

LETTER

Suppression of herbivory by macroalgal density: a critical feedback on coral reefs?

Andrew S. Hoey* and

David R. Bellwood

Australian Research Council Centre of Excellence for Coral Reef Studies and School of Marine and Tropical Biology, James Cook University, Townsville, Qld 4811, Australia

*Correspondence: E-mail:

andrew.hoey@my.jcu.edu.au

Abstract

Coral reefs globally are in decline, with some reefs undergoing phase shifts from coral-dominance to degraded states dominated by large fleshy macroalgae. These shifts have been underpinned by the overharvesting of herbivorous fishes and represent a fundamental change in the physical structure of these reefs. Although the physical structure provided by corals is regarded as a key feature that facilitates herbivore activity, the influence of the physical structure of macroalgal stands is largely unknown. Using transplanted *Sargassum*, the largest coral reef macroalga, we created habitat patches of predetermined macroalgal density (0.25–6.23 kg m⁻²). Remote video cameras revealed both grazing and browsing fishes avoided high density patches, preferring relatively open areas with low macroalgal cover. This behaviour may provide a positive feedback leading to the growth and persistence of macroalgal stands; increasing the stability of phase shifts to macroalgae.

Keywords

Coral reef, feedback, herbivory, macroalgae, phase shift, resilience, *Sargassum*, structural complexity.

Ecology Letters (2011) 14: 267–273

INTRODUCTION

Habitat structure is a fundamental property of all ecological systems (Bell *et al.* 1991). Structurally complex habitats generally support a greater number of species and individuals than less complex habitats (MacArthur & MacArthur 1961; Huston 1979) as predation intensity and competitive interactions are moderated through the provision of a greater number and diversity of microhabitats and refuges (Holbrook & Schmitt 1988; Hixon & Menge 1991). Foraging decisions by consumers may, therefore, be mediated by structural complexity with a trade-off between minimizing the risk of predation and maximizing forage intake. Consumers are likely to favour structurally complex habitats if they provide a spatial refuge from predators (Crowder & Cooper 1982; Kotler *et al.* 1991), or their preferred food resources are facilitated by the physical structure itself (Schmitt & Holbrook 1990). Alternatively, consumers may avoid complex habitats if their ability to detect predators is reduced (Underwood 1982; Riginos & Grace 2008) or the physical structure obstructs their movements, limiting access to preferred food resources (van de Koppel *et al.* 1996). Understanding the potential effects of habitat structure on consumer feeding preferences is becoming increasingly important as anthropogenic and climate-induced stressors are significantly changing the physical and ecological structure of many ecosystems.

Within coral reef systems the importance of hard corals in providing structural complexity, and consequently shaping fish communities, has been well established (Friedlander & Parish 1998). While there is some debate regarding the relative importance of live coral or structural complexity *per se*, marked reductions in coral cover over the past three decades (Gardner *et al.* 2003; Bruno & Selig 2007) have had significant negative effects on the structure and function of reef fish communities (Graham *et al.* 2006; Paddack *et al.* 2009). Reductions in coral cover are, however, typically accompanied by increases in other benthic taxa, in particular algal turfs (filamentous algae and macroalgal propagules), that rapidly colonize the available substrata (Norström *et al.* 2009). Reefs with intact herbivore communities appear to be able to

compensate for this increased algal abundance, maintaining the algal communities in a cropped state (Arthur *et al.* 2006). The removal of herbivorous fishes through overharvesting, however, has limited the capacity of many reefs to absorb the increased algal production; releasing macroalgal propagules from top-down control and ultimately resulting in shifts to a new state dominated by fleshy brown macroalgae (Hughes 1994; Graham *et al.* 2006).

Such phase shifts to macroalgal dominance represent a fundamental change in the physical structure and functioning of these reefs and, as in other ecosystems, these new states may be reinforced or locked in place by positive feedback mechanisms (Scheffer *et al.* 2001; Mumby & Steneck 2008). Although fleshy macroalgae are not the drivers of such shifts, the proliferation of macroalgal biomass increases the frequency and duration of coral–macroalgal interactions, and has been demonstrated to suppress the survival, growth, fecundity and settlement of corals (Jompa & McCook 2002; Hughes *et al.* 2007). This may, in turn, lead to further reductions in coral cover, providing additional substrata for macroalgal colonization. In addition to these coral–macroalgal interactions, the susceptibility of fleshy macroalgae to herbivores changes as the macroalgae grow. Macroalgal propagules may be easily eliminated by a diverse assemblage of grazing herbivores that feed primarily on algal turfs, however, as the macroalgae grow to maturity they become less susceptible to the same suite of herbivores. The removal of larger, mature fleshy brown macroalgae (e.g. *Sargassum*) appears to be restricted to a small suite of species, the macroalgal browsers (Bellwood *et al.* 2006; Hoey & Bellwood 2009). This functional dichotomy is important and highlights the distinction between those species that are capable of preventing (i.e. grazers) and those that are potentially capable of reversing (i.e. browsers) phase shifts to macroalgal dominance (Bellwood *et al.* 2006). Despite their importance in ecosystem dynamics, our current understanding of potential regulatory mechanisms and feedbacks is limited (Scheffer *et al.* 2009). There is a pressing need to identify and understand the role of feedbacks in fish–macroalgal interactions on coral reefs.

