus deep between midday and sunset. The position of large reef fishes under tabular structures also varied among species. Fishes that were observed to use tabular structure more at midday tended to position themselves under the lip (outer edge) of the tabular structure, especially at midday (Table 3.2). Conversely, fishes that sheltered under tabular structures at sunset tended not to show fidelity with any particular location (Table 3.2). No species showed a preference for positioning themselves deep under cover, although large groupers and *Pomacanthus* spp. did occasionally use deeper locations when sheltering (Table 3.2).

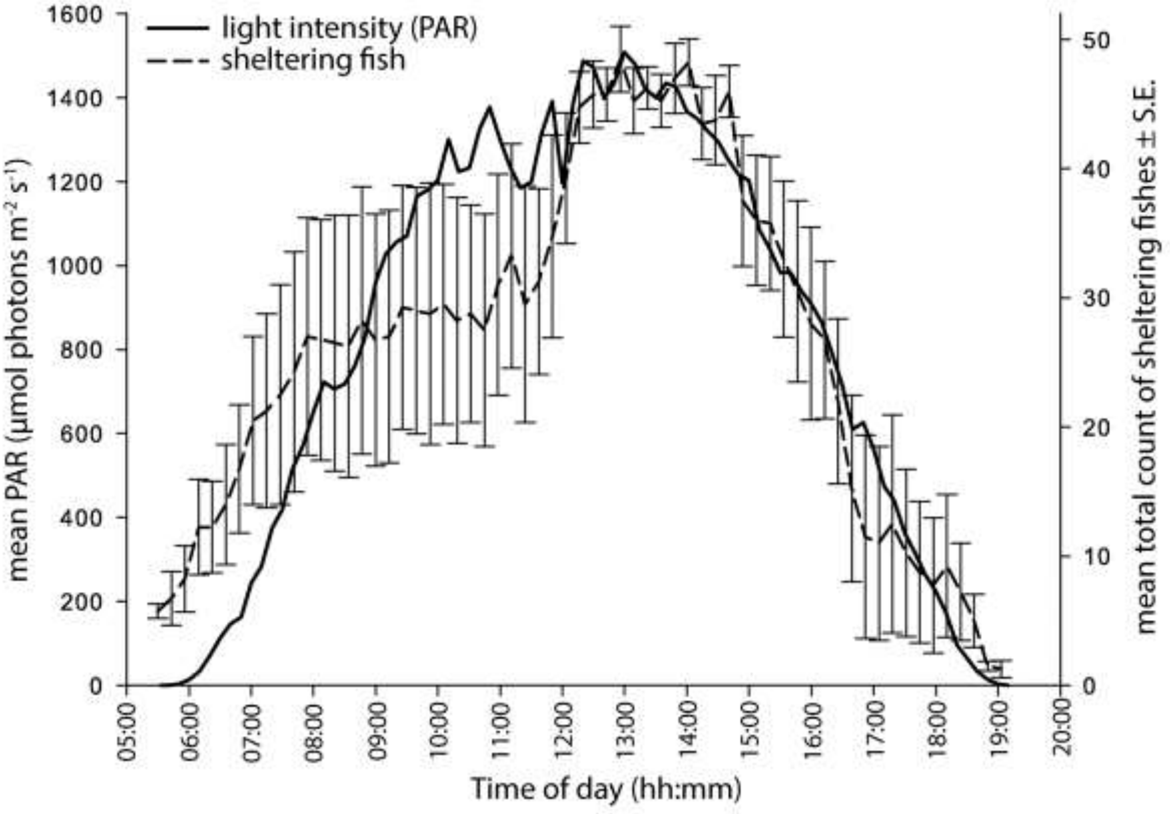

Figure 3.3 Left axis: mean values of photosynthetically active radiation (PAR) measured at Seabird Islet (solid line), Lizard Island over 5 days in late December 2013; values are recorded every 10 minutes. Right axis: mean count (dotted line) ± S.E. of large reef fishes sheltering under a single large table coral in the lagoon at Lizard Island over the same 5 days; values are recorded every 15 minutes. Error bars not shown for PAR data.

Table 3.2 Per cent standardised counts of total numbers of species, genera and groups of large reef fishes sheltering between midday and sunset based on three different locations under tabular structure: 'under lip', 'throughout' and 'deep', ranked by percentage under lip at midday. Groups of fishes used in analyses do not include individual species or genera also considered in the analysis.

	Midday			**Sunset**			
	Under Lip	**Throughout**	**Deep**	**Under Lip**	**Throughout**	**Deep**	**N**
Diagramma pictum	100.00	0	0	0	0	0	11
Lutjanus russelli	100.00	0	0	0	0	0	10
Lutjanus carponotatus	95.56	4.44	0	80.00	20.00	0	96
Plectorhincus	88.89	3.70	7.41	50.00	25.00	25.00	31
Large snappers	76.92	23.08	0	66.67	33.33	0	17
Plectropomus	70.59	5.88	23.53	25.00	50.00	25.00	21
Large grouper	60.00	0.00	40.00	100.00	0.00	0	8
Sargocentron spiniferum	30.00	70.00	0	50.00	50.00	0	18
Acanthurus dussumieri	21.43	78.57	0	0	100.00	0	31
Lethrinus	15.38	84.62	0	16.67	83.33	0	25
Lutjanus gibbus	13.33	86.67	0	25.00	75.00	0	19
Parrotfishes	6.67	93.33	0	12.50	87.50	0	33
Pomacanthus	0	69.23	30.77	9.09	90.91	0	24
Cheilinus undulatus	0	100.00	0	50.00	50.00	0	5
Naso	0	100.00	0	8.33	91.67	0	30
Balistoides viridescens	0	100.00	0	0	100.00	0	5

Discussion

Solar irradiance avoidance

At midday, when light intensity was significantly higher than at sunset, tabular structures were used by significantly more large reef fishes, and for longer time periods; as such, the data presented herein are most consistent with the solar irradiance avoidance hypothesis. It is likely that this behaviour relates, at least in part, to the avoidance of UV-B irradiation, which has been shown to cause significant damage to fish skin in clear, shallow water (Blazer et al. 1997; Sweet et al. 2012; Zamzow et al. 2013). Calculation of UV values from PAR data is difficult because it is affected by several variables including the sun's angle, ozone density and cloud cover (V. E. Brando, *pers comm*). Nevertheless a basic model for solar irradiance in cloudless maritime atmospheres suggests that, UV radiation is approximately 47% of photosynthetically available radiation (Gregg and Carder 1990). In most coral reef habitats, which are often both oligotrophic and shallow, UV wavelengths penetrate to significant depths when the sun is close to its zenith at midday. At sunset, low light levels and surface reflectance greatly reduce UV intensity underwater (Munz and McFarland 1973; Loew and McFarland 1990; Smith et al. 1992). It can therefore be assumed that UV irradiance was significantly higher at midday (mean PAR for study period: 1393 μmol photons m^{-2} s^{-1}) than at sunset (mean PAR for study period: 111 μmol photons m^{-2} s^{-1}).

For large reef fishes that are not actively feeding at midday, avoidance of UV radiation makes physiological sense, given the significant energetic costs of producing UV-blocking MAAs (Zamzow and Losey 2002; Eckes et al. 2008). Thus the preference of certain species of large reef fishes for structures that cut-out UV radiation (cf. Marshall 2000) may help to explain why some families of reef fishes modify their activity spaces in response to changes in the availability of these structures (Kerry and Bellwood 2014). This observation would benefit from further research to discover which fishes on coral reefs produce MAAs and in what quantity.

It is interesting to note that several of the families of fishes observed to consistently shelter under tabular structure at midday in the present study are nocturnally active (e.g. Haemulidae and Lutjanidae; Clark et al. 2009; Farmer and Ault 2011). These individuals would therefore receive the greatest benefit from shelter as they are not constrained by an attachment to feeding grounds (Pittman and McAlpine 2003).

Other large reef fishes, such as *Plectropomus leopardus*, observed sheltering at midday were either absent at sunset or not seen again once they exited the tabular structure. Crepuscular feeders, such as *P. leopardus* (Bunt and Kingsford 2014), probably place priority on feeding over sheltering once light conditions become favourable. They thus vacate the structures during or before sunset. *Plectropomus leopardus* is not thought to actively engage in ambush predation while sheltering during the day (cf. Vail et al. 2013). Even in this predatory species, the attachment to tabular structure appears to relate primarily to UV-avoidance rather than prey capture. Fishes seeking to avoid UV irradiance could instead utilise deeper habitats rather than shelter under tabular structures in shallow environments. The high use of tabular structure in the present study might however be explained by a number of factors, including lack of access to deeper areas within established home ranges, access to prey locations(Pittman and McAlpine 2003; Clark et al. 2013).

Predation avoidance

Strong evidence in the literature for increased predator activity and predation success from late afternoon to twilight (e.g., Danilowicz and Sale 1999; McFarland et al. 1999; Whitney et al. 2007; Vianna et al. 2013) would suggest that if large reef fishes shelter under tabular structure to avoid predation, this occupancy of structure would be greater at sunset than at midday. The data presented herein do not support this conclusion, indeed, by sunset, tabular structures were vacated by most species of large reef fishes observed sheltering at midday. As in previous studies (Munz and McFarland 1973; McFarland 1990), nocturnally-active species continued to be seen in the locality at sunset and until the loss of light prevented further observation. While these species remained in the vicinity of the coral reef they were seldom observed beneath tabular structures, suggesting that these structures provide negligible benefit to most large reef fishes at lower light levels. In one instance, at sunset, when a hammerhead shark (*Sphyrna* spp.) moved through the area, most large reef fishes scattered in the water column, although some swam under the tabular coral (see ESM Video S1). It is worth noting, therefore, that predation avoidance may only require very short periods of time beneath structure as a predator passes by. As such this study may somewhat underestimate the value of tabular structures as a temporary refuge from predation during the crepuscular period. It should also be noted that tabular structure might provide a more important refuge elsewhere on the reef, for example at deeper locations, where predators may be less efficient (Heithaus et al. 2009). In the present study on shallow reefs, however, very little evidence was found for predation-related use of tabular structure by large fishes in shallow water. Nonetheless, *Naso* spp. and *Balistoides viridescens* were more commonly observed sheltering under tabular structures at sunset, suggesting that it continues to maintain some functional role. These diurnal foragers (Hoey and Bellwood 2009; Young and Bellwood 2012) tended not to show an attachment to any particular location under structures and, on average, stayed for significantly shorter periods than their midday counterparts. This behaviour may be explained by the fact that *Naso* spp., at least, remain active during sunset but may visit tabular structures while actively searching for shelter as night approaches (Nagelkerken et al. 2000; Marshell et al. 2011).

If tabular structure helps to avoid solar irradiance at midday, its avoidance at sunset raises the question: are these structures are simply less useful at sunset or do they become disadvantageous locations as light levels fade? At sunset, many large reef fishes were observed to move out from under tabular structures, often being seen in the water column (e.g., Fig. 1b), where the risk of predation would theoretically be greater (Munz and McFarland 1973). One explanation for this behaviour may relate to the very rapid change in the properties of underwater light that occur after sunset, when intensity decreases at approximately 50 % min^{-1} with associated spectral shifts to shorter wavelengths (McFarland and Munz 1975). Dark adaptation in reef fishes is a relatively slow process, taking approximately 1 h to reach full scotopic vision (McFarland and Munz 1973; McFarland et al. 1979). During this transition, large reef fishes may seek to maximise capture of remaining photopic light by moving into the water column where light intensity remains higher for longer (Loew and McFarland 1990). This might be especially relevant in the case of nocturnal fishes, which generally possess fewer cones than diurnal fishes (Munz and McFarland 1973). These nocturnal fishes are thought to be especially vulnerable while they adjust to scotopic vision (Munz and McFarland 1973). It is interesting that they moved into the open at this point, instead of concealing themselves among the reef structure. This suggests that sheltering under tabular structures at this time does not reduce predation risk, indeed, at this critical period it may even increase predation risk.

Increased risk of infestation by parasites may also drive large reef fishes to move away from the benthos at dusk. Benthic parasites (gnathiid isopods) are especially abundant in shallow reef regions (Grutter 1998; Cribb et al. 2000) and are most active during the early morning and near-dusk periods (Chambers and Sikkel 2002). Fishes held in cages on coral reefs during these periods were subject to severe infestations of these parasites (Chambers and Sikkel 2002). Large reef fishes, such as Lutjanidae and Haemulidae, appear to be especially vulnerable, as they provide large targets for parasites and may lack effective anti-parasite defences (Coile and Sikkel 2013). It is interesting to observe that in the present study, Haemulidae and Lutjanidae were common users of tabular structure at midday, but were relatively absent from tabular structure at sunset. Fishes that are near the reef during peak gnathiid activity would be required to expend more energy to develop physiological, anatomical, or behavioural defences to potentially lethal gnathiid infestation (Coile and Sikkel 2013). As such, large reef fishes that move out from under structures outside of peak hours of UV irradiance may do so to reduce infestation by parasites.

Position under structure

The majority of fishes sheltering at midday positioned themselves underneath the outer edge (or lip) of tabular structures. Located here, fishes gain maximum UV protection from the canopy, while maintaining light-adapted, photopic vision, which may be essential should they have to make a sudden exit into the bright surrounding environment (cf. Fig. 3.4). In contrast, at sunset, irradiance becomes irrelevant and photopic acclimation may be hindered by sheltering under tabular structure. Although choosing to shelter deep under a tabular structure should theoretically improve concealment, no species of large reef fish elected to use this as a primary position when sheltering. This may be because any fish sitting deep under the structure has a highly constrained field of vision and would have less time to react to an approaching predator (McCormick and Manassa 2008; Fig. 3.4). The fact that fishes generally did not choose to conceal themselves deep under tabular structures further suggests that these structures have limited utility for large reef fishes in predation avoidance.

Overall, the outcome of the present study was not consistent with the majority of large fishes using shallow tabular structures to avoid predation during the critical crepuscular period at sunset; tabular structures were only used by a few species of large reef fishes at sunset, these fishes tended to stay for shorter periods than their midday counterparts, and they did not shelter in any particular location. At sunset, minimal UV irradiance negates the requirement for large reef fishes to shelter under tabular structures, where such behaviour possibly increases the risk of predation and parasite infestation. However, this study found strong evidence supporting the irradiation-avoidance hypothesis. During midday tabular structures are extensively used by large reef fishes in shallow coral reef environments where they may provide a valuable energetic refuge from harmful solar irradiance.

