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Branching coral as a macroalgal refuge in a marginal coral reef system

S. Bennett · A. Vergés · D. R. Bellwood

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Abstract Marginal coral reef systems may provide valuable insights into the nature of ecosystem processes in systems on the trajectory towards a phase shift to an alternate ecosystem state. This study investigates the process of herbivory in a marginal coral reef system in the Keppel Islands at the southern end of the Great Barrier Reef. Branching *Acropora* coral and the brown macroalga *Lobophora variegata* occupied up to 95% of the reef crest substratum at the three surveyed reefs. Feeding rates of herbivorous fishes and removal rates of *Lobophora* were directly quantified within areas of branching *Acropora* and on planar surfaces. Feeding rates by herbivorous fishes were habitat dependent with the highest bite rates being found in planar habitats for both *Lobophora* and the epilithic algal matrix (EAM) by 1–2 orders of magnitude, respectively. Feeding rates on *Lobophora* were, however, much lower than rates on the EAM. The low rates of *Lobophora* removal and significantly lower rates of herbivory in branching habitats were consistent with the high biomass of this brown alga throughout the Keppel Islands and with its distribution on reef crests, where *Lobophora* biomass was 20 times greater in branching than in planar habitats. This lack of feeding by herbivorous fishes within

branching coral habitats in the Keppel Islands contrasts with the typical role of coral and topographic complexity on herbivores on coral reefs and highlights the potential for complex interactions between algae, corals and fishes on coral reefs. On marginal systems, herbivory may modify algal distributions but may be unable to contain the proliferation of algae such as *Lobophora*.

Keywords Herbivory · *Lobophora variegata* · Ecosystem function · Phase shift · Resilience · Coral reef

Introduction

Evidence of the erosion of ecological resilience on coral reefs has been demonstrated across the globe with a decrease in coral cover (Pandolfi et al. 2003; Bellwood et al. 2004). In some cases, this is associated with a phase shift from a coral to a macroalgal dominated state (Done 1992; Hughes 1994; McClanahan et al. 1999; Mumby 2006; Ledlie et al. 2007). The instances of such phase shifts have been forecast to increase (Hoegh-Guldberg 1999) as anthropogenic influences on coral reef systems continue to rise (Hughes et al. 2003). As a consequence, there is a clear need to develop a sound understanding of the ecological processes which underpin the resilience of coral reef systems (Bellwood et al. 2004). This will enable us to understand the likely trajectory of reefs into the future (Norström et al. 2008; Nystrom et al. 2008) and take measures to limit, and if possible, reverse the current decline of coral reef systems. Herbivory is one such ecological process, which is considered to be important for the persistence of coral-dominated reefs (Choat 1991; Hughes et al. 2003; Bellwood et al. 2004; Mumby 2006). The overfishing of herbivores from coral reef systems has been

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identified as a major cause of large-scale phase shifts to macroalgal dominance (Hughes 1994). Nevertheless, high algal biomass can also occur where herbivores are not targeted by commercial fishing, as in the marginal systems on the inner shelf reefs of the Great Barrier Reef (GBR) (McCook 1997; Bellwood et al. 2006; Wismer et al. 2009).

Marginal systems are defined herein as ecosystems that lie close to the limits of current coral reef growth. Marginal systems may therefore mark the threshold of a system's tolerance to prevailing environmental stressors, beyond which the system may move into alternate stable states. In the case of the GBR, many inshore reefs can be classified as marginal systems. These inshore reefs face chronic disturbance due to poor water quality, which may be a result, at least in part, of the deterioration of terrestrial catchments and waterways, which discharge into inshore waters (McCulloch et al. 2003; Devlin and Brodie 2005). The southern end of the GBR (23°S) is another example of a marginal system situated at the threshold of coral reef development on Australia's east coast and on the margin of a spatial transition into sub-tropical rocky reefs. The southern inshore reefs of the GBR therefore provide an interesting marginal system in which to study reef processes. The ecosystem processes operating within such reefs may provide invaluable insights into the types of functional changes, which ultimately precipitate the transition to an alternative ecosystem state.

The southern GBR is characterised by low coral species richness (DeVantier et al. 2006) and low rates of coral recruitment relative to the central and northern GBR (Hughes et al. 1999). The southern inshore reefs, in particular, lie adjacent to the Fitzroy river catchment, an area of intense agricultural land use, which greatly influences inshore water quality particularly during the wet season (Dec–Mar) (Wooldridge et al. 2006). Southern inshore reefs are dominated by monospecific stands of arborescent *Acropora* (Van Woesik et al. 1995) and have been subject to an influential disturbance regime over the past 20 years (Van Woesik et al. 1995; Jones et al. 2008). Mass coral bleaching events took place in 1998, 2002 (Elvidge et al. 2004) and most recently in 2005–2006, precipitating a major outbreak of the brown fleshy macroalgae *Lobophora variegata* (Lamouroux) Womersley (Diaz-Pulido et al. 2009).