Numerous studies have demonstrated the importance of herbivorous fishes in preventing the development of macroalgal stands on coral reefs (e.g. McCook 1996; Mumby 2006; Hughes *et al.* 2007), however, the potential feedback mechanisms through which macroalgae may influence the foraging behaviour of herbivores are poorly understood, especially in terms of the spatial extent of algal growth. Here, we examine the influence of the physical structure of macroalgal stands on the feeding behaviour of herbivorous coral reef fishes. We use transplanted *Sargassum* (Phaeophyceae), a large canopy-forming macroalga, to experimentally manipulate macroalgal density, and remote underwater video cameras to record the feeding activities of both grazing and browsing fishes. Comparing grazing and browsing rates among habitat patches we demonstrate the effect of macroalgal-mediated habitat structure on those species that appear to prevent and reverse phase shifts, respectively.

METHODS

This study was conducted during April 2008 in Pioneer Bay, Orpheus Island (18°37' S, 146°30' E); an inshore island in the central region of the Great Barrier Reef. To examine the effect of macroalgal density on herbivory, *Sargassum* was transplanted at four predetermined densities (0.25–6.23 kg m⁻²) to two sites on the reef crest; the area of greatest herbivore activity (Hay 1981; Hoey & Bellwood 2008). *Sargassum* was selected as it is the largest coral reef macroalga, and was the dominant taxon following phase shifts to macroalgal dominance on east African reefs (Graham *et al.* 2006), and an experimentally induced phase shift at this location (Hughes *et al.* 2007). Consequently, *Sargassum* is often viewed as a sign of reef degradation. Individual *Sargassum* thalli of similar height (c. 110 cm) were removed by cutting the holdfast as close to the point of attachment as possible. All thalli were placed in raceways with flow-through seawater within 1 h of collection, and were transplanted to the reef within 24 h. A detailed description of the study site and species can be found in Appendix S1(a) in Supporting Information.

Each thallus was spun in a salad spinner to remove excess water, weighed (mean = 561.7 g), and randomly allocated to one of four density treatments: high (25 thalli; c. 6.23 kg m⁻²), medium (13 thalli; c. 3.25 kg m⁻²), and low density (5 thalli; c. 1.25 kg m⁻²), and a single thallus (c. 0.25 kg m⁻²; Fig. 1). All thalli were transplanted to horizontal surfaces covered with algal turfs (1.5 × 1.5 m) shortly after dawn and collected after 8 h. This period encompassed the majority of the herbivore feeding day, with very little activity being recorded at night (Figure S1). An additional thallus was placed inside an exclusion cage to control for the effects of handling. After 8 h, all thalli were collected, spun and weighed, and returned to the raceways where they were held overnight. The *Sargassum* was redeployed in identical configuration the following morning, and continued until < 25% of the *Sargassum* biomass remained (i.e. 4 days). The entire process was replicated three times within each site, with different 1.5 × 1.5 m plots being used for each deployment.

Underwater video cameras were used to record feeding activity on both the transplanted *Sargassum* (i.e. browsing) and the algal-turf covered substratum (i.e. grazing) within each experimental plot. Video recording was continuous for the 8 h experimental period. The video footage for each day was viewed, and the number of bites taken by each fish species from both the *Sargassum* and the algal-turf covered substratum recorded. The presence and size of any potential predators within the experimental plots was also recorded. Grazing taxa were

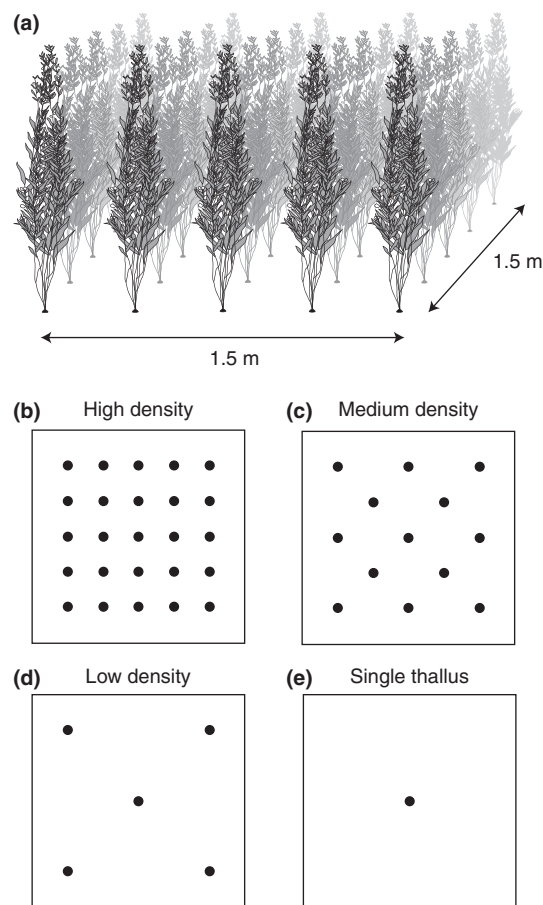


Figure 1 The spatial arrangement of *Sargassum* thalli within each of the macroalgal density treatments. (a) Schematic drawing of a high density macroalgal treatment showing the resultant habitat structure, (b–e) plan diagrams of the distribution of transplanted *Sargassum* thalli within the four macroalgal density treatments. Each experimental plot is 1.5 × 1.5 m.

classified as excavators, scrapers or croppers based on their morphology and feeding behaviour (*sensu* Bellwood *et al.* 2004). To account for body size related variation in the impact of individual bites, a mass standardized bite impact was calculated as the product of body mass (kg) and number of bites (following Hoey & Bellwood 2009). A detailed description of the methods can be found in Appendix S1(b).