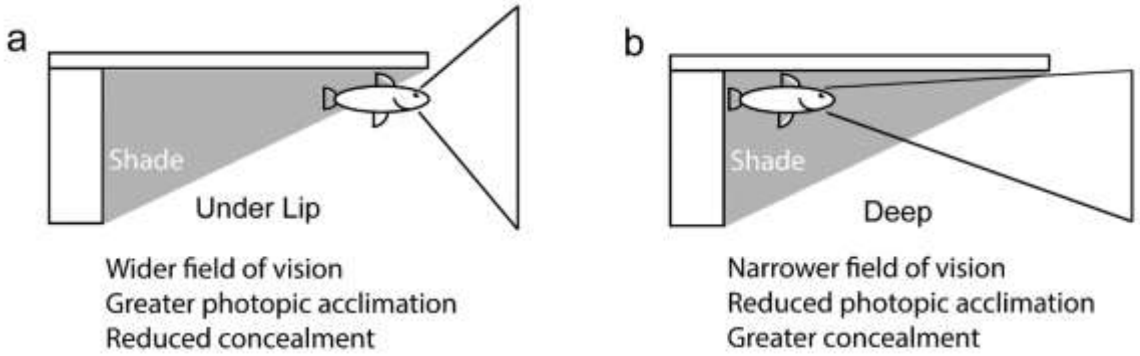

Figure 3.4 Conceptual diagram of potential ecological benefits of different shelter locations under tabular structure. (a) A fish under the lip of a tabular structure lacks concealment but its eyes are better adjusted to current light conditions and it has a reasonable field of vision. (b) A fish deep within a tabular structure is well concealed but its eyes may have adjusted to scotopic vision and its field of vision is restricted (b).

Chapter 4: Competition for shelter in a high diversity system: structure use by large reef fishes

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4.1 Introduction

Competition for resources is common among animals and its study constitutes a fundamental strand of ecology and evolutionary biology.Shelter is a key resource which forms the basis for competitive interactions in a range of systems. Shelter is a highly contested resource : from interspecific competition for shelter between salamander in the USA (Griffis and Jaeger 1998), and competition for nest sites among parrot species in Australia (Heinsohn et al. 2003) to competition for shelter sites among crayfish in Europe (Vorburger and Ribi 1999),. There are, however, very few examples of competition for resources among a high diversity of species and none could be found that relate to competition for shelter. Studying competition in higher diversity systems can provide an increased resolution of interactions, enabling a detailed evaluation of the extent and importance of competition in these systems. For example, Peck and Forsyth (1982) studied 31 species (11 genera) of dung beetles in Ecuador and were able to document size effects in species' ranking, high levels of interspecific aggression and their inverse correlation with reproductive activity.

Tabular structure is present in shallow reef environments where stony corals such as *Acropora hyacinthus* exhibit a tabulate growth form, which along with carbonate overhangs in the reef, provide shade and concealment. Multiple species of large reef fishes seek access to the understorey of these structures in shallow coral reef environments, and have been observed to leave areas where tabular structures are lost (Kerry and Bellwood 2014). This behaviour may be explained by the dependence of large reef fishes on tabular structures to avoid UV irradiance (Kerry and Bellwood 2015), which can be extreme in shallow coral reef environments, and has been shown to cause severe skin damage and melanomas on fishes (Sweet et al. 2012; Zamzow et al. 2013). Intense use of tabular structures by large reef fishes during peak sunlight hours (Kerry and Bellwood 2015) suggests that fish compete for space but this has not been demonstrated. This presents a unique opportunity to study competition in a species rich environment, for a limited resource, shelter.

Increasing competition in response to declining resource availability is well documented in the literature for systems involving smaller numbers of species, which can lead to both sub-lethal and lethal effects on participating species (e.g. Polis and McCormick 1987; Eckardt and Zuberbühler 2004; Boström-Einarsson et al. 2014). This trend is likely to hold true where larger numbers of species compete for the same resource, and may lead to even greater increases in competition. On coral reefs, climate change is already causing a decline in the availability of shelter as tabular corals are among the most susceptible growth forms to wave energy (Madin et al. 2014), coral bleaching (Marshall and Baird 2000) and ocean acidification (Fabricius et al. 2011). As such it is likely that access to tabular structure will become more limited in the future, adding impetus to better understand competition for tabular structure in this system.

This study, therefore, explored the extent and nature of competition among a diverse assemblage of large coral reef fishes for access to shelter provided by tabular structure under natural conditions. Video analysis of competition between reef fishes under tabular structures was used to generate a dominance hierarchy among large, shelter-using fishes on coral reefs, and to analyse the relevance of size and aggression in structuring competitive outcomes.

These interactions are considered in the context of climate change and the potential for competition among large, shelter-using fishes on coral reefs to drive changes in ecosystem function and reef resilience.

4.2 Materials and methods

This study was conducted between November 2013 and January 2014 at Lizard Island, a mid-shelf reef in the northern section of the GBR (14°40’S 145°28’E). Competition for tabular structures was quantified using underwater video observations at 26 reef locations in 2 – 5 m of water bounded by Lizard, South and Palfrey Islands. Tabular structures are herein defined as either living or dead tabular corals (*Acropora hyacinthus* and *Acropora cytherea*, n = 23, mean planar surface area = 3.79 m^2 ± 0.61 SE) or carbonate reef overhangs (n = 3, mean planar surface area = 4.02 m^2 ± 0.86 SE) that provide a shaded canopy greater than 20 cm in height above the substratum.

Focal fishes were large reef fishes (total length (TL) > 20 cm) that were involved in competition for access to the shade provided by the tabular structures. This included 30 species from nine families: Acanthuridae, Balistidae, Ephippidae, Haemulidae, Labridae, Lethrinidae, Lutjanidae, Pomacanthidae and Serranidae (species listed in Electronic Supplementary Material, Table 1).

At each location a single, large tabular structure was filmed from 1000 - 1400 h using two GoPro Hero 3 Silver video cameras (Battery BacPac; 16GB microSD Card; 720p; 25fps; Indicator Light <off>) in underwater housings attached with cable ties to a small dive weight. Filming was only carried out at one location on any given day, equating to 26 days of filming over a three month period in austral summer. Video footage was analysed from 1100 - 1400 h, after one hour of ‘soak’ time to allow fishes to recover from diver disturbance (cf. Dickens et al. 2011) and acclimate to the presence of the camera. Furthermore, this window of observation was selected because usage of tabular structures by large reef fishes reaches a peak during the period when the sun is highest in the sky (Kerry and Bellwood 2015) and this increased density of fishes is likely to increase competition for the resource (Holbrook and Schmitt 2002; Hixon and Jones 2005). Such competition may display elements of both interference and exploitation. While the passive use of tabular structures by fishes may limit access to shelter sites by other fishes (exploitation; Fig. 4.1a), specific acts of aggression from one fish to another may either displace or exclude an individual from a given shelter site (interference; Fig. 4.1b) (Davey et al. 2009).

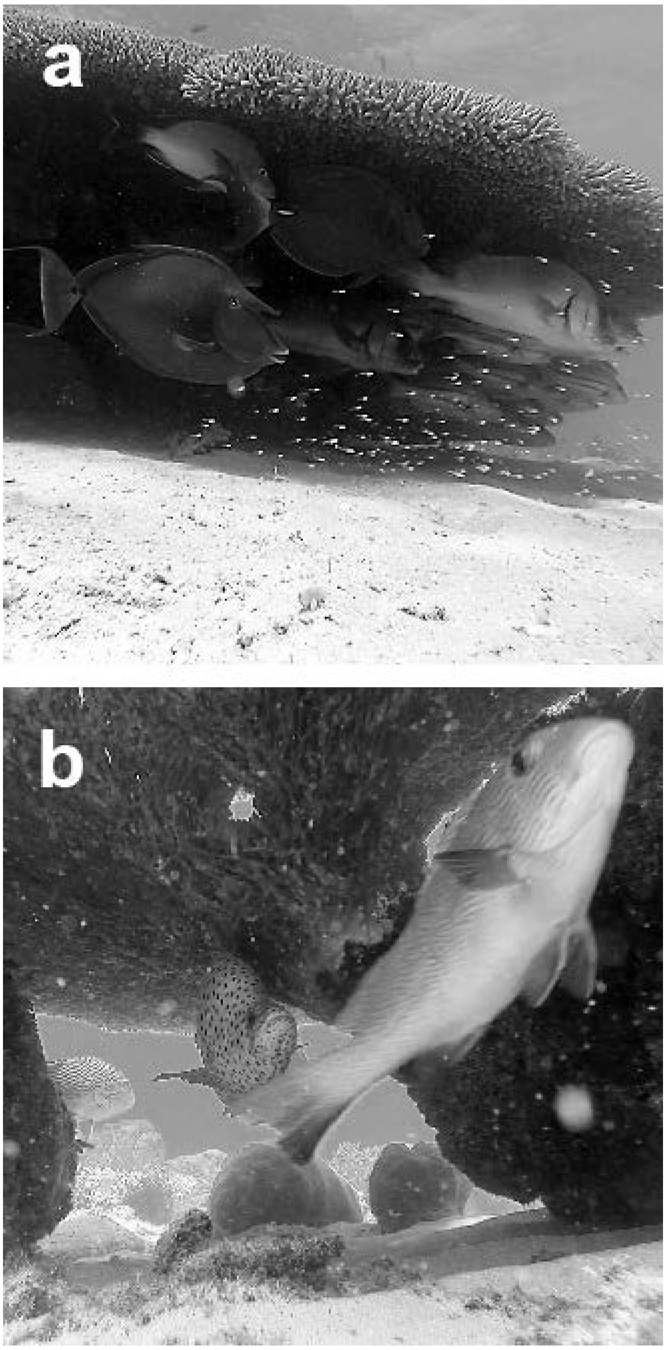

Figure 4.1 (a) A diverse community of large reef fishes occupying a tabular coral, fishes include *Lutjanus gibbus, Naso unicornis, Acathurus dussumieri, Plectorhincus gibbosus* and *Lutjanus carponatatus*. (b) A *Plectorhincus flavomaculatus* is aggressively chased away from the understorey of a tabular coral by a *Cromileptes altivelis*.

For each tabular structure, video analyses was carried out by watching the full 3 h of video footage and observing interactions between fishes occupying or arriving underneath tabular structures. Recorded interactions could be either aggressive or non-aggressive. Aggressive interactions were identified whenever one fish (designated the 'winner') displayed physical aggression towards another fish (designated the 'loser') by either chasing the loser or snapping its jaws at the loser, or both (cf. Gregory and Griffith 1996). Non-aggressive interactions were identified whenever one fish would displace another individual by moving into its shelter space but would not display any physical aggression (cf. Shulman 1985).

There were three possible outcomes from an interaction: 'Displacement' where the losing fish remained under the tabular structure or returned to the structure within 30 seconds, but relocated to a different location therein. 'Vacation' where the losing fish left the structure entirely and did not return for at least 30 seconds (30 seconds was set as a conservative cut-off because fishes tended either to return immediately to the structure or stay away for much longer periods; the mean return time of losing fishes following vacation was 07:38 mm:ss ± 03:03 SE based on the overall average of recorded mean return times, n = 26). The final outcome was 'exclusion' where the losing fish was chased away as it attempted to move under the tabular structure. For each interaction, the species and size (to nearest 5 cm) of each large fish (> 20 cm TL) was recorded. Length estimates were facilitated by placing a graduated rule at several locations under the structure at the start of filming.

A common approach when evaluating competition in systems is to construct a dominance hierarchy. Following Rutberg and Greenberg (1990), a winner-loser relationship was identified where at least three recorded instances of one species winning against another species were recorded (they must also have occurred under at least two separate tabular structures). The dominance hierarchy was constructed from the bottom-up such that the terminal nodes corresponded with those species that did not dominate any other species. Species that were only dominant over terminal species were placed in the rank immediately above. This process was repeated for all remaining species such that each species is located in a rank immediately above the lowest ranked species over which it is dominant. For each species, the mean percentage win was calculated based on the mean percentage of wins versus losses for that species at each tabular structure where an interaction was recorded (i.e. a mean of means from each structure). Species were grouped into one of three categories based on their mean percentage win: top-ranked competitors (>80%), mid-ranked competitors (80-50%) and bottom-ranked competitors (<50%).

Student's *t*-tests were used to investigate the impact of fish size in the outcome of competitive interactions, specifically, comparing the overall mean size of winners and losers, and the mean size of winning and losing fishes in displacement, vacation and exclusion interactions, respectively ($n = 26$). Data were $\log_{10}(x + 1)$-transformed to meet assumptions of normality and homoscedasticity. A linear regression was used to test for a significant trend in the percentage of wins in response to fish size.

A student's *t*-test was also used to compare the percentage likelihood that a fish would vacate tabular structure. Differences in the aggression of fishes based on their length of stay were compared using multiple two-tailed Fisher's exact tests, with length of stay being categorised as either short (less than 30 s), medium (30 s to 10 min) or long (more than 10 min). Fisher's exact tests were used given the comparison of two nominal variables: *aggression* and *length of stay*, and are more robust than the chi-square or *G*-test of independence for small sample sizes. Given the multiple pairwise comparisons the P-value was Bonferroni corrected to be significant at $P < 0.017$ (Gardner and MacDonald 2000). Data were $\log_{10}(x + 1)$-transformed to meet assumptions of normality and homoscedasticity. Three linear regressions were conducted to test for significant trends in the percentage of aggressive versus non-aggressive interactions based on size difference of interacting fishes, percentage of won interactions by species, and mean size of species, respectively.

4.3 Results

Fish assemblages

In total, 404 individuals were recorded sheltering under 26 tabular structures (which had a combined surface area of 84.6 m^2). At any given time there was a mean number of 199.4 fishes sheltering under the 26 tabular structures, which equated to a total biomass of 398.4 kg, or 4.71 kg m^{-2}. A total of 475 competitive interactions were recorded, involving 326 individuals from 30 species of large reef fishes from nine families (Table 4.1). Of the 475 interactions, 307 resulted in displacement, 123 in vacation and 44 in exclusion.