Lobophora variegata (hereafter *Lobophora*) and branching coral have previously been shown to have a competitive interaction on inshore reefs of the central GBR, an interaction that is mediated by the presence of herbivores (Jompa and McCook 2002). The high cover of *Lobophora* on southern inshore reefs, therefore, raises questions about the functional role of herbivores in the southern marginal system. Currently, few studies have investigated the process of herbivory on the southern margins of the GBR, particularly on inshore reefs that are

dominated by *Lobophora* and branching *Acropora* (Diaz-Pulido et al. 2009). By understanding the process of herbivory at the threshold of coral reef tolerance, we can begin to understand the potential functional role of herbivores in ecosystems on the trajectory towards alternate, undesirable stable states.

The aim of the current study was to examine the interaction between roving herbivorous fishes, *Lobophora* and branching corals on a southern inshore fringing reef. Using measurements of algal biomass removal and remote underwater video cameras, we quantified consumption rates of *Lobophora* between different habitat types and compared herbivore feeding rates between different habitat types. These results were then compared to the benthic composition and *Lobophora* biomass within different habitats on fringing reefs surrounding three southern inshore islands.

Materials and methods

Study site and benthic surveys

The study was carried out during December 2008 at three inshore fringing reefs within the Keppel Island Group: Olive Point (23° 09.710'S 150° 55.218'E), Middle Island (23° 10.234'S, 150° 55.182'E) and Halfway Island (23° 11.849'S 150° 58.140'E). At each reef, benthic cover was quantified along 8 × 20 m transects along the reef crest using a diver-operated underwater video (DUV; Sony DCR-HC1000E camera, with an Amphibico housing). For each transect, the camera lens was maintained approximately one metre above the substratum, at a height necessary to produce a 50 × 70 cm field of view. Each transect ran alongside a tape measure to provide a scale of reference during video analysis. For video analysis, the transect duration was divided equally to provide 20 still frames captured from the video. The substratum directly under each of three points within the captured frame was then recorded. The benthic surface under each point was classified into one of seven functional categories: hard coral, soft coral, turf algae, macroalgae, crustose coralline algae, sand and sponge. Hard corals were further categorised according to six growth form categories: branching, digitate, encrusting, foliose, massive and plate. Coral and algae were classified to the generic level where possible, with the exception of turf algae, which were categorised as epilithic algal matrix (EAM) (sensu Wilson and Bellwood 1997).

Lobophora variegata biomass

Lobophora biomass was quantified within live branching coral, dead branching coral and planar habitats on the crest

of each of the three reef locations (Olive Point, Middle Island and Halfway Island). Live branching coral commonly displayed a ‘crown’ of live tissue, on the apical end of the branch, whilst the lower branch frequently did not bear living coral tissue. Whilst *Lobophora* does not grow on living coral tissue (Diaz-Pulido et al. 2009), the living coral on the outer portion of branches defined the habitat. Dead branching habitat was defined as an area, which maintained the full structural integrity of live branching habitat, without live coral tissue, whilst planar habitat was defined as dead, eroded *Acropora* plates or flat consolidated surfaces on the reef crest. All *Lobophora* within a 50 × 50 cm quadrat was carefully collected and bagged from within each habitat type. Where necessary, coral was temporarily displaced from the quadrat area to remove algae living beneath the coral framework. In dead branching and planar habitats, quadrats were laid at the first appropriate habitat patch encountered during a transect swim along the reef crest. At each of the three reefs, three replicate quadrats per habitat were collected ($n = 9$ quadrats per habitat total). All *Lobophora* collected from the quadrats was returned to the laboratory where it was spun for 15 s in a salad spinner and weighed to the nearest 0.1 g.

Lobophora variegata removal

The impact of roving herbivorous fishes on *Lobophora* within branching and planar habitats was quantified at one of the three study sites (Olive Point). Individually weighed and labelled assays of *Lobophora* (average size \pm SE: 23.1 ± 0.5 g) were attached to the reef crest substratum within live branching, dead branching and planar habitats. Each assay was attached to the reef using gardening wire, passed through a loop in a rubber band (secured around the base of the algal assay). For each habitat type, two treatment and two control sites were used. Control assays were caged to exclude herbivores and control for handling loss. Control sites were set up identically to treatment sites, however, a wire cage (100 × 50 × 20 cm with a 1.44 cm² mesh size) was secured to the reef, to cover the control assays and prevent roving herbivores from feeding. Whilst the control cages did not prevent mesograzers (e.g., crustaceans, gastropods or small fish) from feeding on the *Lobophora*, neither the presence of these herbivores nor their feeding scars were observed, therefore their impact was assumed to be limited. *Lobophora* assays in the branching habitat were attached beneath the crown of living coral tissue to simulate natural conditions on the reef. For the purpose of the experiment, live branching habitat was selected, which displayed predominantly EAM rather than *Lobophora* beneath the crown of live tissue. Assays were deployed for a 48-h period, then were collected, returned to the laboratory and reweighed. The loss in