Statistical analyses

To determine if the relative removal rates of *Sargassum* biomass varied among density treatments, sites and days, a repeated measure MANOVA was used. As the spatial separation of treatments within each site may have been smaller than the likely foraging ranges of herbivorous fishes, independence among treatments could not be assumed. Feeding in one treatment may have been dependent on the presence of other treatments. Therefore, a MANOVA was used to account for these dependencies among density treatments (Pfister & Hay 1988; Roa 1992). There was no significant spatial variation in removal rates among thalli within each of the density treatments (Table S1; Figure S2). Consequently, the analysis was based on the proportion of the initial *Sargassum* biomass (pooled across thalli and $\sqrt{}$ transformed

to improve normality and homoscedasticity) that remained after each consecutive day.

Variation in feeding by browsing fishes among density treatments, sites and days was analysed using two repeated measures MANOVAS. MANOVAS were used to account for the lack of independence among treatment responses (Roa 1992). The analyses were based on the total mass standardized bites ($\sqrt[4]{}$ transformed to improve multivariate normality and homoscedasticity) taken from the *Sargassum* assays within each experimental plot by the two dominant browsing species (accounting for > 97% bites), with a separate analysis performed for each species. The influence of macroalgal density on grazing intensity and the biomass of potential predators was examined using regressions. The regressions were based on daily estimates of each variable within each of the experimental plots.

RESULTS

The total biomass of *Sargassum* removed was relatively constant among days with an average of $10.37 \text{ kg day}^{-1}$ ($\pm 0.76 \text{ SE}$) being removed from the two sites combined. The relative removal rates of *Sargassum* biomass were, however, influenced by density treatment ($F_{3,2} = 36.22$, $P = 0.03$) and day within each deployment ($F_{1,4} = 113.09$, $P < 0.001$; Table S2). The single thallus and low density treatments displayed similar trajectories over the 4-day period with the majority of the *Sargassum* biomass being removed within the first 2 days of each deployment (75.2–86.4%; Fig. 2). In contrast, the medium and high density treatments displayed relatively low but constant reductions in biomass over the 4-day period (Fig. 2), with removal rates of 10.0–25.2% day^{-1} .

Video footage revealed that browsing activity was dominated by two species, the kyphosid *Kyphosus vaigiensis* (Quoy & Gaimard) and the acanthurid *Naso unicornis* (Forsskal) (Fig. 3). In total, 70 685 bites from 30 fish species were recorded on the transplanted *Sargassum* across all treatments, with *K. vaigiensis* and *N. unicornis* accounting for 89.1 and 7.6% of the total mass standardized bites, respectively. The only other species to take a substantial number of bites from the *Sargassum* was the siganid *Siganus doliatus* Cuvier, accounting for 1.9% of the standardized bites. Each of the remaining 27 species accounted for < 0.4% of the standardized bites.

Both *K. vaigiensis* and *N. unicornis* fed more intensively on the *Sargassum* within the lower density patches, as opposed to the higher density patches, on the first day of each deployment (Fig. 3). *Kyphosus*

vaigiensis favoured the low macroalgal density patches, whereas *N. unicornis* favoured the single *Sargassum* thallus treatment. On subsequent days feeding by these two browsers shifted (*K. vaigiensis*: $F_{3,2} = 33.93$, $P = 0.028$; *N. unicornis*: $F_{3,2} = 20.60$, $P = 0.046$; Table S3) as the *Sargassum* biomass was depleted from the single thallus and low density patches (Fig. 2). Feeding by *K. vaigiensis* decreased within the single thallus and low density patches, and increased markedly within medium and high macroalgal density patches (Fig. 3). Similarly, feeding by *N. unicornis* decreased on the single thallus, and increased within the low and medium macroalgal density patches (Fig. 3). This temporal variation in feeding by both species led to significant negative relationships between *Sargassum*

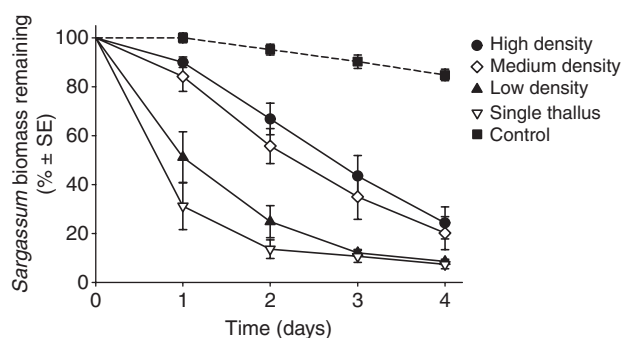


Figure 2 Variation in the removal rates of *Sargassum* among four density treatments on the reef crest of Orpheus Island. The mass remaining was calculated as the proportion of the initial, or transplanted, biomass that remained after each consecutive day (summed across all thalli).