Competition and dominance

A clear hierarchy was found to exist between species, with balistids, large labrids and a pomacanthid occupying the upper ranks, serranids, large haemulids and a large lutjanid occupying the intermediate ranks, and an ephippid, acanthurid, lethrinids and smaller lutjanids and haemulids occupying the bottom ranks (Fig. 4.2).

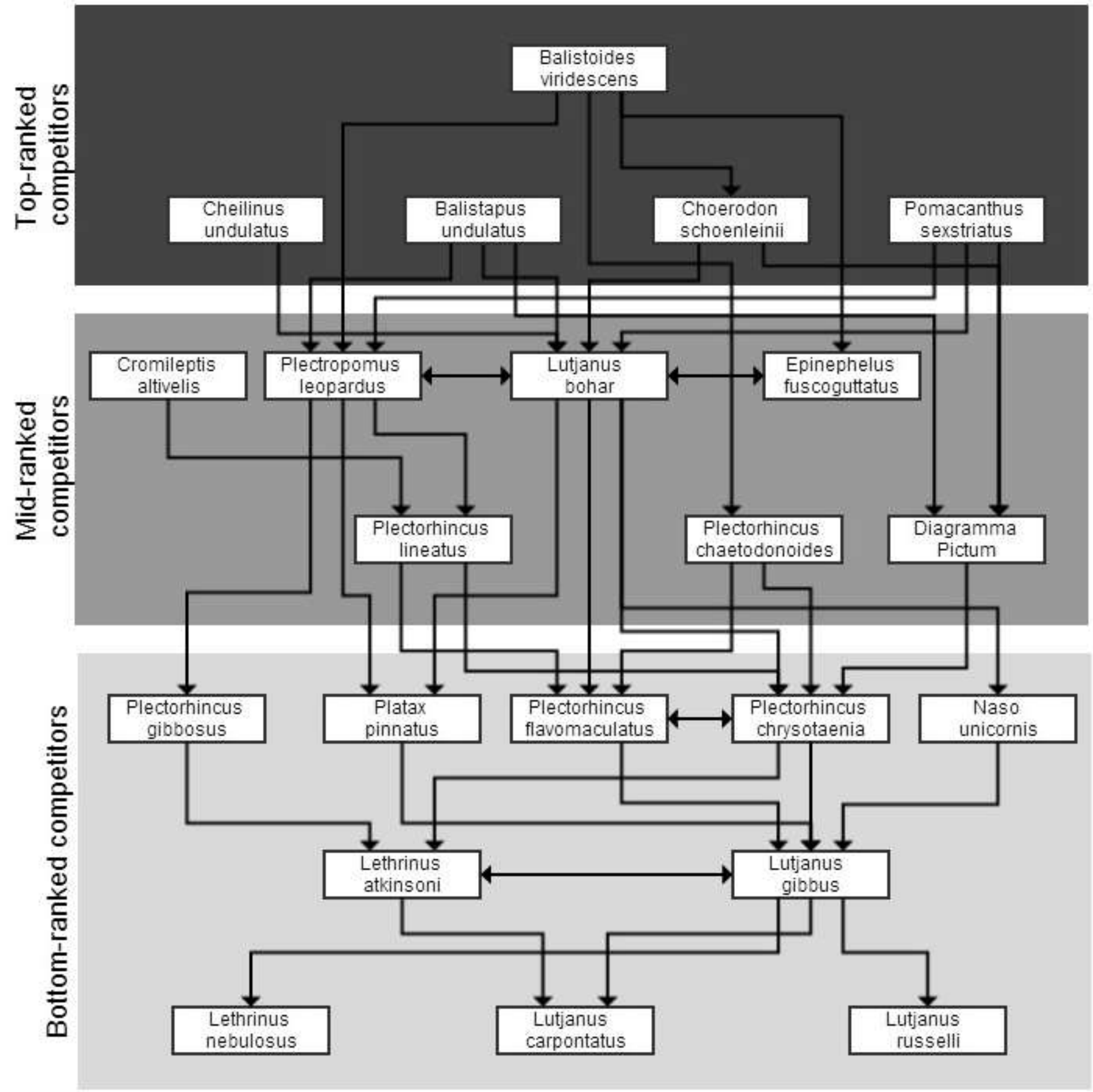

Figure 4.2 A dominance hierarchy showing relative rankings among 22 species of large reef fishes. Arrows indicate a winner-loser relationship pointing from the winning species to the losing species. Where two species were mutually dominant they are identified by a double-headed arrow pointing at both species. In order to reduce complexity, dominance relationships are not shown for species in non-adjacent ranks when transitive connections exist via other species in the hierarchy.

Table 4.1 Species of large reef fish involved in competitive interactions

Family	Species
Acanthuridae	
	Acanthurus dussumieri
	Naso unicornis
Balistidae	
	Balistapus undulatus
	Balistoides viridescens
Ephippidae	
	Platax pinnatus
Haemulidae	
	Diagramma pictum
	Plectorhincus chaetodonoides
	Plectorhincus chrysotaenia
	Plectorhincus flavomaculatus
	Plectorhincus gibbosus
	Plectorhincus lineatus
Labridae	
	Bolbometopon muricatum
	Cheilinus undulatus
	Choerodon schoenleinii
Lethrinidae	
	Lethrinus atkinsoni
	Lethrinus erythracanthus
	Lethrinus harak
	Lethrinus nebulosus
Lutjanidae	
	Lutjanus bohar
	Lutjanus carponatatus
	Lutjanus gibbus
	Lutjanus russelli
	Symphorichthys spilurus
	Symphorus nematophorus
Pomcanthidae	
	Pomacanthus sexstriatus
Serranidae	
	Cephalopholis argus
	Cromileptes altivelis
	Epinephelus fuscoguttatus
	Plectropomus laevis
	Plectropomus leopardus

Fish size was an important factor in interactions, with mean size of winners (50.4 ± 1.52 cm SE) being significantly greater than the mean size of losers (41.3 ± 1.30 cm SE; $T_{50} = 4.59$, $P < 0.0001$). This applied to displacement interactions (50.6 ± 1.64 cm SE vs. 40.4 ± 1.40 cm SE; $T_{50} = 4.71$, $P < 0.0001$) and vacation interactions (50.6 cm ± 1.80 SE vs. 42.7 ± 1.48 cm SE; $T_{48} = 3.43$, $P < 0.005$). However, no significant difference was found between the sizes of fishes involved in exclusion interactions. The size of fishes was also positively correlated with the proportion of wins vs. losses (Fig. 4.3), i.e. bigger fishes tended to win more often. Of all individual interactions, 85.2% were won by fishes that were equal or larger in size than the respective losing individual.

However, contrary to expectations, the ratio of aggressive to non-aggressive interactions was found to be greater among fishes that tended to lose interactions more often than winning (Fig. 4.4), i.e. fishes lower down the dominance hierarchy were more likely to be aggressive when they won interactions. Aggressive interactions were more likely to cause the losing fish to vacate the tabular structure (45.6% ± 6.55) than non-aggressive interactions (16.1% ± 4.50; $T_{48} = 3.29$, $P < 0.005$). Exclusion interactions were always aggressive in nature.

The proportion of aggressive interactions undertaken by sheltering fishes also appeared to correlate with the length of stay. Short-stay fishes (<30 s) performed aggressive interactions 32.2 ± 5.9% SE of the time, compared with medium-stay (30s – 10 min); 42.6 ± 6.3% SE and long-stay fishes (>10 min); 68.8 ± 5.4% SE with a significant difference in aggressive behaviour between short- and long-stay fishes ($P < 0.0001$, two-tailed Fisher's exact test) and between medium- and long-stay fishes ($P < 0.0001$, two-tailed Fisher's exact test). Finally, difference in size between fishes was found to be strongly negatively correlated with the number of aggressive interactions (Fig. 4.5), i.e. similarly sized fishes were most aggressive.

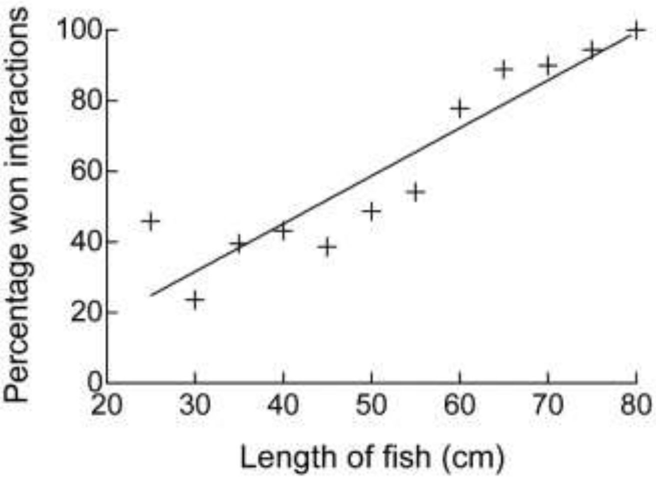

Figure 4.3. Percentage of interactions won (vs. lost) as a measure of the overall length of individuals involved in interactions (to the nearest 5 cm). $r^2 = 0.8605$ and $P < 0.0001$

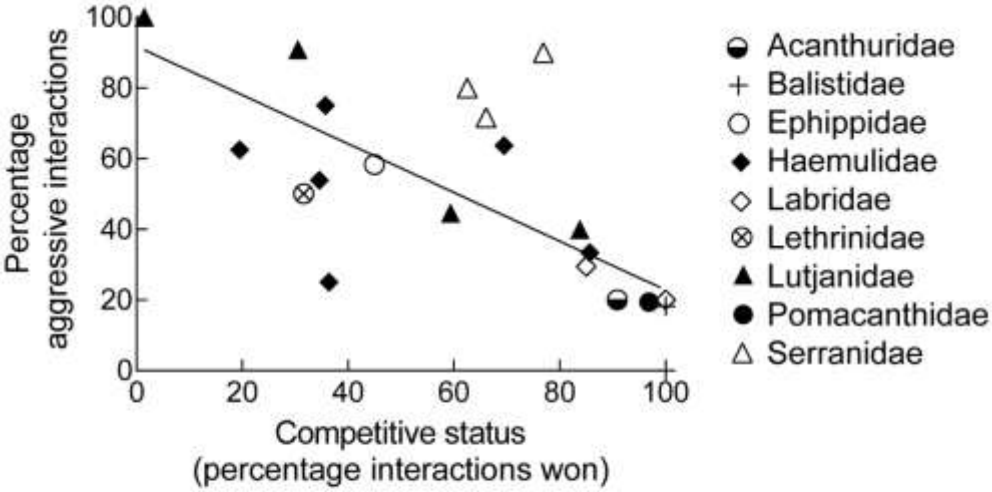

Figure 4.4 Percentage of aggressive winning interactions carried out by each species, as a measure of how likely each species is to win (vs lose) an interaction. $r^2 = 0.5038$ and $P = 0.0002$

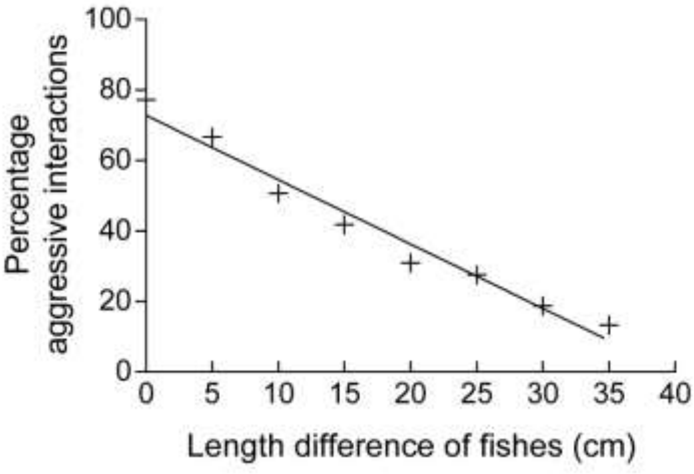

Figure 4.5 Percentage of aggressive interactions based on the length difference of the two interacting individuals. $r^2 = 0.9710$ and $P < 0.0001$

Discussion

The concentrations of sheltering large reef fishes in the present study are by far the highest densities of fishes recorded on coral reefs. The mean biomass of sheltering fishes was 4.71 kg m^{-2}, which is one to two orders of magnitude greater than typical coral reef estimates (between 0.031 to 0.1 kg m^{-2} (Mora et al. 2011 and Ackerman and Bellwood 2000, respectively)). Thirty species of large reef fishes from nine families were recorded engaging in competition for this resource, which may be the highest recorded diversity of vertebrates competing for a single resource. By strict definition, competition can be said to occur when negative demographic effects are shown for competing species. Nonetheless, tabular structures are a finite resource on coral reefs and the strong interactions observed here among multiple species of large reef fishes for access to this structure imply that there are significant benefits from sheltering under tabular structure. Notably, access to shade is likely to moderate energetic expenditure that would otherwise be required to deal with harmful UV irradiance (Kerry and Bellwood 2015), although these costs need to be formally evaluated.

Despite the species rich community of large reef fishes that seek shelter under tabular structures during peak sunlight hours, a clear dominance hierarchy was generated. The system is relatively linear and based predominantly on the size of fishes, agreeing with other studies on competition for resources, including small reef fishes (Shulman 1985; Robertson 1996), insects (Peck and Forsyth 1982), birds (Robinson and Terborgh 1995), arachnids (Polis and McCormick 1987) and mammals (Rutberg and Greenberg 1990). This is perhaps logical given that larger species may have a physical advantage, while smaller species may, in general, be discouraged from provoking their larger counterparts (Rutberg and Greenberg 1990).