Lobophora fresh mass (g) was recorded per assay for both treatment and controls. Each assay was standardised by the proportion of its initial mass (g) lost during exposure. To assess the removal rates by herbivores, the proportional loss in mass was compared between treatment and control assays for each habitat type. Because no statistically significant differences in *Lobophora* removal were recorded between sites, the removal rates of *Lobophora* assays from each site were pooled in each habitat for the analysis ($n = 10$ assays per habitat treatment).

Feeding rates

To quantify the feeding rates of individual herbivore species on *Lobophora* within branching coral and planar habitats, treatment assays were filmed using a stationary remote underwater video camera (RUV, Sony DCR-HC1000E, with an Amphibico housing). Each camera was mounted onto a cement block positioned 2–4 m from the algae. In the initial seconds of recording, a 1-m² quadrat was placed over the site to provide a frame of reference when viewing the footage and for a standardised survey area. Cameras recorded for 3 × 4.5-h sampling periods over the 48-h *Lobophora* exposure period, with tape changes at 90-min intervals. Tape changes took less than 5 min. This procedure was repeated at both sites and in each of the live branching coral and planar habitats, yielding 27 h of video footage per habitat. To quantify the relative feeding rates on *Lobophora* between the different habitat types in Olive Point, the total number of herbivore bites was recorded from video footage for each 4.5-h sampling period. A foray, where consecutive bites by an individual fish took place without a discernable pause, was conservatively classed as a single bite (Bellwood and Choat 1990; McClanahan et al. 1999). As a result of the low overall number of bites by herbivores on *Lobophora*, all species were pooled into the total number of herbivore bites per 4.5-h replicate per habitat ($n = 6$ per habitat). Feeding rates by herbivores on the EAM within each 1-m² site were similarly recorded. Once again, as a result of the low and highly variable feeding rates, all species were pooled into the total number of herbivore bites per 4.5-h replicate per habitat.

Roving herbivore censuses

Abundances of roving nominally herbivorous fishes (*sensu* Choat et al. 2002) were quantified within each site, using underwater visual censuses (UVC) (10-min-timed swims) by divers on SCUBA (Bellwood and Wainwright 2001). Censuses were conducted along the reef crest recording roving herbivores within 4-m-wide transect. Twelve replicate censuses were conducted over 3 days within each of

the three study reefs. The length of each transect was subsequently measured using tapes (116 ± 8.7 m mean \pm SE) then standardised to give abundance per 400 m² (all censuses by SB). Roving herbivorous fishes (>10 cm TL) belonging to the families Labridae (parrotfishes), Acanthuridae, Siganidae and Kyphosidae were recorded. Due to difficulties in identification, individuals belonging to the species *Acanthurus auranticavus*, *A. grammoptilus* and *A. blochii* were grouped as *Acanthurus* spp.

Statistical analyses

The effect of habitat type, location (both fixed factors) and the interaction of these two factors on *Lobophora* biomass were tested using a full factorial analysis of variance (ANOVA). Biomass data were square-root transformed to adequately satisfy the assumptions of normality and homogeneity of variance. The effect of habitat type (fixed factor), treatment (fixed factor; herbivore exclusion vs. open plot) and the interaction of these two factors on *Lobophora* removal rates were likewise tested using a full factorial ANOVA. Removal rate data were arcsine transformed to reflect the structure of proportional data. In both factorial ANOVA's, Tukey's HSD *a posteriori* analysis were carried out to assess the source of differences for significant effects. Bite rates were compared between both branching and planar habitats for *Lobophora* and similarly for EAM using a one-way ANOVA. Due to low numbers of bites, bite rates were pooled for the entire herbivore community, for both *Lobophora* and EAM analyses. Bite rates were log ($n + 1$) transformed to adequately satisfy the assumptions of normality and homogeneity of variance. In all tests, the assumptions of normality and homogeneity of variances were tested using a P-plot of residuals and predicted vs. residual plots.

Results

The brown macroalga *Lobophora* and the branching hard coral *Acropora* (mainly *A. formosa*) dominated benthic communities within each of the three reef locations surveyed in the Keppel Islands group (Fig. 1). Abundance of *Lobophora* ranged between 13 and 60% of total benthic cover (31–100% of total macroalgal cover), whilst arborescent *Acropora* ranged between 15 and 57% of total benthic cover (71–95% of total coral cover) (Fig. 1). Of the other taxa present, the brown macroalga *Dictyota* sp. was prevalent around Halfway Island, as were tabular *Acropora* corals, whilst the macroalga *Asparagopsis* sp. (P: Rhodophyta) and *Caulerpa* sp. (P: Chlorophyta) were abundant at Olive Point.