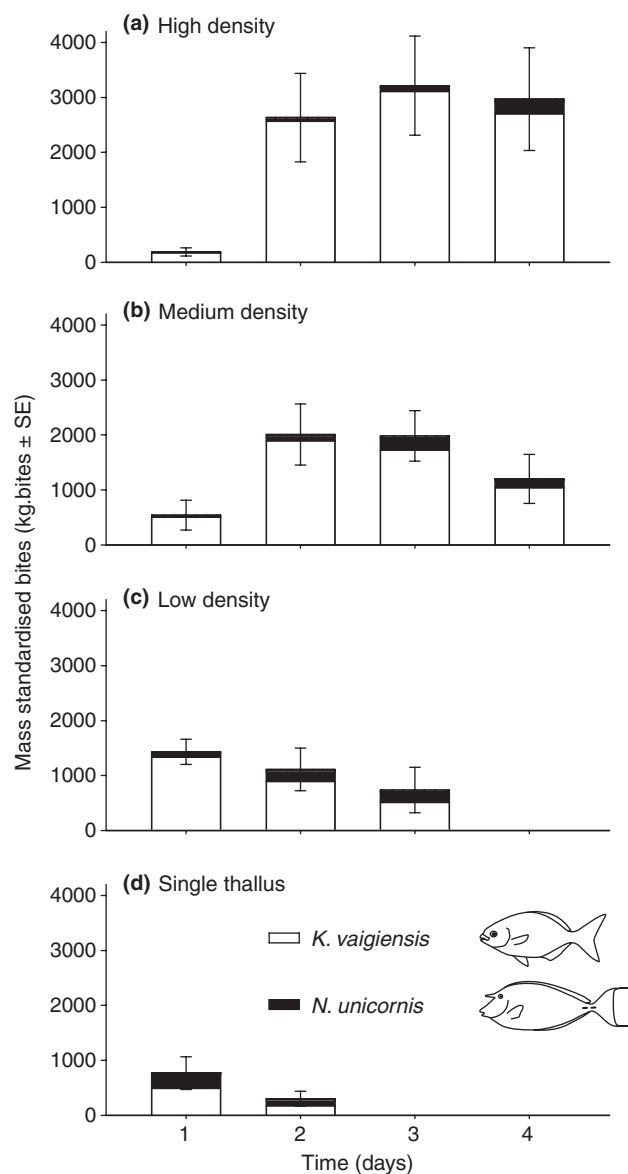


Figure 3 Influence of *Sargassum* density on the browsing intensity by herbivorous fishes. Temporal variation in the total mass standardized bites taken from *Sargassum* within each of the four density treatments (a–d). The relative contributions of the two dominant species are shown. The remaining 28 species included in the figure are not distinguishable as collectively they accounted for < 2.3% of all bites. The single thallus (d) and low density (c) treatments were only filmed for the first 2 and 3 days of each deployment, respectively.

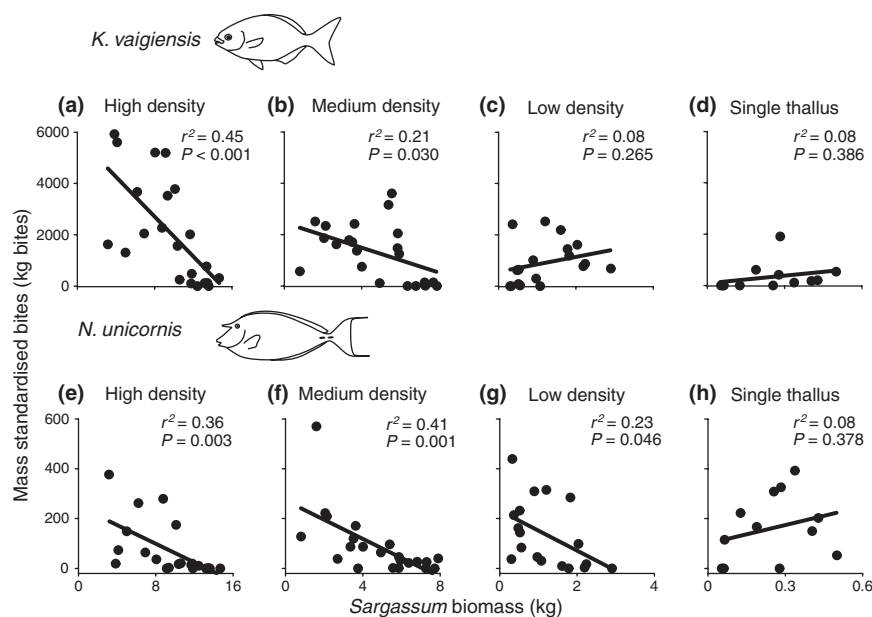


Figure 4 Relationship between *Sargassum* density and browsing intensity by *Kypbosus vaigiensis* (a–d) and *Naso unicornis* (e–h) within each of the density treatments. The best-fit relationships (linear) are given as solid lines, along with r^2 and P values.

biomass and browsing rates within the high and medium density patches (Fig. 4). There was no significant effect of site on the feeding of these two species, either independently or through interactions with density treatment and day (Table S3).

Over 15 000 bites from 28 species were recorded from the substratum within the habitat patches. Scraping and excavating parrotfishes (primarily *Scarus rivulatus* Valenciennes and *Chlorurus microrhinos* Bleeker, respectively) were the dominant grazers, accounting for 52.2 and 37.8% of the total mass standardized bites, respectively. Grazing intensity within the habitat patches, as proxied by the mass standardized bites taken from the substratum, displayed a significant negative relationship with *Sargassum* biomass. This pattern was observed every day and for each grazing functional group independently (Figure S3). Overall, there was an exponential decline in grazing intensity with increasing *Sargassum* biomass, for all grazers collectively and the three grazing functional groups independently (Fig. 5).