In the present study, when one individual engaged another individual of a similar size, the interaction was significantly more likely to be aggressive, suggesting that when sizes are similar individuals need to assert their dominance through other means. This supports previous studies of fishes in both marine and freshwater environments, where similar sized individuals were more likely to engage in agonistic behaviour (Orpwood et al. 2003; Nanami and Yamada 2008; Nanami and Yamada 2009). Aggressive interactions under tabular structures were also more likely to cause the loser to vacate the shelter space. This outcome may simply be a by-product of the aggression involved in establishing dominance of one individual over another, but it may also be the intended outcome. For excluded fishes this appears to be the case, although it is unclear why certain fishes will not tolerate co-habitation by other fishes, especially when there is sufficient space for both fishes to shelter under the tabular structure. One possible explanation for such territorial behaviour is to monopolise access to feeding sites (Namani and Yamada 2008).

Unlike several other studies (Shulman 1985; Robinson and Terborgh 1995; Robertson 1996; Mac Nally and Timewell 2005), the present study did not find that higher levels of aggression were correlated with size or with those species in higher ranks of the dominance hierarchy. Aside from increased aggression when two individuals were similar or matched in size, aggressive interactions were more commonly observed for species that tended to lose more often than they won. This suggests that in the rare instances when species with a lower competitive rank won interactions they needed to adopt an aggressive approach in order to be successful.

How then do species at the top of the dominance hierarchy maintain their position without frequently carrying out aggressive interactions? This is especially pertinent in the current study because two species in the upper ranks are relatively small in size when compared to the rest of the assemblage: *Balistapus undulatus* and *Pomacanthus sexstriatus*.

High dominance rank and reduced involvement in aggression may be explained by an adaption of the ‘teaching hypothesis’, which proposes that full-grown adults who establish dominance over immature individuals can maintain that relationship when challenges are rare (Hauser and Tyrrell 1984; Rutberg and Greenberg 1990). In the present case, once an individual has asserted dominance over another, the loser may then accept the status quo and defer to the winner on subsequent occasions without the need for further aggressive behaviour from the dominant individual. This ‘social conditioning’ has been found in numerous other animals including mammals (Haag et al. 1980; Thouless and Guiness 1986), crustaceans (Fero et al. 2007) and fish (McDonald et al. 1968; Beacham and Newman 1987), such that individuals will give way to others who have beaten them in the past. Indeed, the apex competitor in this study, *Balistoides viridescens*, was never observed undertaking an aggressive interaction, despite its position at the top of the hierarchy. Given the longevity of reef fishes (Depczynski and Bellwood 2006) and increasing evidence of limited home ranges (Welsh and Bellwood 2012; Nash et al. 2015) it is likely that shelter-using fishes on coral reefs have been in contact for several years and have well established dominance hierarchies.

Deference of one individual to another may explain why the majority of interactions only involved displacement (rather than vacation) of the losing fish, allowing both winner and loser to occupy the tabular structure. Toleration of the losing fish by the winning fish potentially represents a win-win, as the winner occupies its location of choice underneath the tabular structure without having to expend more energy in driving the losing fish from the structure altogether. Why then does the winning fish not simply occupy a vacant location under the structure without engaging in any interaction? One explanation might be that by displacing the loser, the winner reinforces its dominant position (Thouless and Guiness 1986), another may relate to the importance of position underneath the structure. The physical position of dominant capuchin monkeys (Robinson 1981) and feral pony mares

(Rutberg and Greenberg 1990) within their groups are thought to provide them with increased feeding opportunities and reduced predation vulnerability. For sheltering large reef fishes, position under tabular structure may affect predation vulnerability, field of vision, and phototopic acclimation in case a sudden escape into open water is required (Kerry and Bellwood 2015). Moreover, fishes sheltering under tabular structure may tolerate each other because they gain an antipredation defence by having multiple sets of eyes watching for any approaching threat (cf. Eckardt and Zuberbühler 2004).

Nonetheless, such tolerance may lose relevance as physical access to tabular structure becomes more limited. If, as predicted, climate change and ocean acidification cause a substantial decline in the availability of tabular structures on coral reefs (Pratchett et al. 2008), a decline in the local abundance of large reef fishes might be expected – as shown experimentally by Kerry and Bellwood (2014). The mechanism for this is unknown but when the availability of shelter decreases those species in the higher ranks of the dominance hierarchy may establish their occupancy more forcefully, vacating or excluding subordinate fishes (cf. Almany 2004). Perhaps one precedent for this can be found in the behaviour of fishes that remain under tabular structure for longer periods of time. In these instances, individuals became progressively more likely to behave aggressively towards other fishes, presumably to maintain their position underneath the tabular structure.

Examples of habitat loss leading to increased competition for shelter have been found in other aquatic communities, including juvenile salmonids (Harwood et al. 2002), crayfish (Vorburger and Ribi 1999) and small reef fishes (Boström-Einarsson et al. 2014). This not only causes significant increased metabolic costs through increased competitive interactions (Forrester et al. 2006) but also increased mortality among losing species that are outcompeted for shelter (Holbrook and Schmitt 2002; Hobbs and Munday 2004; Hixon and Jones 2005). Should a loss of tabular structures on coral reefs induce a similar, fundamental change in the structure of large reef fish communities, ecosystems may lose key species that play an important role in ecosystem function and resilience. At least two species found in the lower ranks of the dominance hierarchy presented herein, *Naso unicornis* and *Platax pinnatus*, have been identified as critical for reef recovery through their removal of macroalgae (Bellwood, et al. 2006; Hoey and Bellwood 2009). Additionally, several species in the mid- to low-ranks of the dominance hierarchy are predators on the sediment apron of reefs (Appeldoorn et al. 2009), a role whose impact on the ecosystem is not well understood. It should be noted, however, that there may be alternate shelter options for displaced fishes, which may redistribute themselves in the event that tabular structures are only lost at small scales (cf. Kerry and Bellwood 2014).

In conclusion, the present study found that tabular corals and overhangs on coral reefs are the loci of major concentrations of large reef fishes that compete, sometimes aggressively, for access to the shelter provided by these structures. Despite the high diversity of fishes involved in this competitive system, a relatively linear and simple dominance hierarchy emerges in which fish size appears to be the primary driver, with larger fishes tending to be found in higher ranks. Position in the dominance hierarchy did not however correlate with aggression, which was more common in interactions between similarly sized individuals or fishes seeking to establish longer-term occupancy. The community dynamics shown here may be aggravated by a future reduction in the availability of tabular structures as a result of climate change, which may in turn fundamentally shift the balance of the dominance hierarchy towards the more dominant species. This presents cause for concern given the critical functional roles played by certain species of large reef fishes that utilise tabular structures for shelter, and which occupy the lower ranks of the dominance hierarchy.

Chapter 5: Environmental drivers of sheltering behaviour in large reef fishes?

Submitted to *PLoS One*

5.1 Introduction

Sheltering behaviour is a key facet in the ecology of species throughout the animal kingdom. Shelter can provide multiple benefits to individuals, and may serve distinct functions for different species (Webb and Shine 1998; Hinsley and Bellamy 2000; McMaster and Downs 2006). Studies of shelter usage reveal important details about species' ecology and can aid in conservation planning and effective habitat restoration for threatened populations (Dover et al. 1997; Webb and Shine 2000; Manning et al. 2006; Pratchett et al. 2008).

For many species, shelter can be a critical resource and its availability has direct implications for their survival, enabling them to avoid predation (e.g. Olsen 1973; Eggleston and Lipcius 1992; Heinsohn et al. 2003; Almany 2004) or lethal stress from environmental extremes (e.g. Schwarzkopf and Alford 1996; Langkilde et al. 2003). Shelter sites may also provide individuals with more routine functions, allowing them to conserve energy and maximise fitness on a daily basis. For terrestrial animals, these functions include, proximity to food sources (Hinsley and Bellamy 2000), enhanced predation success (Webb and Shine 1998), avoidance of sub-lethal environmental stresses (Merckx et al. 2010), provision of long-term habitat (McMaster and Downs 2006), thermoregulation (Walsberg 1986), and simply, locations in which to rest (Lucherini et al. 1995). Many of these shelter functions are also relevant for fishes on coral reefs.

As the principle architects of coral reefs, hermatypic corals are largely responsible for structural complexity on coral reefs (Done et al. 1996), and provide a key source of shelter for reef-associated fishes (Jones et al. 2004; Wilson et al. 2006; Kerry and Bellwood 2014). Aside from being relatively permanent shelter locations, corals have been shown to improve access to food (Clarke 1992), both enhance and diminish predation rates (Almany 2004), and to mitigate environmental stresses such as wave energy (Fulton and Bellwood 2002).

A recent study suggested that sheltering behaviour of large reef fishes beneath tabular corals was primarily to avoid high levels of ultraviolet (UV) irradiance in shallow reef environments (Kerry and Bellwood 2015). This behaviour is thought to reduce energetic expenditure for fishes, which would otherwise secrete costly protective substances to block UV radiation or have to invest in repairing epidermal damage (Kerry and Bellwood 2015). It remains, however, unclear whether there are other environmental factors that might be relevant in the occupation of tabular corals by large reef fishes. In addition to wave energy and UV radiation mentioned above, other potentially important environmental factors include temperature, tides and turbidity. Temperature changes may affect fish physiology (Rummer et al. 2013) and cause them to seek out more favourable environments. Tides can physically restrict the shelter options of large reef fishes (Harborne et al. 2015), while turbidity has significant impact on in-water irradiation (Anthony et al. 2004). Assessing shifts in the usage of tabular corals by large reef fishes due to changes in each of these environmental factors may reveal their relevance to large reef fishes in shallow coral environments. The response of large reef fishes in terms of sheltering behaviour may also highlight mechanisms by which large reef fishes cope with changing environmental parameters.

This study, therefore, investigated changes in the sheltering behaviour of a diverse assemblage of large coral reef fishes to changes in tides (and depth), irradiance, wind speed (as a proxy for wave energy), water temperature and visibility over a 10 week period. Video and statistical analyses were used to identify the most relevant environmental factors driving sheltering behaviour and to generate a best-fit model for predicting large reef fish usage of tabular corals.

5.2 Materials and methods

This study was conducted between October 2013 and January 2014 at Lizard Island, a mid-shelf reef in the northern section of the GBR (14°40'S 145°28'E). Over 10 weeks, the sheltering behaviour of large reef fishes (total length (TL) > 20 cm) beneath four tabular corals (*Acropora hyacinthus*) was quantified using underwater video observations at two sites within the lagoon (Fig. C1). The four tabular corals provided a shaded canopy greater than 20 cm in height above the substratum, and had a similar planar surface area (mean = 2.78 m^2 ± 0.41 SE).

Video analysis

At each site the two large tabular corals were filmed from 1000 hrs to 1400 hrs using GoPro Hero 3 Silver video cameras (Battery BacPac; 16GB microSD Card; 720p; 25fps; Indicator Light <off>) in underwater housings attached with cable ties to a small dive weight. The tabular corals were no further than 50 m apart at both sites. The two sites were filmed on separate days of the week over the 10 week period, with the same site being filmed on the same day each week (leading to a total of 10 days of filming per site). Video footage was analysed from 1100 hrs to 1400 hrs, after one hour of 'soak' time to allow fishes to recover from diver disturbance (cf. Dickens et al. 2011) and to acclimate to the presence of the camera. For each tabular coral, video analysis was carried out by watching the full 3 hrs of video footage and recording any large reef fishes that stopped to shelter beneath the corals.

Over the 10 week period, 22 species of large reef fishes from nine families were observed sheltering beneath the four tabular corals: Acanthuridae, Balistidae, Ephippidae, Haemulidae, Labridae, Lethrinidae, Lutjanidae, Pomacanthidae and Serranidae.

Abundances of fishes using both tabular corals at a site were pooled so that the level of replication is a single day i.e. one data point represents the usage of two corals based on prevailing environmental conditions for that day. Care was taken not to record the same individual more than once, especially as it is possible that an individual fish might use both structures during the 3 hr filming window. This was possible given the low numbers of any given species of large reef fish observed in this study, and because individuals could be clearly identified based on their size and distinctive markings (such as scarring or fin damage). Additionally, synchronous video footage from the two tabular structures could be cross-referenced to check if an individual might feasibly have moved from one structure to another.

Environmental data

Data were collected for five environmental variables over the same 10 week period: visibility, depth, temperature, wind speed and photosynthetically active radiation (PAR). Visibility (m) was determined *in situ* at each site prior to deployment of the video cameras. Two divers moved apart along a transect tape, as soon as the diver moving along the transect lost sight of the diver at the beginning, the distance between the two divers was recorded to the nearest metre to give a relative measure of visibility. The same diver always performed the same role and the orientation, equipment and clothing of the both divers was the same in each instance.

Depth (every 5 min; m) and seawater temperature (every 5 min; ºC) data were obtained from Sensor Float 2 (Blue Lagoon South; Fig. C1), which is located within the lagoon at Lizard Island and is part of the Integrated Marine Observing System (IMOS; source: Australia Institute of Marine Science). For the purpose of analyses, the following data were calculated for each period of video analysis: mean depth (average depth over the 3 hr filming window, n = 37), tide change (the relative change in depth over the 3 hr filming window), and mean temperature (average temperature over the 3 hr filming window, n = 37).

Wind speed (scalar average every 10 min; km h^{-1}) and PAR (every 10 min; µmol photons m^{-2} s^{-1}) data were obtained from Relay Pole 2 (Seabird Islet; Fig. C1), which is also located within the study zone at Lizard Island (IMOS; source: Australian Institute of Marine Science). During the study period, wind direction was overwhelming south-easterly (137° ± 11 SE). For the purpose of analyses, the following data were calculated for each period of video analysis: mean wind speed (average wind speed over the 3 hr filming window, n = 19) and mean PAR (average PAR over the 3 hr filming window, n = 19). The following six predictor variables were, therefore, available for each window of observation (3 hr video analysis): mean depth, tide change, mean PAR, mean wind speed, mean water temp and visibility.

Data analyses

Variation in the assemblages of large reef fishes sheltering under tabular structures over the 10 week period were visualised using non-metric multi-dimensional scaling (nMDS) based on a Bray-Curtis similarity matrix. The rank-correlation Bio-Env + Stepwise routine (BEST analysis) was then run (999 permutations) to assess which combination of the predictor variables best correlated with variation in assemblages of large reef fishes sheltering beneath tabular structures. Prior to this, all six variables were normalised to put them on the same scale.