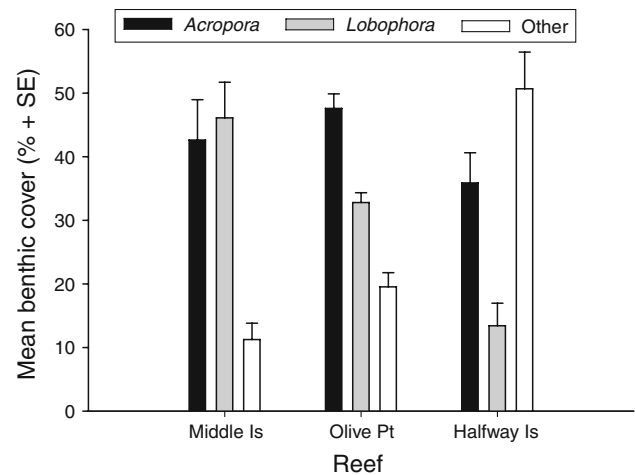


Fig. 1 Mean proportional benthic cover of branching *Acropora* (black), *Lobophora variegata* (grey) and the combined mean cover of all other substratum types (open) (\pm SE) on the crest of southern inshore fringing reefs ($n = 8$ transects per location)

Lobophora was unevenly distributed between habitat types on the reef crest in the Keppel Islands (Fig. 2a). Live and dead branching corals supported 333 ± 30 g and 381 ± 55 g 0.25 m² (mean \pm SE) fresh weight of *Lobophora* per quadrat, respectively. This was significantly greater than planar habitats that averaged just 17 ± 6 g 0.25 m² of *Lobophora* per quadrat (Table 1). No effect of location was detected between the three reefs, nor was an interaction between location and habitat type detected (Table 1).

The decrease in biomass of *L. variegata* in both planar habitat treatments (herbivore exposed and herbivore protected) was significantly greater than that recorded from all branching habitats over the 48-h sampling period (Table 2). Biomass of *L. variegata* in planar habitat treatments declined by $7.0 \pm 3.0\%$ (mean \pm SE) compared with $2.2 \pm 1.3\%$ in live branching coral and $1.9 \pm 4.0\%$ in dead branching coral habitat. Assays of *Lobophora* exposed to herbivore feeding did not exhibit significantly greater decreases in biomass than control (herbivore protected) assays in live branching, dead branching or planar habitats (Fig. 2). No significant interaction between habitat type and treatment type was recorded (Table 2).

Feeding rates by herbivorous fishes on *Lobophora* were significantly greater in the planar habitat than the branching habitat (ANOVA, $F_{(1,10)} = 5.026$, $P = 0.048$) with 20 times more bites occurring in the planar than the branching habitat. Despite this, bite rates on *Lobophora* were relatively low in both habitat types (Fig. 3a). Within planar habitats, a total of just 43 bites were recorded on *Lobophora* assays, primarily from *Siganus doliatus* (24 bites) and *Kyphosus vaigiensis* (10 bites). The branching habitat recorded just two bites on *Lobophora* over the 27 h of video footage.