In marked contrast to all herbivores, the biomass of potential predators displayed a significant, but generally weak, positive relationship with *Sargassum* biomass within the habitat patches over the first 3 days of each deployment (Figure S4). The predator community was dominated by relatively small (< 30 cm total length) generalist carnivores, with few larger piscivorous species being recorded (Table S4). Consistent with a hypothesis that predation risk affected grazing intensity, grazing intensity was negatively related to predator biomass across all days ($r^2 = 0.202$, $F_{1,72} = 18.26$, $P < 0.001$). Browsing intensity was also negatively related to predator biomass for the first day of each deployment ($r^2 = 0.387$, $F_{1,22} = 13.92$, $P = 0.001$), but displayed no relationship across all days ($r^2 = 0.015$, $F_{1,72} = 1.10$, $P = 0.299$).

DISCUSSION

Habitat choice is a key determinant of an organisms fitness, with individuals selecting habitats that maximize their energy intake while

minimizing their risk of predation (Houston *et al.* 1993; Brown & Kotler 2004). Within coral reef systems, habitat structure has a major influence on fish communities with increased structural complexity moderating predation intensity and competitive interactions (Holbrook & Schmitt 2002; Wilson *et al.* 2008) and facilitating key ecological processes, such as herbivory (Randall 1965; Graham *et al.* 2006). The vast majority of these studies have focused on the role of corals, or artificial surrogates, in providing physical structure and have reported positive relationships between coral cover and fish faunas. Our results stand in marked contrast, with a strong negative relationship between herbivore activity and the structure provided by macroalgal stands. Herbivorous coral reef fishes at our study sites preferred relatively open habitat patches with lower structural complexity (i.e. lower cover and biomass of macroalgae), as opposed to areas of high macroalgal cover. Given the importance of herbivorous fishes in structuring benthic communities, these preferences may have positive feedbacks on the growth and stability of macroalgal stands. If these observations on Orpheus Island are applicable at larger scales, this type of feedback may be important in reinforcing phase shifts to fleshy macroalgal dominance on coral reefs around the world.

Habitat associations are often related to differences in the quantity or quality of food resources among habitat patches (McNaughton 1988; Bakker *et al.* 2005), however, such bottom-up forcing appears not to be operating within the Pioneer Bay system. The experimental framework in this study ensured food availability to grazers was broadly comparable among macroalgal density treatments. The availability of macroalgae to browsers was directly related to the biomass of *Sargassum*, yet the two dominant browsing species displayed a preference for the single thallus and/or low macroalgal density patches; only switching to the higher density patches after the *Sargassum* biomass within the lower density patches had been depleted. Taylor & Shiel (2010) reported similar reductions in fish browsing under the canopy of kelps in New Zealand.

Alternatively, herbivore habitat preferences may be determined by top-down effects if the availability of refuges or the ability to detect

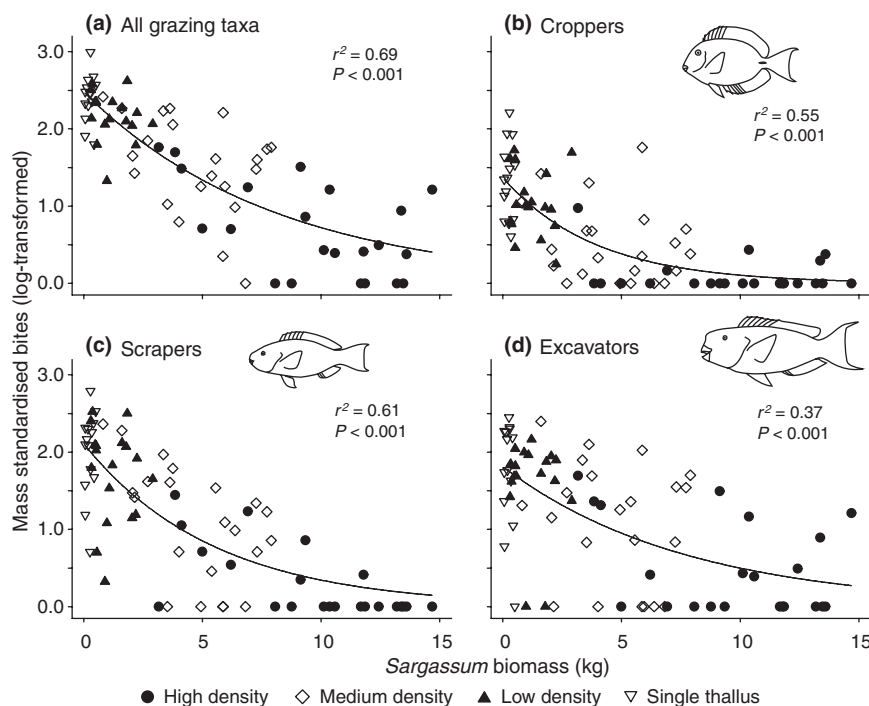


Figure 5 Influence of *Sargassum* biomass on the grazing intensity of herbivorous fishes. The relationship between the total number of mass standardised bites taken from the substratum and the biomass of *Sargassum* within each of the experimental plots for (a) all species combined, (b–d) three herbivore functional groups independently. The best-fit relationships (log-linear) are given as solid lines, along with r^2 and P values.

and escape from predators are functions of habitat structure. In marine systems, physical complexity is generally regarded as a feature that reduces predation intensity. Increased complexity associated with corals in tropical systems, and macroalgae or kelps in temperate systems, have been demonstrated to reduce the mortality of fishes, presumably through the provision of spatial refuges from predators (Anderson 2001; Holbrook & Schmitt 2002). In terrestrial systems, however, the physical structure provided by woody vegetation has been shown to have both positive and negative effects on predation risk. Prey have been shown to favour open habitats when the ability to detect predators and initiate an escape response is perceived to be more important than concealment (Riginos & Grace 2008). Conversely, bush habitats are favoured by prey when concealment is perceived to be important (Kotler *et al.* 1991). The physical structure provided by the macroalgal patches in this study differs markedly from that of other structural features (i.e. corals and woody vegetation) which impede movement and predator access as they present solid physical barriers. The flexible nature of *Sargassum*, while representing a visual barrier to predator detection, is unlikely to provide a physical barrier to the movement of predators. It may, therefore, be the functional characteristics of structural features that are most important in shaping fish behaviour.