The BEST routine computes rank-correlations for all possible combinations of predictor variables, and converges on the combination with the strongest relationship to the dependent fish assemblage dataset (Clarke and Gorley 2015). However, the BEST routine does not demonstrate which variables take high or low values for which samples. Therefore, for each environmental predictor variable identified by the BEST routine, a linear regression was performed based on their relationship to fish abundance and MDS primary axis scores.

Finally, distance-based redundancy analysis (dbRDA) was performed on the fish assemblage dataset using both the best and second-best combination of predictor variables. dbRDA performs a multivariate multiple regression of principle component axes on predictor variables and is, therefore, able to determine the per cent variation in the dataset that is explained by the selected variables (Anderson et al. 2008). Examination of the optimal (best) and sub-optimal (second best) combinations of predictor variables in this manner indicates the level of confidence that can be placed in the optimal model as the best predictor of variance in the fish assemblages throughout the 10 week study. All analyses were conducted using the software *Primer 7 & Permanova+* (PRIMER-E Ltd, Plymouth, UK).

5.3 Results

Over the 10 week period, 343 fishes were recorded sheltering under the four tabular structures (174 on site 1 and 169 on site 2). The BEST analysis revealed that most variation in fish assemblage could be attributed to the predictor variables with v*isibility* and *wind speed* as the best combination (rho = 0.485, $p < 0.01$), although *visibility* by itself was also a strong predictor of fish assemblage (Table 5.1).

Table 5.1 BEST BIO-ENV results for fish assemblages based on six predictor variables

No. variables	Rho	Variables selected
2	0.485	wind speed, visibility
3	0.451	tide, wind speed, visibility
1	0.426	visibility
3	0.403	depth, wind speed, visibility
2	0.371	tide, visibility

Potential predictor variables included were depth, tide, PAR, wind speed, water temperature, visibility

Exploration of the data using nMDS also suggested that environmental variables played an important role in influencing sheltering behaviour by large reef fishes. Assemblages of large reef fishes were overwhelmingly associated with *visibility* and *wind speed*, and to a lesser extent, *tide change* and *PAR* (Figs. 5.1 and 5.2). Linear regressions showed that increasing abundance of large reef fishes was significantly and positively related to increases both *visibility* ($P < 0.01$; Fig 5.3a and Fig D2a) and *wind speed* ($P < 0.05$; Fig. 5.3b and Fig. D2b). Basically, as in-water visibility and above water wind speed increased, so did the numbers of sheltering large reef fishes.

The dbRDA using the two best predictor variables identified by the BEST analysis produced a spatial arrangement of sample points that was similar to the data cloud of sample points based on the nMDS analysis (Fig. D3). This suggests that the combination of these two predictor variables (*visibility* and *wind speed*) provide a good model to describe the most salient patterns of the variation across the unconstrained data cloud as a whole (Anderson et al. 2008). More formally, the dbRDA using the *visibility-wind speed* model was able to explain 44.7% of the variation in the data in two-dimensional space. This value is only improved marginally (to 47.4%) when adding the next-best predictor variable: *tide change*. This suggests that visibility and wind speed are the key environmental factors driving sheltering behaviour by large reef fishes.

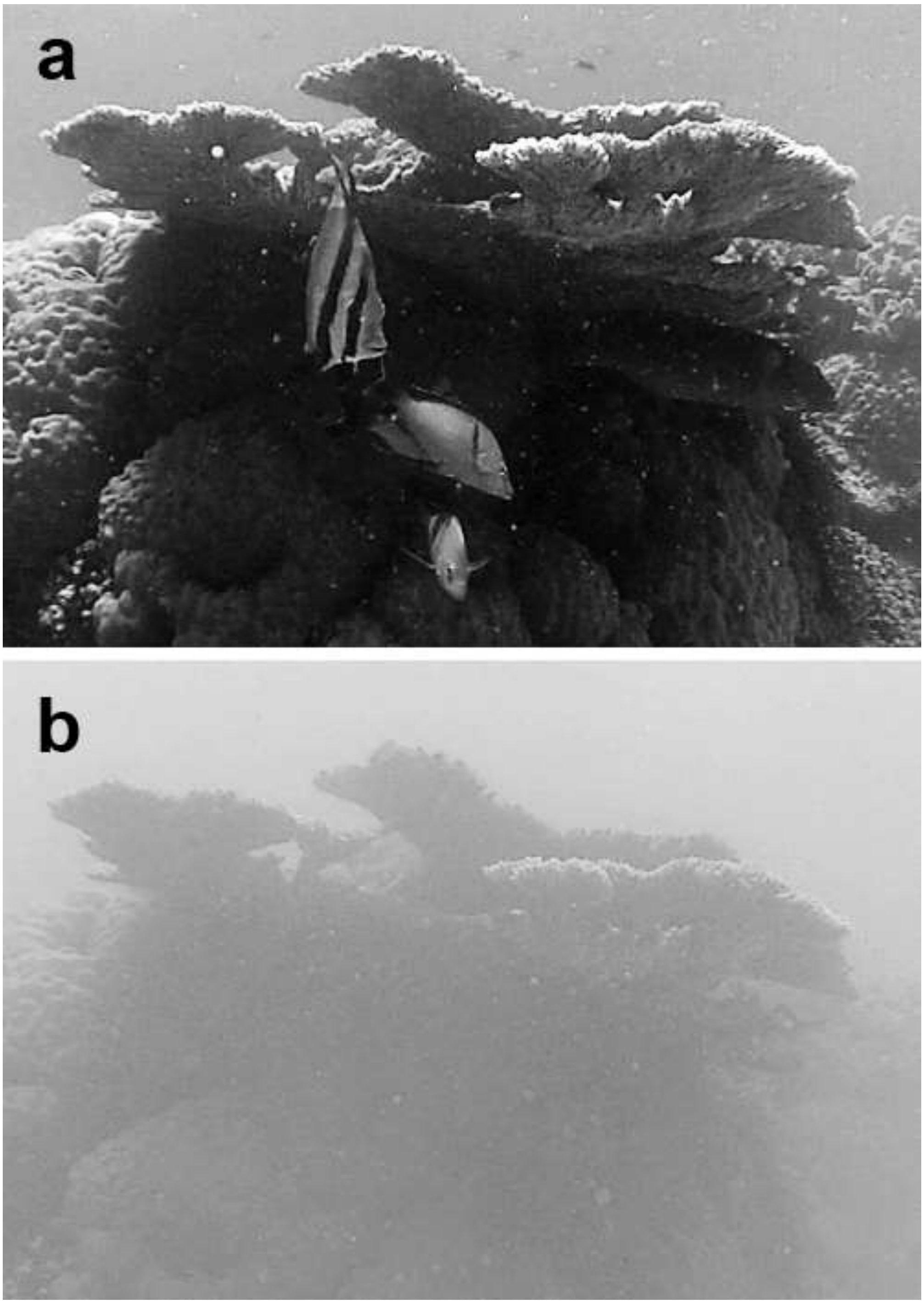

Figure 5.1 Images showing the difference in shelter usage by large reef fishes underneath a coral in the lagoon at Lizard Island. **a** Example of high visibility (6 m) scenario, taken at

1200 hrs on week 7, sheltering species: *Platax pinnatus*, *Plectropomus leopardus* and *Lutjanus gibbus*. **b** Example of low visibility (2 m) scenario, taken at 1200 hrs on week 5, no fishes are sheltering.

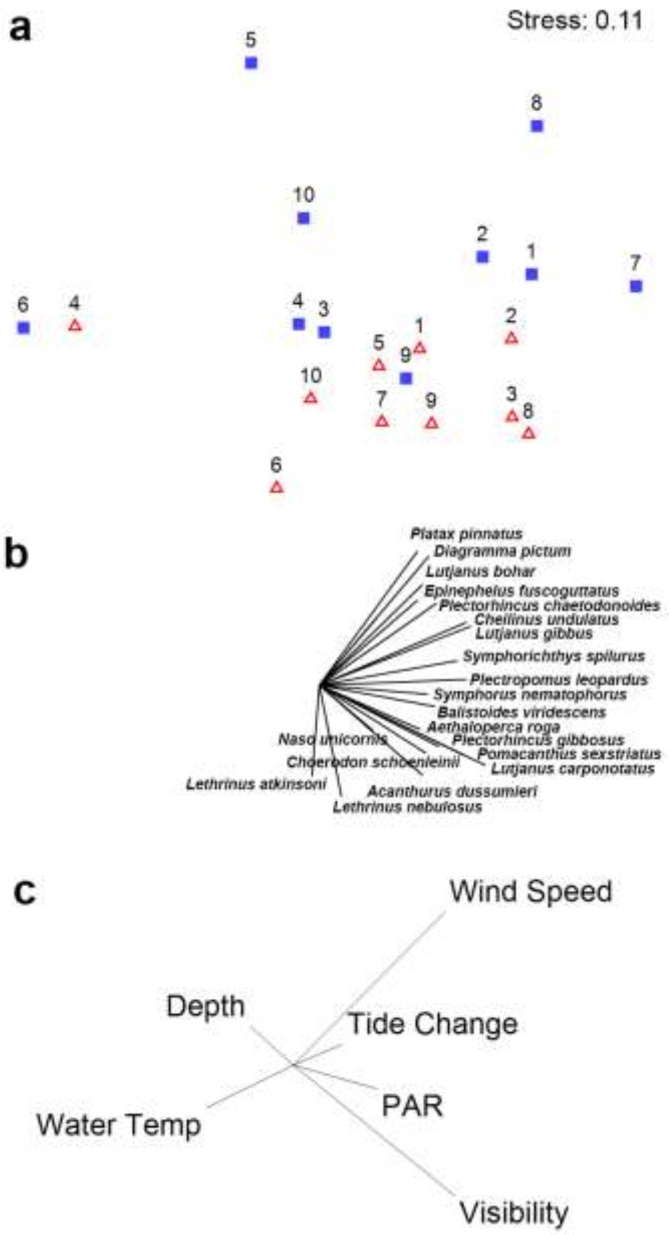

Figure 5.2 Non-metric multi-dimensional scaling analysis showing the spatial variation in sheltering behaviour by large reef fishes at two sites at Lizard Island over a 10 week period. **a** Ordination plot showing the relationship between site 1 (blue squares) and site 2 (red triangles) over the 10 week period, numbers associated with sample points refer to individual

weeks. **b** Species loadings showing the relative contribution of each species to observed differences in shelter usage. **c** Environmental variables showing their characterisation of the data cloud.

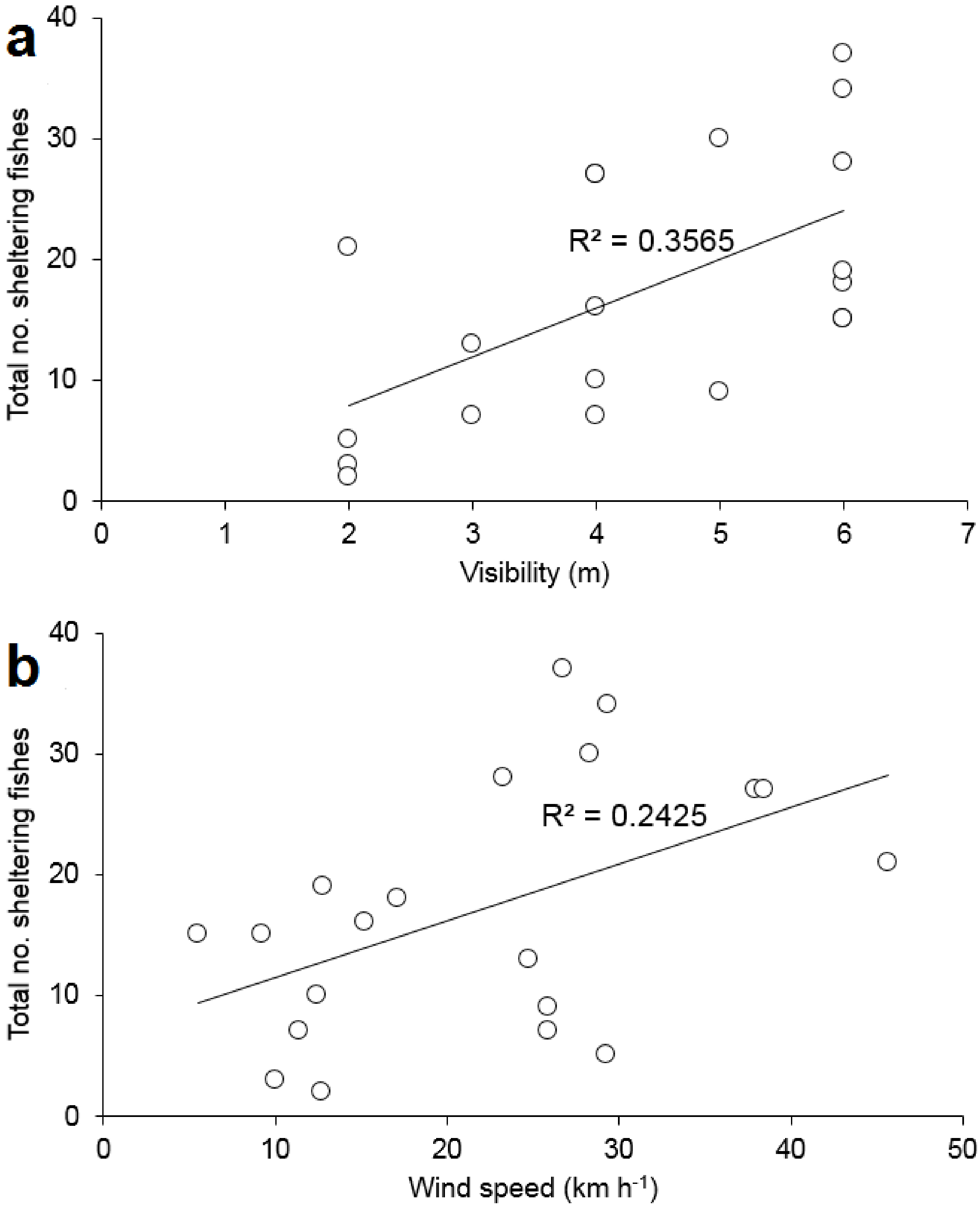

Figure 5.3 Regressions of total numbers of large reef fishes sheltering at two sites at Lizard Island over a 10 week period, based on 20 3 hr observation periods against **a** visibility, and **b** mean wind speed (for the same window of observation).