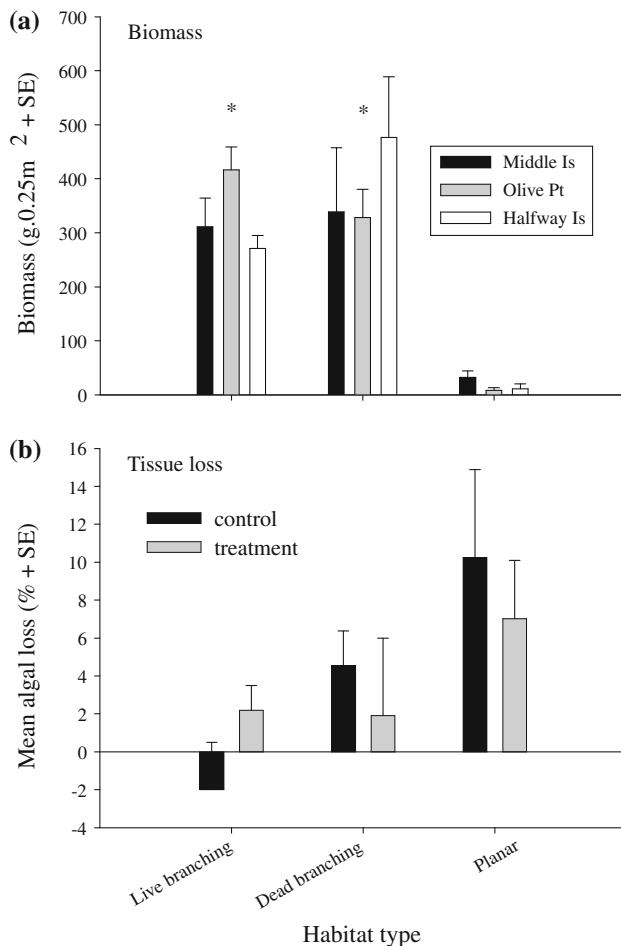


Fig. 2 Comparison between live branching, dead branching and planar habitat surfaces in the **a** mean standing biomass of *Lobophora variegata* (g 0.25 m⁻² ± SE) across the three surveyed reefs and **b** mean proportional decrease in *Lobophora* following 48-h exposure period ± SE. Black columns represent assays from which herbivores were excluded, grey columns represent assays exposed to herbivores. Asterisks (*) denotes significantly higher biomass and removal rates ($P < 0.05$) than columns without. Columns with asterisks do not differ significantly from each other ($P > 0.05$)

Table 1 Full factorial ANOVA testing the effect of habitat type (fixed factor: live branching, dead branching and flat) and location (random factor) on the biomass of *Lobophora variegata*

	SS	df	MS	F	P
Location	3,670	2	1,835	0.102	0.905
Habitat type	703,509	2	351,755	19.517	0.009
Location*habitat type	72,093	4	18,023	1.546	0.231
Error	209,834	18	11,657		

Data were square-root transformed to adequately satisfy the assumptions of homogeneity of variance and normality. Asterisks (*) denotes significance ($P < 0.05$)

Feeding rates on EAM also revealed a stark differentiation between branching and planar habitat types (Fig 3b). In the planar habitats, 261 ± 126 bites 4.5 h⁻¹ (mean ± SE)

Table 2 Full factorial ANOVA assessing of effect of habitat type (live branching dead branching and flat) and treatment (herbivore access and herbivore exclusion) on *Lobophora variegata* removal rates (%)

Source of variation	SS	df	MS	F	P
Habitat type	0.019	2	0.010	3.226	0.047*
Treatment	0.001	1	0.0012	0.399	0.530
Habitat type*treatment	0.002	2	0.0012	0.413	0.664
Error	0.163	54	0.0030		

Removal rates were square-root and arcsine transformed to adequately satisfy assumptions of homogeneity of variance and normality and for the use of proportional data. Asterisks (*) denotes significance ($P < 0.05$)

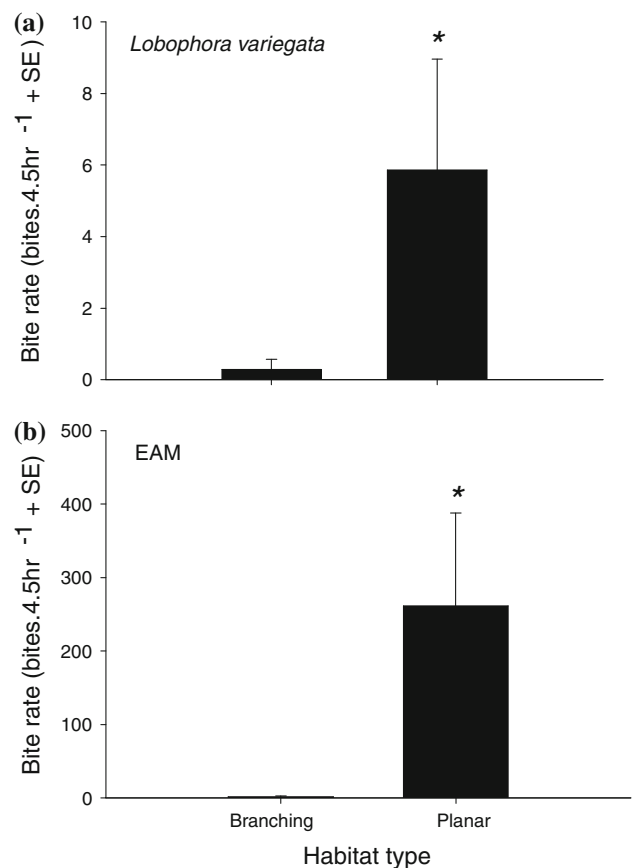


Fig. 3 Comparison of mean herbivore feeding rates between branching and planar habitat surfaces on **a** *Lobophora variegata* and **b** Epilithic Algal Matrix per 4.5-h period. Note the different y-axis scale. Asterisks (*) denote significant difference in feeding rates between habitat types ($P < 0.05$)

were taken (totalling 1,830 bites over a 27-h period). This level of herbivore feeding was significantly greater than that observed in branching habitats, where the video recorded an average of just 1.7 ± 1.1 bites 4.5 h⁻¹ (ANOVA, $F_{(1,10)} = 22.637$, $P = 0.001$). This was over an order of magnitude more bites than recorded on *Lobophora* in this habitat. Of the species feeding on EAM, *S. doliatus* took the greatest