The preference for open patches in this study suggests that the higher density macroalgal patches did not provide spatial refuges from predation, but may have been perceived as potentially hazardous environments. Although the relationship was generally weak, the higher density macroalgal patches tended to support a higher biomass of potential predators. However, the predator assemblage was dominated by generalist carnivores (i.e. mixed invertebrate and fish predators) of comparable sizes to the herbivores and consequently was unlikely to pose a direct threat to the grazing or browsing fishes.

The apparent avoidance of these patches by herbivorous fishes may have reflected a general aversion to a habitat in which predators are likely to be found, rather than the presence of predators *per se* (reviewed by Verdolin 2006). For example, the distribution of African savanna browsers has been shown to be negatively related to the long-term risk of lion predation, avoiding areas that lions frequent irrespective of their presence (Valeix *et al.* 2009).

Herbivores are widely regarded as a key group determining the benthic community structure and resilience of coral reefs (Bellwood *et al.* 2004; Mumby *et al.* 2006). Reductions in herbivorous fishes (primarily grazing species), through regional overharvesting (Hughes 1994; Graham *et al.* 2006) or experimental exclusion (Hughes *et al.* 2007), can result in an increase in macroalgal biomass following large scale coral mortality or ecosystem disruption. Our results suggest that the physical structure provided by the macroalgae may further reduce herbivore activity, forming a feedback that could facilitate the continued expansion and stability of macroalgal patches on coral reefs. Konar & Estes (2003) reported a similar feedback in a temperate marine system where the wave-induced sweeping motions of kelps exclude herbivorous sea urchins from kelp forests and boundary regions. Areas of increased macroalgal cover on coral reefs are not only likely to enhance the local supply of macroalgal propagules (Stiger & Payri 1999), but also lead to a reduction in grazing which may release these propagules from top-down control. This would allow them to reach a size at which they are no longer susceptible to grazing herbivores. Macroalgae are not the drivers of community change on coral reefs. This appears to be largely a result of decreased herbivore densities, with the change triggered by local perturbations (e.g. coral bleaching). Nevertheless, macroalgae once established may, through feedbacks, become the dominant player in an altered benthic state.

Previous studies at this location have suggested that macroalgal density has a marked influence on browsing taxa. *Siganus canaliculatus* (Park) and *K. vaigiensis* have been reported to dominate feeding on bioassays of individual *Sargassum* thalli (Fox & Bellwood 2008; Cvitanovic & Bellwood 2009) but were rarely observed feeding on dense stands of *Sargassum* ($5.3\text{--}8.1\text{ kg m}^{-2}$) from previously caged 25 m^2 areas (Bellwood *et al.* 2006). Instead the batfish, *Platax pinnatus* (Linnaeus), was largely responsible for removing *Sargassum* biomass from these areas. We found no evidence for such a marked transition. Although our results indicate there was a shift in the relative importance of *K. vaigiensis* and *N. unicornis* among the four macroalgal densities (Figure S5), both species were recorded feeding within each of the density treatments. Surprisingly, batfish were not observed to feed on the *Sargassum* in this study despite being regularly observed in the immediate vicinity of the habitat patches. This apparent lack of feeding by batfish is difficult to explain but may be related to differences in the size of the macroalgal stands, height of the macroalgal canopy or condition of the *Sargassum* among studies.

Overall, the consistency of the daily removal rates of *Sargassum* (pooled across density treatments and sites) suggest that there is a limit to the macroalgal biomass that can be consumed by the browsing community within the study location. Based on an algal removal rate of 10.37 ± 0.76 (SE) kg day^{-1} (the mean rate in this study) and a seasonally adjusted growth rate of $1.7\% \text{ day}^{-1}$ for *Sargassum* (Schaffelke & Klumpp 1998), there is a threshold of $c. 610 \pm 45$ (SE) kg standing biomass, beyond which algal production would exceed consumption leading to further biomass accumulation. Conversely, below this threshold, consumption will exceed production resulting in a reduction in macroalgal biomass and density. This threshold equates to an established stand of *Sargassum* ($c. 5.3\text{--}8.1\text{ kg m}^{-2}$; Bellwood *et al.* 2006) with a spatial extent of just $75\text{--}115\text{ m}^2$. While this simplistic model does not account for seasonal variation in growth rates of *Sargassum* or browsing intensity, it does provide an interesting insight into the potential limits of browsing fishes to regulate macroalgal biomass on these reefs.

This study was conducted within an area of the Great Barrier Reef Marine Park that has been protected from all commercial and recreational fishing for over 20 years and is likely to have intact herbivorous and predatory fish communities. The response of herbivorous fishes to variation in macroalgal density in other coral reef systems, particularly those in which predatory and/or herbivorous fish communities have been impacted through fishing, may be a key factor in understanding the future of coral reefs and the processes that regulate benthic community structure on exploited coral reefs.