5.4 Discussion

Two environmental factors emerged as the primary drivers of tabular structure usage by large reef fishes, visibility and wind speed. Together, these two variables explain almost half the variation in the assemblages of large reef fishes sheltering under tabular corals over the 10 week period. This finding both complements and extends previous research, which suggested that UV avoidance was the primary factor driving sheltering behaviour in large reef fishes (Kerry and Bellwood 2015).

Visibility and UV irradiance

The positive correlation of increased shelter usage with increased visibility strongly supports the earlier suggestion that UV avoidance is the primary reason for sheltering behaviour in large reef fishes. Suspended particles in the sea both absorb and scatter light, and this scattering further increases the probability that photons will be absorbed by other suspended particles, or by molecules of water and the substances dissolved in it (Wozniak and Dera 2007). As such, more turbid waters cause significant attenuation of UV-light (Lesser 1995, Lee et al. 2005). In Hawaii, the difference between clear and turbid tropical waters is so marked that it can alter the intensity of UV-B irradiance by several orders of magnitude at shallow depths (Lesser 1995). On the Great Barrier Reef, periods of strong southeasterly winds (occasionally experienced during this study) generate swells which can produce near-bed suspended sediment concentrations two orders of magnitude greater than typical values (Larcombe 1995). Here, turbidity has been shown to account for 74-79% of the total annual variation in irradiance (Anthony et al. 2004). Therefore, the drop off in shelter usage during periods of high turbidity (low visibility) is likely to reflect the response of large reef fishes to reduced levels of UV irradiance in their environment. Variation in turbidity may thus explain variation in shelter usage during the day, as observed in a previous study, which on occasion only loosely tracked incident (above water) irradiance values (Kerry and Bellwood 2015).

McFarland and Hillis (1982) found similar results for resting schools of Haemulidae following five days of high turbidity (visibility <1 m), where only one in ten individuals remained at shelter sites. They hypothesised, however, that high turbidity interfered with navigation and increased susceptibility to predation. Although evidence for predation avoidance by large reef fishes occupying tabular corals is limited (cf. Kerry and Bellwood 2015), it is possible that this factor may play a role. Given that water turbidity negatively affects fish reactive distance (Newcombe 2003) and disrupts chemical cues (Wenger et al. 2011) it might be prudent for fishes to avoid structures that constrain flight options during highly turbid conditions, although these hindrances also apply to predators (Miner and Stein 1996).

Wind speed and flow refuge

The other environmental driver found to influence sheltering behaviour by large reef fishes was wind speed. In shallow reef environments, wind speed is a good proxy for wave energy (Fulton and Bellwood 2005; Pequignet 2011), and in an earlier study conducted in the lagoon at Lizard Island, wave energy was found to be intermediate when compared with exposed and sheltered sites (Fulton and Bellwood 2005). Higher levels of wave energy and associated water velocity can affect swimming performance and place extra energetic demands on fishes that are trying to maintain station or conduct daily activities (Fulton and Bellwood 2002; Webb 2004). Station-holding fishes, such as those observed in this study, may therefore seek out water flow refuges to avoid the need for excessive swimming. This behaviour has been documented for fishes in freshwater streams, which lower swimming costs by residing behind large woody debris that reduces current speeds (Webb 2006). Similar behaviour has been observed for fishes on coral reefs, which occupy substratum holes, allowing them to station-hold for significantly longer periods (Johansen et al. 2007; Johansen et al. 2008). However, unlike tabular corals, substratum holes do not provide shade, nor would they typically be able to accommodate large reef fishes.

Large reef fishes in this study tended to increase usage of tabular corals when wave energy increased suggesting that this structure may also provide respite from higher water velocities. Similarly shaped overhanging structures have been shown to retard incident flow velocity owing to the canopy surface area, which creates drag, thereby absorbing water momentum. Furthermore, these structures reduce turbulence because the canopy layer separates the surface flow from understory flow, preventing mixing (Leonard and Luther 1995; Wilson et al. 2003; Munson et al. 2013). It is, therefore, probable that flow velocity and turbulence is significantly retarded beneath tabular corals, and that this location offers large reef fishes respite from both excessive UV radiation and wave energy.

It should be noted, however, that because high wind speeds may create more turbid conditions (Larcombe 1995), it is possible that the two associated environmental drivers – UV irradiance and wave energy – somewhat offset each other, i.e. if higher wind speeds increase turbidity, this may reduce UV irradiance and moderate tabular coral usage by large reef fishes. Given, however, the greater contribution of visibility when compared with wind speed in driving usage patterns in this study, it is possible that large reef fishes treat UV avoidance as the primary driver, and will shelter beneath tabular corals when UV is high (low turbidity) even if wind speed is low. Interestingly, Mackenzie and Greenbery (2006) found a comparable result for stone loach (*Barbatula barbatula*) in streams, which prioritised shelter from predation over flow refuging.

Other environmental factors

Perhaps one unexpected result is the absence of PAR as an apparent environmental driver in the sheltering behaviour by large reef fishes. Whilst it is likely that once incident light enters the water, turbidity becomes a more relevant factor in determining irradiance levels, PAR may not have registered in the present study because levels were so uniform throughout the observation period. Only on two cloudy days did PAR drop noticeably below typical midday values. It is possible, therefore, that under typical conditions, PAR levels are more relevant in structuring shelter usage by large reef fishes over the diurnal cycle (Kerry and Bellwood 2015), rather than across different days.

Water temperature also showed little variation over the study period and was not found to influence the sheltering behaviour of large reef fishes, although it is less clear how this factor might affect such behaviour if the range was greater. A longer, seasonal study would be required to resolve this question and might also reveal a greater effect of PAR, which is also likely to decline outside the austral summer months.

Tide change and depth were related factors in this study, and neither was found to be especially relevant in influencing sheltering behaviour of large reef fishes. Tides have been shown to be critically important in mangrove habitats where changing water levels can physically prevent fishes from accessing important nursery habitats (Igulu et al. 2014; Harborne et al. 2015). Tide changes in the present study did not prevent access of fishes to tabular corals, but it is possible that they play an indirect role, as large tides can resuspend settled sediment, increasing turbidity (Kleypas 1996). At low tide, the strength of wave energy may also increase in shallow reef areas where most tabular corals are found, while at high tide irradiance levels are somewhat reduced owing to greater depth (Anthony et al. 2004).

In conclusion, the present study has found further evidence that tabular corals are important shelter sites for large fishes on coral reefs, potentially offering both shade from down-welling UV irradiance and a refuge from wave energy. By utilising tabular corals, large reef fishes may save considerable energetic costs that would otherwise be invested in preventing or repairing UV-damage, and in additional swimming activity. This finding helps to explain why tabular corals are used so consistently and in such high densities by large reef fishes, and emphasises the importance of ensuring that these structures are a conservation priority.

Chapter 6: Concluding Discussion

The ecology of an organism is defined by its relationship with the environment. On coral reefs, for example, corals offer reef fishes a number of important functions including access to food (Wilson et al. 2006; Pratchett et al. 2008), camouflage (Coker et al. 2009; McCormick 2009), recruitment habitat (Jones et al. 2004; Bonin 2012), and shelter (Munday and Jones 1998; Holbrook and Schmitt 2002). Numerous studies have identified the structural complexity of reefs as a positive, primary correlate with reef fish abundance and diversity (reviewed by Graham and Nash 2013), but have been unable to identify specific functional properties of habitat structure that drive these associations (Harborne et al. 2012; Kerry and Bellwood 2012). This thesis offers a contrasting approach, exploring in detail the function and importance of tabular structure for large reef fishes, a functionally diverse and relatively understudied component of coral reefs. Specifically, to achieve this, the present thesis has answered four questions that were posed in the introduction (Chapter 1).

Question 1: “Does the loss of tabular structures affect large reef fishes?” Even the loss of a single important structure might critically alter shelter availability in an environment. Chapter 2 highlighted that the exclusion (or “loss”) of tabular structures had a significant effect on the distribution of large reef fishes, even though these structures only constituted a small fraction (4%) of benthic cover. Changes in the availability of tabular structure at the spatial scale of this chapter (200 m^2) shifted activity spaces of large reef fishes away from these localities. More importantly, the exclusion effect simulated here could occur at reef-wide scales during major disturbance events (e.g. cyclones), with the displacement of multiple species of large fishes, which may severely impact ecosystem function. The higher order effects identified in smaller reef fishes further suggests that tabular structures may constitute keystone structures on coral reefs.

Question 2: "Why do large reef fishes shelter beneath tabular corals?" Predation avoidance is often cited as the principle cause of structure usage by coral reef fishes; however, Chapter 3 did not find strong evidence for this behaviour in sheltering large reef fishes. Tabular structure usage appeared to reach a peak during the middle of the day when predation risk would be relatively low, while incident solar irradiance would reach its zenith. Although tabular structure may offer some benefit in predation avoidance, the data suggest that the large reef fishes are primarily sheltering beneath tabular structure to protect themselves from harmful UV irradiance, which can be extreme in shallow, oligotrophic waters. Given the significant costs of producing UV-blocking mycosporine-like amino acids, fishes may achieve considerable energetic savings by station-holding beneath tabular structure.

Chapter 3 also observed that absence of large reef fishes from tabular structure at sunset may relate to the increased risk of acquiring parasites during that time, which would also require greater energetic expenditure to develop physiological, anatomical, or behavioural defences to combat potentially lethal gnathiid infestation.

Question 3: "Do large reef fishes have unrestricted access to tabular corals?" Tabular structure is a finite resource on coral reefs and given its intense use during peak sunlight hours, suggests that fishes may compete for space beneath it. Chapter 4 found an exceptionally high mean biomass of sheltering fishes beneath tabular structure (4.71 kg m^{-2}, which is one or two orders of magnitude greater than typical coral reef estimates between 0.031 to 0.1 kg m^{-2}). This chapter also documented strong interactions among 30 species of large reef fishes, which resulted in displacement and exclusion of losing individuals from the understory of tabular structure. When large reef fishes did elect to share tabular structure this was attributed to increased anti-predation defence gained by having multiple sets of eyes. Nonetheless, position beneath structure may still be important: potentially affecting predation vulnerability, field of vision and phototopic acclimation.

Question 4: "What environmental factors drive tabular coral usage by large reef fishes?" While the study presented in Chapter 3 found greater evidence for UV avoidance as a driver of shelter usage when compared to predation avoidance, there are a number of other environmental factors that may be relevant. Chapter 5 identified two environmental factors as key drivers of sheltering behaviour in large reef fishes: increased visibility (decreasing turbidity) and increasing wind speed (increasing wave energy). Turbidity is the primary determinant of in-water irradiance (including UV) and, therefore, as water clarity improves large reef fishes are more likely to seek out shelter as observed in Chapter 3. Increasing wave energy places energetic costs on swimming or station holding fishes, which seek refuge from higher wave velocities. Tabular structures likely reduce water momentum by creating drag and also reduce turbulence by preventing mixing of surface flow with understory flow. Chapter 5, therefore, provides further evidence that tabular structures are important energetic refuges for large reef fishes, offering both shade from down-welling UV-irradiance and respite from wave energy.

Concluding remarks

Shelter use by fishes appears to be a common feature of aquatic environments, having been documented in estuarine rivers (Webb 2006), kelp beds (Holbrook et al. 1990), seagrass beds (Heck and Wetstone 1977), and on coral reefs (Bonin 2012; Johansen et al. 2008). Shelter can serve as a critical resource, with its availability having direct implications for population survival, through predation avoidance or lethal environmental disturbance. Shelter sites may also provide individuals with more routine functions, allowing them to conserve energy and maximise fitness on a daily basis. In this thesis, Chapters 3 and 5, both found support for the latter function of tabular structures for large reef fishes on coral reefs, identifying energetic savings in UV-avoidance and respite from wave energy. These observations would benefit from more formal analyses of energetic expenditure by large reef fishes in producing UV-blocking compounds and in flow retardation beneath tabular structures.

Climate change and other anthropogenic stresses present a clear threat to the longer term availability of tabular structure on coral reefs, given that tabular corals are one of the most susceptible growth forms to coral bleaching (Marshall and Baird 2000), storms (Madin et al. 2014), ocean acidification (Fabricius et al. 2011), and crown-of-thorns starfish outbreaks (Baird et al. 2003). It should be noted, however, that with respect to crown-of-thorns outbreaks and coral bleaching, these structures may remain in place for months or even years after the coral has died, such that they may still be utilised by large reef fishes (Kerry and Bellwood 2012). Alternate shelter may also be available on coral reefs in the form of carbonate overhangs, but the physical loss of tabular corals nonetheless represents a significant reduction in the abundance and distribution of shelter options for large reef fishes. It is also noteworthy that alternate stable states of 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 reef fishes. Chapter 2 suggests that the abundances of large reef fishes may decline locally following the loss of tabular corals. This displacement of large reef fishes may place increasing demand on remnant tabular structures, in turn increasing competition for these shelter sites. If the competition documented in Chapter 4 should increase, this would likely place increased metabolic costs on shelter-using fishes (Forrester et al. 2006; Boström-Einarsson et al. 2014) and increased mortality among losing species that are outcompeted for shelter (Holbrook and Schmitt 2002; Hixon and Jones 2005). Given that at least two species of functionally important fishes were documented in the lower ranks of the dominance hierarchy (*Naso unicornis*, *Platax pinnatus*), coral reef ecosystems could lose key functionality following the loss of tabular structure. This observation should prompt formal analysis of the activity spaces of large reef fishes, and especially, their response to loss of shelter sites.

Keystone structures have a disproportionate effect on their ecosystems relative to their abundance, providing shelter or ‘services’ crucial for other species, but their identification remains relatively scarce and largely restricted to terrestrial and shoreline environments. Tabular corals may, however, fit the description of a keystone structure based on the findings presented in this thesis. Their vulnerability to contemporary environmental and biological pressures presents real concerns about their availability on coral reefs, and concomitant shifts in coral reef fish communities. Nonetheless, their importance demonstrated herein, highlights the need for conservation planning to preserve these key structures.