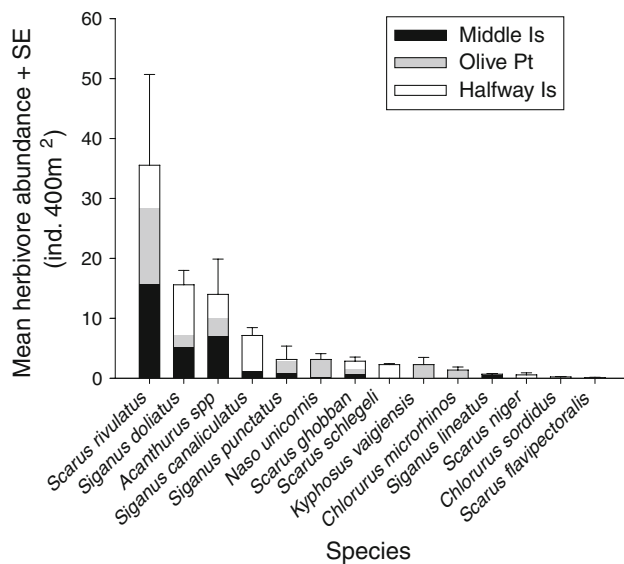


Fig. 4 Cumulative mean herbivore abundance in the three reefs examined (density per 400 m² in each bay, $n = 12$; error terms summed over three reefs)

number of bites, recording 1,348 on the planar habitat, whilst no bites were recorded within the branching habitat. *Scarus rivulatus* and *Acanthurus* spp. also recorded high numbers of bites (330 and 137, respectively), on the planar habitat over the 27-h period. *S. rivulatus* recorded only a single bite in the branching habitat, whilst *Acanthurus* spp. did not record any bites.

A total of 14 species of roving herbivores from the families Acanthuridae, Kyphosidae, Labridae and Siganiidae were recorded on UVC's, within Middle Island, Olive Point and Halfway Island (Fig. 4). *S. rivulatus* was the most abundant roving herbivore, accounting for 40.5% of the total number of individuals recorded, whilst *S. doliatus* and *Acanthurus* spp. accounted for 17.8 and 14.6% of total individuals, respectively. The macroalgal grazers *Naso unicornis* and *K. vaigiensis* accounted for 11.0 and 10.6% of Olive Point herbivore abundance, respectively.

Discussion

On the marginal coral reef system of the Keppel Island Group on the southern inner shelf of the GBR, feeding rates by herbivorous fishes were significantly higher in planar than branching habitats for both *Lobophora* and the EAM. Despite this, bite rates on *Lobophora* were relatively low, with both habitats displaying less than 10% consumption of *Lobophora* assays. In contrast, herbivorous fish feeding rates on EAM were much higher with feeding rates on planar habitats being two orders of magnitude higher than in areas of branching corals. The overall low rates of *Lobophora* removal and low rates of herbivory in

branching habitats were consistent with the high biomass of this brown alga throughout all three study sites in the Keppel Islands and with its distribution on reef crests, where *Lobophora* biomass was 20 times greater in branching than in planar habitats. Given that branching *Acropora* and *Lobophora* jointly comprise between 50 and 95% of the reef crest benthos in the surveyed reefs, it is probable that the coral-mediated suppression of herbivory is widespread, thus markedly changing the nature of ecosystem function in crest habitats on surveyed Keppel Island reefs.

Unlike the case of reefs impacted by over-fishing (Hughes 1994; Mumby et al. 2006) or cold water marine systems (Harmelin-Vivien 2002; Floeter et al. 2005), the reduced impact of herbivores in the Keppel Islands on the southern GBR was observed despite relatively intact herbivore populations. Herbivore composition and density in the current study was comparable to reports from reefs surrounding Orpheus Island (Cvitanovic and Bellwood 2009), which are considered to be typical of the herbivore communities on the inshore GBR (Bellwood et al. 2006). The findings of the current study, therefore, provide an indication of the potential role of some corals in limiting the key role played by herbivores in controlling macroalgae on coral reefs, a coral-mediated limitation that may apply to reefs elsewhere on the GBR and around the world.