Within coral reef systems, habitat complexity, particularly that provided by corals, has been widely regarded as a feature that promotes herbivore activity (Randall 1965). However, our results have shown that in an experimental situation the physical structure provided by large canopy-forming macroalgae yielded the opposite response, with all herbivorous fishes preferring relatively open areas and avoiding high macroalgal density patches. This pattern was consistent across both grazing and browsing taxa and was independent of the availability of their preferred food resources, suggesting that these fishes are responding directly to the density of the macroalgae. The difference in the response of herbivorous fishes to coral and macroalga appears to be related to the nature of the structures they create, potentially mediated through relative predation risk. Given the importance of herbivores in structuring coral reef benthic communities (Hughes *et al.* 2007), the avoidance of areas of

high macroalgal density may have a cascading effect leading to further expansion and stability of macroalgal stands on coral reefs. Such feedbacks may be particularly important as climate- and human-induced disturbances are fundamentally changing the structure and function of coral reefs around the globe.

ACKNOWLEDGEMENTS

We thank C. Goatley, J. Hoey and C. Lefèvre for field assistance, J. Hoey for assistance with video analysis, S. Connolly, N. Graham, M. McCormick and C. Syms for statistical advice, and the staff at the Orpheus Island Research Station for invaluable field support. Comments by three anonymous referees greatly improved the manuscript. Financial support was provided by the Australian Coral Reef Society, the Great Barrier Reef Marine Park Authority and the Australian Research Council.

REFERENCES

- Anderson, T.W. (2001). Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology*, 82, 245–257.
- Arthur, R., Done, T.J., Marsh, H. & Harriott, V. (2006). Local processes strongly influence post-bleaching benthic recovery in the Lakshadweep atolls. *Coral Reefs*, 25, 427–440.
- Bakker, E.S., Reiffers, R.C., Olff, H. & Gleichman, J.M. (2005). Experimental manipulation of predation risk and food quality: effect on grazing behaviour in a central-place foraging herbivore. *Oecologia*, 146, 157–167.
- Bell, S.S., McCoy, E.D. & Mushinsky, H.R. (1991). *Habitat Structure: The Physical Arrangement of Objects in Space*. Chapman Hall, London.
- Bellwood, D.R., Hughes, T.P., Folke, C. & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, 429, 827–833.
- Bellwood, D.R., Hughes, T.P. & Hoey, A.S. (2006). Sleeping functional group drives coral-reef recovery. *Curr. Biol.*, 16, 2434–2439.
- Brown, J.S. & Kotler, B.P. (2004). Hazardous duty pay and foraging cost of predation. *Ecol. Lett.*, 7, 999–1014.
- Bruno, J.F. & Selig, E.R. (2007). Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS ONE*, 2, e711.
- Crowder, L.B. & Cooper, W.E. (1982). Habitat structural complexity and the interaction between bluegills and their prey. *Ecology*, 63, 1802–1813.
- Cvitanovic, C. & Bellwood, D.R. (2009). Local variation in herbivore feeding activity on an inshore reef of the Great Barrier Reef. *Coral Reefs*, 28, 127–133.
- Fox, R.J. & Bellwood, D.R. (2008). Remote video bioassays reveal the potential feeding impact of the rabbitfish *Siganus canaliculatus* (F. Siganidae) on an inner-shelf reef of the Great Barrier Reef. *Coral Reefs*, 27, 605–615.
- Friedlander, A.M. & Parish, J.D. (1998). Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *J. Exp. Mar. Biol. Ecol.*, 224, 1–30.
- Gardner, T.A., Côté, I.M., Gill, J.A., Grant, A. & Watkinson, A.R. (2003). Long-term region-wide declines in Caribbean corals. *Science*, 301, 958–960.
- Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Bijoux, J.P. & Robinson, J. (2006). Dynamic fragility of oceanic coral reef systems. *Proc. Natl. Acad. Sci. USA*, 103, 8425–8429.
- Hay, M.E. (1981). Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. *Aquat. Bot.*, 11, 97–109.
- Hixon, M.A. & Menge, B.A. (1991). Species diversity: prey refuges modify the interactive effects of predation and competition. *Theor. Popul. Biol.*, 39, 178–200.
- Hoey, A.S. & Bellwood, D.R. (2008). Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs*, 27, 37–47.
- Hoey, A.S. & Bellwood, D.R. (2009). Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. *Ecosystems*, 12, 1316–1328.
- Holbrook, S.J. & Schmitt, R.J. (1988). The combined effects of predation risk and food reward on patch selection. *Ecology*, 69, 125–134.
- Holbrook, S.J. & Schmitt, R.J. (2002). Competition for shelter space causes density-dependent mortality in damselfishes. *Ecology*, 83, 2855–2868.