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Appendix A: Supplementary Material for Chapter 2

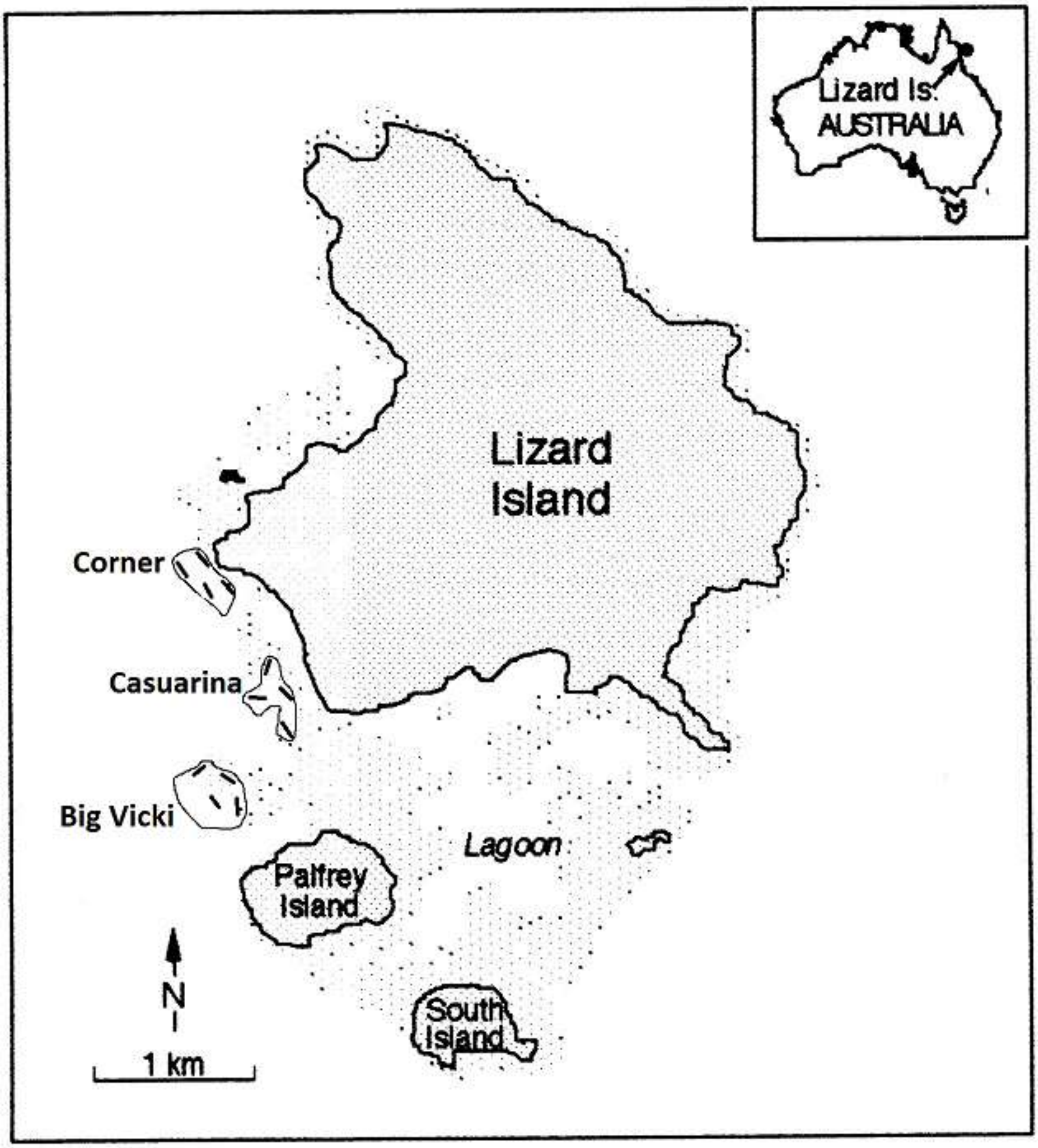

Figure A1. Map of three reef sites (Corner, Casuarina, Big Vicki) used in study showing approximate location of transects (solid lines).

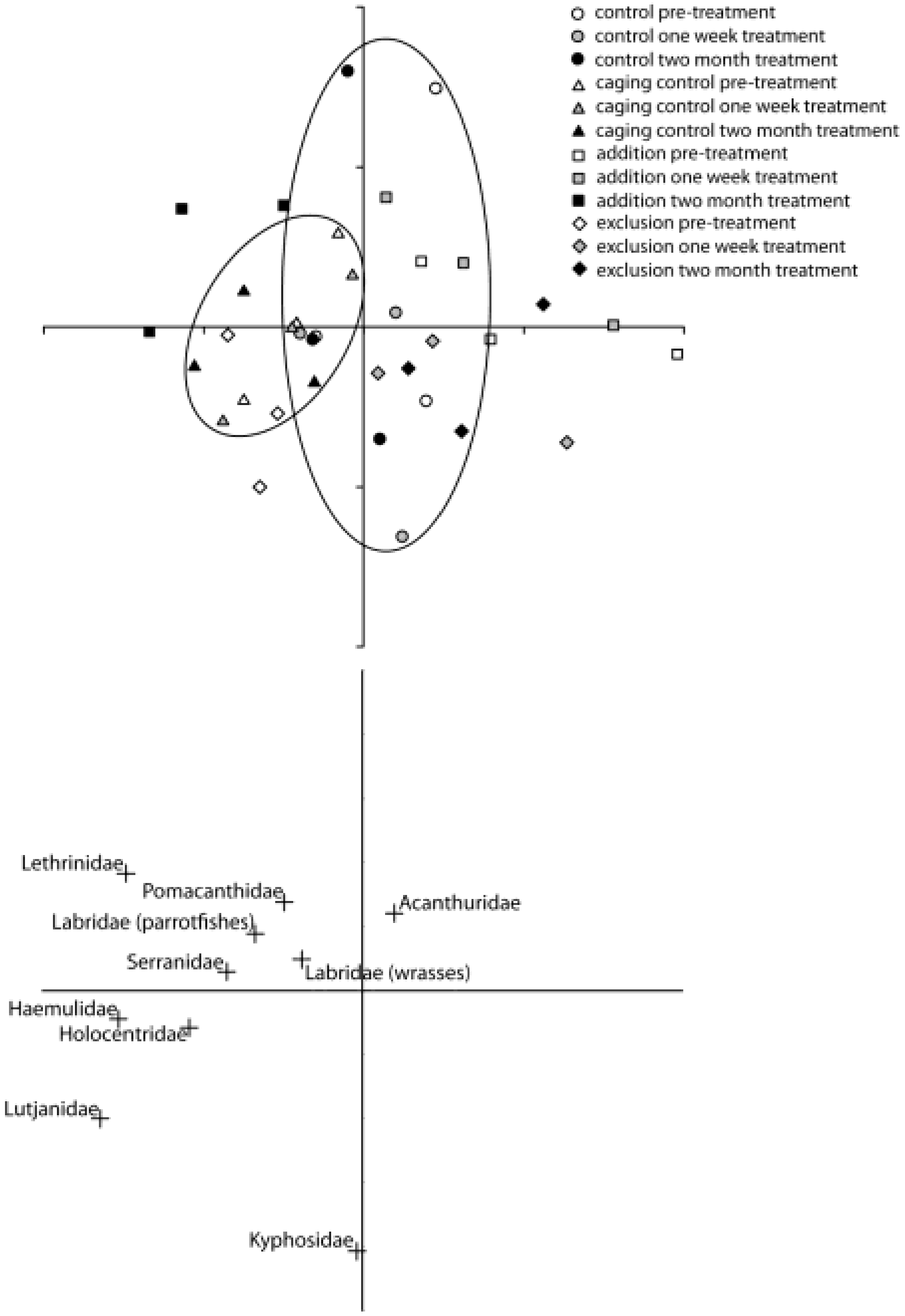

Figure A2. Non-metric multi-dimensional scaling analysis showing the relationships between families of large reef fishes across four different structure treatments at Lizard Island, GBR. (a) Ordination plot showing the relationship between three different sites and three different time periods for each treatment. (b) Families loadings showing the relative contribution of each family to the observed differences in usage of the two different treatments. Circles group together control and caging-control transects.

Table A1. Summary of available and manipulated surface area (SA) of tabular structure on three reefs at Lizard Island, GBR

Site	Treatment	No of tabular structures	Total SA per transect (m^2)	Mean SA per tabular structure (m^2)	Total modified SA (m^2)	Post-treatment SA (m^2)	% SA change post-treatment
Big Vicki	Control	9	4.89	0.54	0.00	4.89	0
Big Vicki	Caging Control	10	7.81	0.78	5.34	7.81	0
Big Vicki	Exclusion	10	10.07	1.01	-7.91	2.15	-78.6
Big Vicki	Addition	0	0.00	0.00	3.84	3.84	100.0
Casuarina	Control	8	5.01	0.63	0.00	5.01	0
Casuarina	Caging Control	8	7.46	0.93	6.23	7.46	0
Casuarina	Exclusion	9	7.70	0.86	-5.83	1.88	-75.6
Casuarina	Addition	0	0.00	0.00	3.84	3.84	100.0
Corner Beach	Control	9	5.10	0.57	0.00	5.10	0
Corner Beach	Caging Control	7	7.27	1.04	5.25	7.27	0
Corner Beach	Exclusion	10	8.33	0.83	-6.75	1.58	-81.0
Corner Beach	Addition	0	0.00	0.00	3.84	3.84	100.0

Tabular structures with a mean diameter <= 0.2 m were present but uncommon on all transects and have not been included in analyses because field observation suggests they are insufficient to support the length of focal fishes (>= 0.2 m).

Table A2. Results of analysis of similarities (ANOSIM: Primer-e) based on Bray-Curtis similarities of $\log_{10}(x + 1)$- transformed abundance data comparing large reef fish assemblages between all treatments at three sites, over three survey periods. Global $R = 0.352$, $P < 0.01$

Treatment (Period)	Control (1)	Control (2-3)	Caging-Control (1)	Caging-Control (2-3)	Addition (1-2)	Addition (3)	Exclusion (1)	Exclusion (2-3)
Control (1)		0.56	0.3	0.048*	0.048*	0.1	0.2	0.381
Control (2-3)	0.56		0.429	0.024*	0.02*	0.083	0.369	0.084
Caging-Control (1)	0.3	0.429		0.345	0.012*	0.1	0.4	0.06
Caging-Control (2-3)	0.048*	0.024*	0.345		0.002*	0.012*	0.095	0.02*
Addition (1-2)	0.048*	0.02*	0.012*	0.002*		0.036*	0.012*	0.022*
Addition (3)	0.1	0.083	0.1	0.012*	0.036*		0.1	0.012*
Exclusion (1)	0.2	0.369	0.4	0.095	0.012*	0.1		0.024*
Exclusion (2-3)	0.381	0.084	0.06	0.02*	0.022*	0.012*	0.024*	

Survey periods are grouped in line with cluster analysis for addition and exclusion transects, and consist of survey period pre-treatment (1), survey period after one-week treatment (2) and survey period after two-months treatment (3). Significant values are marked with an asterisk.

Table A3. Species list including total counts of families of large reef fishes surveyed.

Acanthuridae	**326**
Acanthurus blochii	
Acanthurus dussumieri	
Acanthurus nigricauda	
Ctenochaetus striatus	
Naso tonganus	
Naso unicornis	
Zebrasoma veliferum	
Haemulidae	**81**
Diagramma pictum	
Plectorhincus albovittatus	
Plectorhincus chaetodonoides	
Plectorhincus chrysotaenia	
Plectorhincus flavomaculatus	
Plectorhincus lineatus	
Holocentridae	**65**
Sargocentron spiniferum	
Kyphosidae	**43**
Kyphosus bigibbus	
Kyphosus vaigiensis	
Labridae (non-parrotfishes)	**240**
Cheilinus chlorourus	
Cheilinus fasciatus	
Cheilinus trilobatus	
Cheilinus undulatus	
Choerodon schoenleinii	
Epibulus insidiator	
Haliochores hortulanus	
Hemigymnus melapterus	
Novaculichthys taeniourus	
Oxycheilinus diagrammus	
Scarus schlegeli	
Lethrinidae	**132**
Lethrinus atkinsoni	
Lethrinus laticaudus	
Lethrinus obsoletus	
Lutjanidae	**211**
Lutjanus bohar	
Lutjanus carponotatus	
Lutjanus fulviflamma	
Lutjanus gibbus	
Lutjanus russelli	
Symphorichthys spilurus	
Symphorus nematophorus	
Pomacanthidae	**57**
Pomacanthus sexstriatus	
Labridae (parrotfishes)	**613**
Bolbometopon muricatum	
Cetoscarus bicolor	
Chlorurus microrhinos	
Chlorurus sordidus	
Hipposcarus longiceps	
Scarus altipinnis	
Scarus flavipectoralis	
Scarus frenatus	
Scarus ghobban	
Scarus niger	
Scarus oviceps	
Scarus rivulatus	
Scarus schlegeli	
Scarus spinus	
Serranidae	
Anyperodon leucogrammicus	**70**
Epinephelus hexagonatus	
Epinephelus merra	
Plectropomus laevis	
Plectropomus leopardus	

Appendix B: Supplementary Material for Chapter 3

Table B1. Species observed during study

Species group		Total count
Acanthurus dussumieri		31
Pomacanthus		24
	Pomacanthus semicirculatus	
	Pomacanthus sexstriatus	
Cheilinus undulatus		5
Plectropomus		21
	Plectropomus leopardus	
	Plectropomus laevis	
Diagramma pictum		11
Lethrinus		25
	Lethrinus atkinsoni	
	Lethrinus nebulosus	
	Lethrinus obsoletus	
Lutjanus carponotatus		95
Lutjanus gibbus		19
Lutjanus russelli		10
Naso		30
	Naso annulatus	
	Naso brachycentron	
	Naso tonganus	
	Naso unicornis	
Parrotfishes		33
	Chlorurus microrhinos	
	Chlorusus sordidus	
	Scarus altipinnis	
	Scarus frenatus	
	Scarus ghobban	
	Scarus rivulatus	
Plectorhincus		31
	Plectorhincus chaetodonoides	
	Plectorhincus chrysotaenia	
	Plectorhincus flavomaculatus	
	Plectorhincus gibbosus	
	Plectorhincus lineatus	
Sargocentron spiniferum		18
Balistoides viridescens		5
Large Groupers		8
	Aethaloperca rogaa	
	Anyperodon leucogrammicus	
	Cromileptes altivelis	
	Epinephelus caerulopunctatus	
	Epinephelus fuscoguttatus	