The dominance of branching *Acropora* and *Lobophora* on southern inshore reefs reported in the current study is broadly consistent with the findings of Diaz-Pulido et al. (2009). Although the mean abundance of *Lobophora* recorded on the reef crest in the current study (13–60%) is higher than the reported values from the reef slope in Diaz-Pulido et al. (2009) (approximately 10–30% in February 2008 on Halfway Island and Middle Island), this is probably a consequence of the difference in reef zone and season. The interaction between *Lobophora* and branching coral has been demonstrated previously on an inshore reef of the central GBR (Jompa and McCook 2002), showing that whilst *Lobophora* was the slight competitive superior to *Porites cylindrica*, it was only following the exclusion of herbivores that *Lobophora* proliferated. In the current study, the suppression of herbivory in structurally complex branching habitats appears to be a mechanism contributing to the high density of *Lobophora*. However, the low rates of consumption of *Lobophora* also appear to be a significant factor that may underpin the proliferation of *Lobophora* in a range of habitats in the Keppel Islands.

The low removal rates of *Lobophora* by herbivores reported in the current study supports the findings of studies conducted in aquaria and parts of the Caribbean (Hay 1981b; Paul and Hay 1986; Pillans et al. 2004; Weidner et al. 2004), but conflicts with reports of relatively high *Lobophora* removal rates in other parts of the

Caribbean and Western Australia (Hay 1984; Vansteveninck and Breeman 1987a, b; Coen and Tanner 1989; Steinberg and Paul 1990). Of the studies that have reported high removal rates of *Lobophora*, the herbivores driving the patterns have often been *Diadema* urchins (Vansteveninck and Breeman 1987a, b), which only occur in very low densities on reef crests in the Keppel Island group (S. Bennett, pers. obs.). Other studies, which have reported high rates of fish herbivory, have not reported the apparent ‘removal’ rates of control assays with herbivore exclusion (Hay 1984; Steinberg and Paul 1990), which as demonstrated by the current study, can be relatively high. Losses due to handling, deployment and wave action may, therefore, partially explain the high removal rates observed previously. By using RUV’s, the current study was able to provide independent evidence of low removal rates, based on the very low feeding rates by herbivores. Feeding rates on *Lobophora* in the planar habitat were two orders of magnitude lower than feeding rates on EAM and between 2 and 3 orders of magnitude lower than previously reported feeding rates on the brown macroalgae *Sargassum* sp., from inshore reefs of the central GBR (Cvitanovic and Bellwood 2009).

The low feeding rates on *Lobophora* in the current study may be partly explained by the defence mechanisms adopted by plant species in protection against herbivory. Two common plant defence mechanisms are escape and deterrence (Hay and Fenical 1988). For *Lobophora*, it is possible that these two mechanisms contribute to the low removal rates. Spatial and temporal escape of herbivores has been reported as one of the key driving forces of algal zonation across reefs (Lubchenco and Gaines 1981). On fringing coral reefs, escape from herbivory is often discussed in terms of cross reef zonation patterns (Hay 1981a; Hay et al. 1983; Lewis and Wainwright 1985), whereby macroalgae is most prevalent on the inner reef flat where grazing intensity is low (Hay et al. 1983; McCook 1997; Fox and Bellwood 2007) and environmental stress often restricts coral cover. Escape from herbivory in the southern inshore reefs, however, also appears to be operating over smaller spatial scales. The high biomass of *Lobophora* and low herbivore feeding rates in branching environments suggests that *Lobophora* is provided with an ‘escape’ from herbivores within the branching coral framework, facilitating the persistence of *Lobophora* within the reef crest, the zone of highest herbivory on inshore reefs in the central GBR (Fox and Bellwood 2007). This contrasts with the low *Lobophora* biomass recorded in the planar habitat and high feeding rates, particularly on EAM, which suggests that herbivores may be preventing the successful recruitment and growth of *Lobophora* in this habitat.

The second mode of defence that may have contributed to the low feeding rates on *Lobophora* is deterrence. The

deterrence of herbivores by plants is achieved primarily through the use of secondary metabolic compounds, structural features (e.g., size, shape, tough or calcareous foliage) and other nutritional constraints of the plant (Herms and Mattson 1992). In laboratory studies, grazer-induced chemical defences have been recognised in *Lobophora* (Weidner et al. 2004), and *Lobophora* has been shown to rank low in preference, from feeding choice experiments in aquaria (Pillans et al. 2004). In other studies, however, polyphenolic and other non-polar compounds, which are effective deterrents to temperate water herbivores and in closely related species to *Lobophora*, were found to be ineffective in deterring tropical herbivores from *Lobophora* (Steinberg and Paul 1990).