- Houston, A.I., McNamara, J.M. & Hutchinson, J.M.C. (1993). General results concerning the trade-off between energy and avoiding predation. *Philos. Trans. R. Soc. Lond. B*, 341, 375–397.
- Hughes, T.P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, 265, 1547–1551.
- Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L. *et al.* (2007). Phase-shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.*, 17, 360–365.
- Huston, M.A. (1979). A general hypothesis of species diversity. *Am. Nat.*, 113, 81–101.
- Jompa, J. & McCook, L.J. (2002). The effects of nutrients and herbivory on competition between a hard coral (*Porites cylindrica*) and a brown alga (*Lobophora variegata*). *Limnol. Oceanogr.*, 47, 527–534.
- Konar, B. & Estes, J.A. (2003). The stability of boundary regions between kelp beds and deforested areas. *Ecology*, 84, 174–185.
- van de Koppel, J., Huisman, J., van der Wal, R. & Olff, H. (1996). Patterns of herbivory along a productivity gradient: an empirical and theoretical investigation. *Ecology*, 77, 736–745.
- Kotler, B.P., Brown, J.S. & Hasson, O. (1991). Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology*, 72, 2249–2260.
- MacArthur, R.H. & MacArthur, J.W. (1961). On bird species diversity. *Ecology*, 42, 594–598.
- McCook, L.J. (1996). Effects of herbivores and water quality on *Sargassum* distribution on the central Great Barrier Reef: cross-shelf transplants. *Mar. Ecol. Prog. Ser.*, 139, 179–192.
- McNaughton, S.J. (1988). Mineral nutrition and spatial concentrations of African ungulates. *Nature*, 334, 343–345.
- Mumby, P.J. (2006). The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecol. Appl.*, 16, 747–769.
- Mumby, P.J. & Steneck, R.S. (2008). Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends Ecol. Evol.*, 23, 555–563.
- Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R. *et al.* (2006). Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*, 311, 98–101.
- Norström, A.V., Nyström, M., Lokrantz, J. & Folke, C. (2009). Alternative states on coral reefs: beyond coral macroalgal phase shifts. *Mar. Ecol. Prog. Ser.*, 376, 295–306.
- Paddack, M.J., Reynolds, J.D., Aguilar, C., Appeldoorn, R.S., Beets, J., Burkett, E.W. *et al.* (2009). Recent region-wide declines in Caribbean reef fish abundance. *Curr. Biol.*, 19, 590–595.
- Pfister, C.A. & Hay, M.E. (1988). Associational plant refuges: convergent patterns in marine and terrestrial communities result from differing mechanisms. *Oecologia*, 77, 118–129.
- Randall, J.E. (1965). Grazing effects on sea grasses by herbivorous reef fishes in the West Indies. *Ecology*, 46, 255–260.
- Riginos, C. & Grace, J.B. (2008). Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. *Ecology*, 89, 2228–2238.
- Roa, R. (1992). Design and analysis of multiple-choice feeding-preference experiments. *Oecologia*, 89, 509–515.
- Schaffelke, B. & Klumpp, D.W. (1998). Nutrient-limited growth of the coral reef macroalga *Sargassum baccularia* and experimental growth enhancement by nutrient addition in continuous flow culture. *Mar. Ecol. Prog. Ser.*, 164, 199–211.
- Scheffer, M., Carpenter, S.R., Foley, J., Folke, C. & Walker, B.H. (2001). Catastrophic shifts in ecosystems. *Nature*, 413, 591–596.
- Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V. *et al.* (2009). Early-warning signals for critical transitions. *Nature*, 461, 53–59.
- Schmitt, R.J. & Holbrook, S.J. (1990). Contrasting effects of giant kelp on dynamics of surfperch populations. *Oecologia*, 84, 419–429.
- Stiger, V. & Payri, C. (1999). Spatial and temporal patterns of settlement of the brown macroalgae *Turbinaria ornata* and *Sargassum mangroveense* in a coral reef on Tahiti. *Mar. Ecol. Prog. Ser.*, 191, 91–100.
- Taylor, D.I. & Shiel, D.R. (2010). Algal populations controlled by fish herbivory across a wave exposure gradient on southern temperate shores. *Ecology*, 91, 201–211.
- Underwood, R. (1982). Vigilance behavior in grazing African antelopes. *Behaviour*, 79, 81–104.
- Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. *et al.* (2009). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations in habitat use. *Ecology*, 90, 23–30.
- Verdolin, J.L. (2006). Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behav. Ecol. Sociobiol.*, 60, 457–464.
- Wilson, S.K., Fisher, R., Pratchett, M.S., Graham, N.A.J., Dulvy, N.K., Turner, R.A. *et al.* (2008). Exploitation and habitat degradation as agents of change within coral reef fish communities. *Glob. Change Biol.*, 14, 2796–2809.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Methodological details.

Figure S1 Variation in the removal rates of transplanted individual *Sargassum* thalli between diurnal and nocturnal periods on the reef crest of Pioneer Bay, Orpheus Island.

Figure S2 Spatial and temporal variation in removal rates of *Sargassum* thalli positioned within each of the macroalgal density treatments.

Figure S3 Influence of *Sargassum* biomass on the grazing intensity of herbivorous fishes for each day of the deployments.

Figure S4 The relationship between the biomass of potential predators and the biomass of *Sargassum* within the each of experimental patches.

Figure S5 Proportion of total mass standardized bites taken from each of the *Sargassum* density treatments by the two dominant browsing fish species, *Kyphosus vaigiensis* and *Naso unicornis*.

Table S1 Results of repeated measures ANOVA comparing the spatial variation in removal rates among thalli within the high, medium and low density macroalgal treatments.

Table S2 Results of repeated measures MANOVA comparing relative removal rates of *Sargassum* biomass among sites, density treatments and days.

Table S3 Results of repeated measures MANOVA comparing the feeding intensity of the two dominant browsing species among sites, density treatments and days.

Table S4 Summary of predatory fishes recorded within the habitat patches.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Editor, Tim Wootton

Manuscript received 5 August 2010

First decision made 14 September 2010

Second decision made 30 November 2010

Manuscript accepted 10 December 2010