Large Snappers		17
	Lutjanus bohar	
	Symphoricthys spilurus	
	Symphorus nematophorus	
Total		**383**

Appendix C: Supplementary Material for Chapter 5

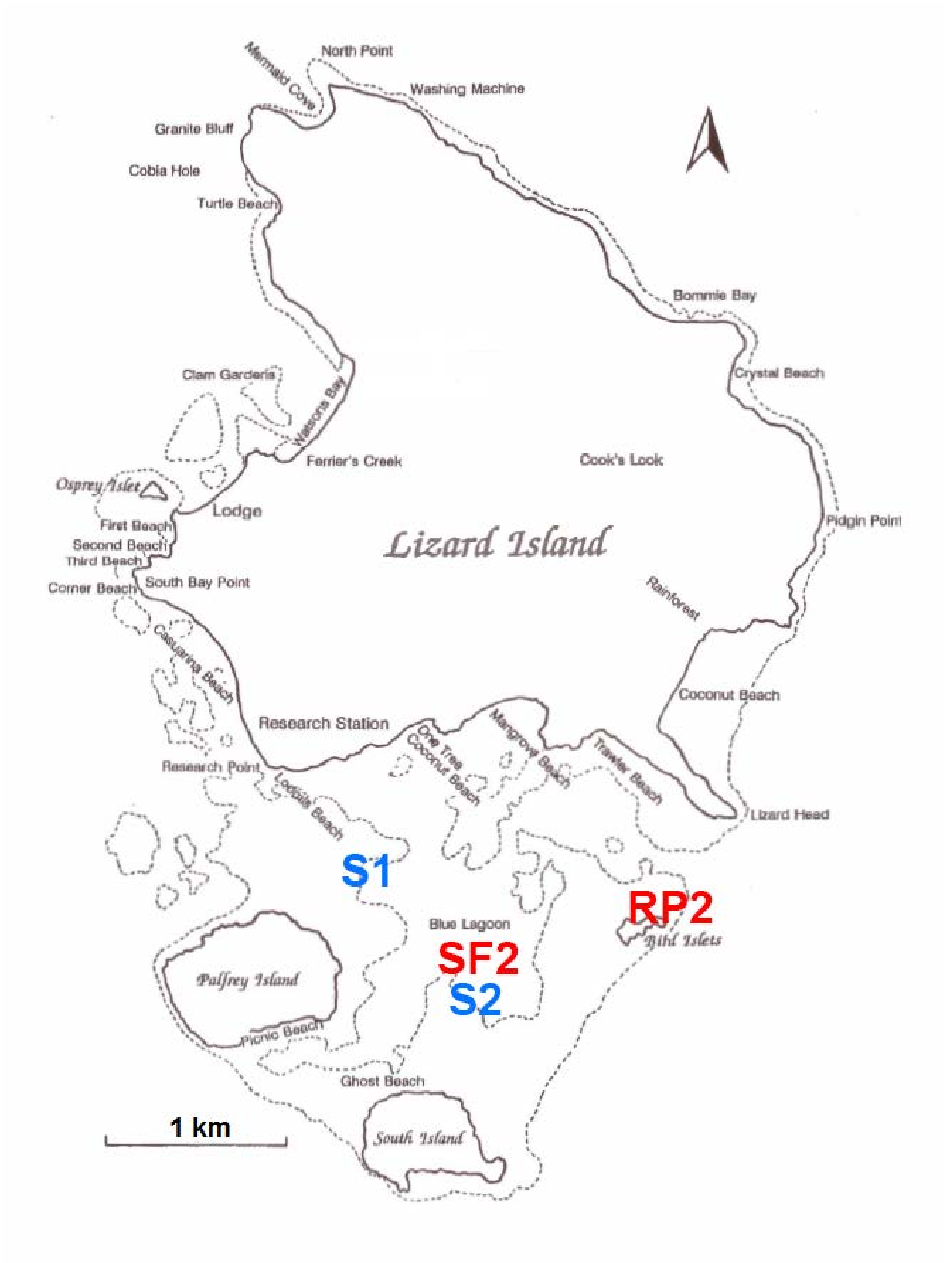

Figure C1. Map of Lizard Island (Australia), showing study sites (blue): Site 1 (S1) and Site 2 (S2). Locations of Sensor Float 2 (SF2) and Relay Pole 2 (RP2) from which environmental data were drawn (red).

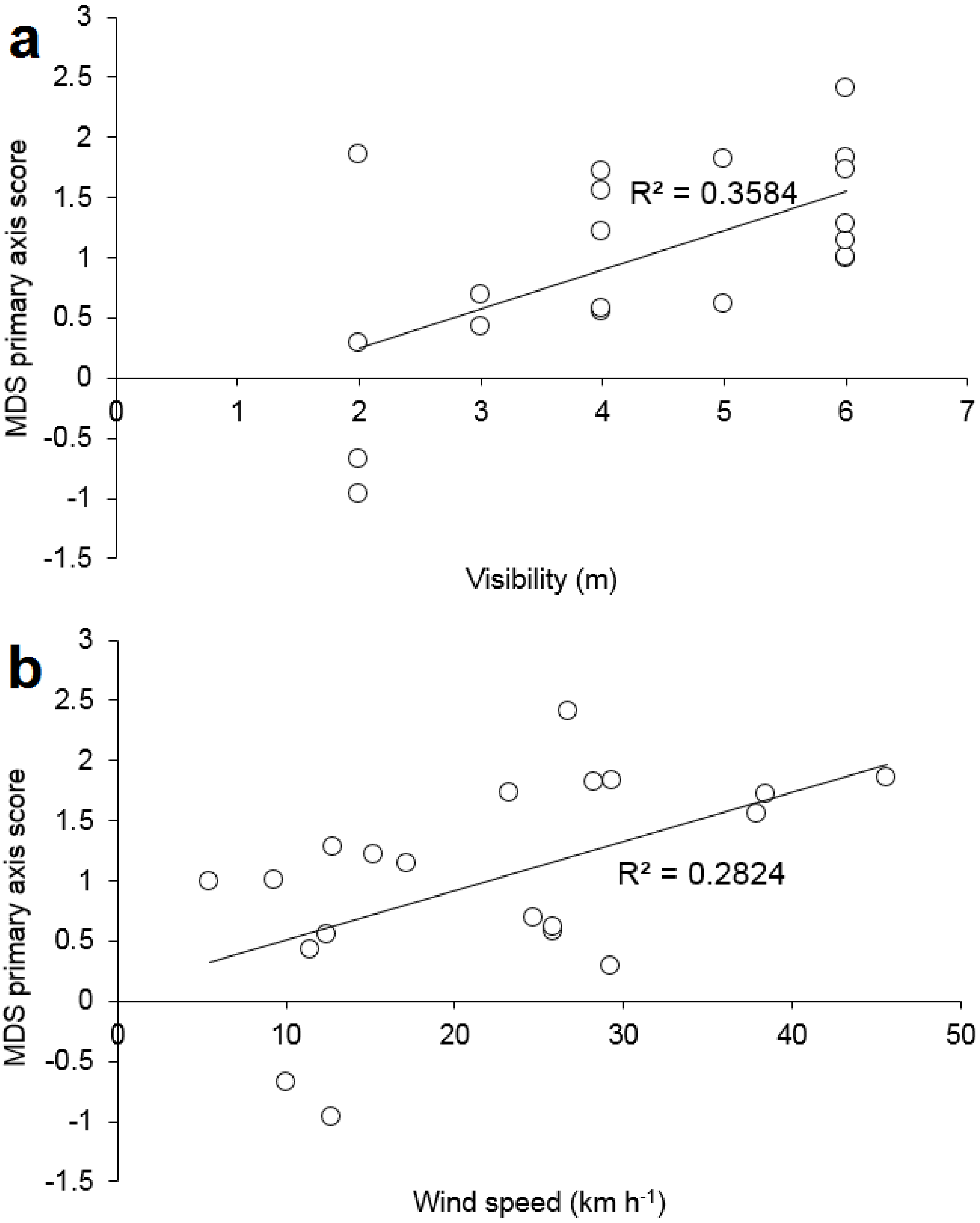

Figure C2. Regressions of primary axis scores of individual samples based on nMDS of sheltering by large reef fishes at two sites at Lizard Island over a 10 week period, based on individual 3 hr observation periods against **a** visibility, and **b** mean wind speed (for the same window of observation).

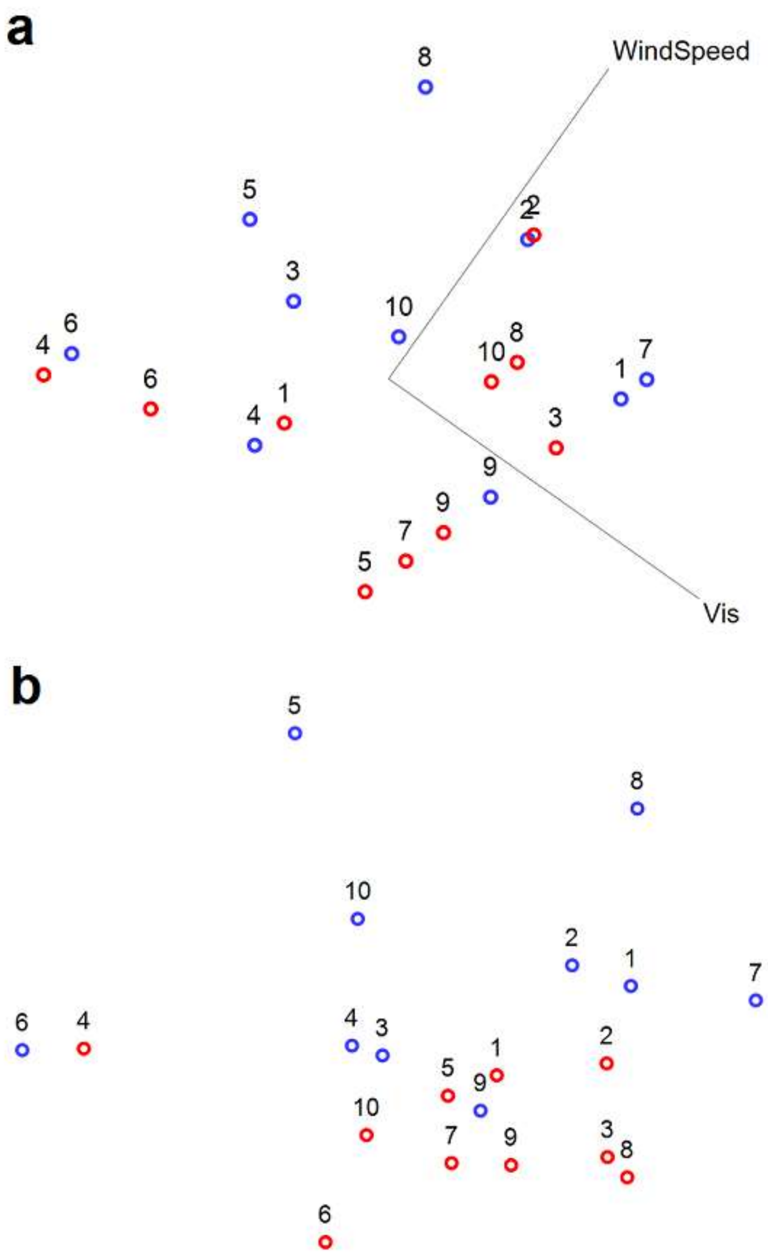

Figure C3. a Distance-based redundancy analysis (dbRDA) showing the spatial variation in two sites at Lizard Island over a 10 week period, as described by the two best predictor variables according to the BEST analysis: *visibility* and *wind speed*. **b** non-metric multi-dimensional scaling analysis (nMDS) showing the spatial variation in sheltering behaviour by large reef fishes at two sites in the lagoon at Lizard Island over a 10 week period. The full data cloud of the unconstrained nMDS is shown to allow comparison with the BEST-model above; the similarity of the patterns of sample points suggest that the dbRDA model provides a good fit for the salient patterns observed in the nMDS.

Table C1. Species of large reef fish observed sheltering during 10 week study

Family	**Species**
Acanthuridae	
	Acanthurus dussumieri
	Naso unicornis
Balistidae	
	Balistoides viridescens
Ephippidae	
	Platax pinnatus
Haemulidae	
	Diagramma pictum
	Plectorhincus chaetodonoides
	Plectorhincus chrysotaenia
	Plectorhincus gibbosus
	Plectorhincus lineatus
Labridae	
	Cheilinus undulatus
	Choerodon schoenleinii
Lethrinidae	
	Lethrinus atkinsoni
	Lethrinus nebulosus
Lutjanidae	
	Lutjanus bohar
	Lutjanus carponatatus
	Lutjanus gibbus
	Symphorichthys spilurus
	Symphorus nematophorus
Pomcanthidae	
	Pomacanthus sexstriatus
Serranidae	
	Aethaloperca roga
	Epinephelus fuscoguttatus
	Plectropomus leopardus

Appendix D: Publications arising from thesis

Kerry JT, Bellwood DR (2014) Do tabular coral constitute keystone structures on coral reefs? Coral Reefs 34(1):415-424

Kerry JT, Bellwood DR (2015) The functional role of tabular structures for large reef fishes: avoiding predators or solar irradiance? Coral Reefs 34(2):693-702

Kerry JT, Bellwood DR (2015) Competition for shelter in a high-diversity system: structure use by large reef fishes. Coral Reefs (online)

Kerry JT, Bellwood DR (*submitted*) Environmental drivers of sheltering behaviour in large reef fishes. PLoS ONE