An important additional mechanism of protection against herbivores may be provided by a ‘resource saturation’ effect similar to the predator-saturation hypothesis that is suggested to partly explain masting events in plants (Janzen 1974, 1976). The high densities of *Lobophora* on southern reefs precipitated by mass coral bleaching events may mean that populations of *Lobophora* are ‘saturating’ the herbivore community. The dominance of branching coral habitat within these systems may provide an additional positive feedback on *Lobophora* populations, by providing a refuge and enabling proliferation even in the presence of herbivores. Saturation of herbivores may provide an alternate explanation as to why feeding was recorded on *Lobophora*, but only at low rates. Therefore, longer sampling periods of weeks or months may be necessary to observe significant removal rates of assays. The three herbivore defences described herein (escape, deterrence and resource saturation) are not mutually exclusive, and there is evidence to suggest that they may all contribute to the low feeding rates on *Lobophora* on southern inshore reefs.

It is not clear why branching *Acropora* are herbivore deterrents, as topographic complexity is widely regarded as a feature, which facilitates herbivore activity (e.g., Randall 1961; Graham et al. 2006; Fox and Bellwood 2007). However, it appears that it is the spatial scale of complexity which is critical. At a scale of tens of metres, a topographically complex reef may provide cover from predation and increase herbivory in the general area. However, at a scale of tens of centimetres (e.g., between *Acropora* branches), high topographic complexity may limit the manoeuvrability of fish to feed and provides shelter for algae. The high cover of branching *Acropora* and *Lobophora* in the Keppel Islands suggests that these small-scale interactions may influence larger scale patterns in topographic complexity and benthic structure across the reef ecosystem.

Acropora stands may also be good algal substrata for reasons other than protection from herbivory. Removal

rates of *Lobophora* showed an unexpected pattern with both control and herbivore treatments in the planar habitat losing significantly more mass than assays in the branching habitat, indicating that there is a potential for dislodgement of algae independent of herbivory. Flow rates within branching colonies have been shown to be lower than ambient flow outside of colonies (Helmuth et al. 1997) and, therefore, flow rates may be influential in the distribution of *Lobophora*. Greater sediment build-up and the lower surface area of planar compared with branching habitats could also partly explain the observed distribution patterns of *Lobophora*. The decumbent growth form of *Lobophora*, characteristic of the reef crest, grows flat forming a mat on the substratum (Coen and Tanner 1989). The three-dimensional framework of branching corals provides a greater surface area and reduced sediment build-up than the two-dimensional flat surfaces, upon which sediment could smother decumbent *Lobophora*. The synergy of such processes may well assist in the maintenance of *Lobophora* on southern reefs. Of these factors, evidence from the current study suggest that both the structure of branching habitat and low rates of herbivory are important in shaping the current ecosystem state of these reefs.

It is important to recognise that the state of the southern inshore reefs documented in the current study is dynamic. Monospecific stands of branching *Acropora* in the Keppel Islands have been dominant on the reef crest for at least 20 years (Van Woessik et al. 1995) up until the 2006 bleaching event, which precipitated the dramatic outbreak of *Lobophora*. Following the 2006 bleaching event, vegetative growth of branching *Acropora* has been rapid, resulting in the reduced proportional cover of *Lobophora* (Diaz-Pulido et al. 2009), leading to the current state of the system. Interestingly, herbivores are likely to have been passengers (*sensu* Walker 1992) responding to, not driving this change. As such, they are probably unable to control the increase in algal biomass on reef crests throughout these benthic dynamics. This stands in marked contrast to the understood role of herbivores throughout the rest of the GBR and presents interesting questions about the resilience and future trajectory of marginal systems such as the Keppel Islands.

Previously, a functional herbivore population has been regarded as a requisite for a resilient coral reef system (Bellwood et al. 2004; Mumby 2006), whilst more recently Diaz-Pulido et al. (2009) have identified the Keppel Is reefs as “highly resilient” due to the rapid vegetative recovery of branching *Acropora*. Both aspects of resilience appear to be important in the Keppels, yet both are spatially limited. The current findings suggest that herbivore-based resilience is primarily operational in non-branching habitats and plays a very limited role in branching *Acropora*. Conversely, the findings from Diaz-Pulido et al. (2009) indicate that the rapid vegetative growth of *Acropora* provides

resilience to remnant areas of branching *Acropora* yet not to areas beyond branching habitat or in the event of mass mortality of the branching *Acropora* colonies. The resilience of these marginal systems, therefore, appears to be spatially limited and vulnerable to large-scale disturbance events.

In the marginal coral reef ecosystems observed in this study, the critical role of herbivory appears to be constrained, at least in part, by small-scale topographic complexity. The low rates herbivory within branching *Acropora* compared with planar surfaces, illustrates a mechanism that may contribute to the proliferation of fleshy macroalgae on coral reefs without necessarily losing important herbivore species. Presence/absence of species, or even their abundance, therefore may not necessarily be the best measures of reef resilience. Instead, an understanding of the role of processes within the context of the local system may be required to assess the resilience of coral reef systems.

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