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The ecosystem role of macroalgal browsing fishes on coral reefs

Thesis submitted by

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in June 2010

for the degree of Doctor of Philosophy in Marine Biology
within the School of Marine and Tropical Biology and
the ARC Centre of Excellence for Coral Reef Studies,
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Statement on the Contribution of Others

This thesis includes some collaborative work with my supervisor Prof. David Bellwood. While undertaking these collaborations, I was responsible for the project concept and design, data collection, analysis and interpretation, and the final synthesis of results into a form suitable for publication. My collaborator provided intellectual guidance, equipment, financial support, and editorial assistance.

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Abstract

Herbivory is a key process structuring plant communities in both terrestrial and aquatic ecosystems, with variation in herbivory often being related to shifts between contrasting groups of primary producers. On coral reefs, regional reductions in herbivores have underpinned shifts from coral-dominance to dominance by fleshy macroalgae. The capacity to remove macroalgae is, therefore, viewed as a key process in both preventing and reversing such transitions. The present study compared the role of macroalgal browsing fishes across two distinct exposure gradients, both among habitats within a single reef and across several reefs spanning the continental shelf, and among patches of differing macroalgal densities. Finally, the role of a second group of herbivorous fishes, the territorial damselfishes, in influencing macroalgal removal rates and shaping macroalgal distributions was explored.

Browsing intensity was quantified across eight habitats of varying depth and wave exposure on a mid-shelf reef in the northern Great Barrier Reef (GBR) using assays of two species of *Sargassum*. Removal rates of *Sargassum* varied significantly amongst habitats, with both species displaying broadly similar patterns. Reductions in *Sargassum* biomass were highest within the shallow habitats on the exposed aspect of the reef (81.4–91.6 %.d^{-1}), lowest within the deeper exposed habitats (3.8–13.4 %.d^{-1}), and intermediate within the sheltered habitats (37.9–76.5 % d^{-1}). Surprisingly the rates of removal of *Sargassum* displayed no relationship with visual census estimates of the density or biomass of all roving herbivorous fishes or macroalgal browsing fishes, either collectively or independently. Stationary underwater video cameras revealed that, despite the reef supporting over fifty herbivorous fish species and six macroalgal browsing species, a single species, *Naso unicornis*, was almost solely responsible for

the removal of *Sargassum* biomass. Of the 42,246 bites taken from the *Sargassum* across all habitats, *N. unicornis* accounted for 89.8 % (37,982) of the total bites, and 94.6 % of the total mass standardized bites.

Sargassum assays revealed a distinct pattern in browsing across the continental shelf in the northern GBR, with the highest rates of removal recorded on mid-shelf reefs (55.2–79.9 %.d^{-1}) and decreasing significantly on inner-shelf reefs (10.8–17.0 %.d^{-1}). The low removal rates on inner-shelf reefs appeared to be directly related to the high cover of macroalgae on those reefs. Reductions in *Sargassum* biomass were also initially low on outer-shelf reefs (10.1–10.4 %.d^{-1}), but increased markedly (32.1-73.4 %.5h^{-1}) after the resident fishes were allowed several days to familiarize themselves with the *Sargassum*. Despite considerable cross-shelf variation in the rates of removal of *Sargassum*, there was little variation in the agents of macroalgal removal across all reefs. Feeding on the transplanted *Sargassum* was again dominated by a single browsing species. *N. unicornis* accounted for 82 % of all mass standardized bites and explained over 80 % of the total variation in the reduction in *Sargassum* biomass across all reefs and habitats. Although the majority of this feeding activity was recorded on the mid- and outer-shelf reefs, *N. unicornis* accounted for over 72 % of the recorded feeding on the inner-shelf reefs.

The territory composition and effect of resident damselfish on the removal of *Sargassum* was quantified for six common species of damselfish on a mid-shelf reef in the northern GBR. The functional composition of algal communities within territories varied markedly among species. The territories of four species were characterized by algal turfs, while the territories of two species were characterized by foliose and leathery brown macroalgae. *Sargassum*, a generally rare alga on mid-shelf reefs, was a particularly common alga within *Dischistodus prosopotaenia* territories. *D.*

prosopotaenia was the only species to retain the transplanted *Sargassum*, with only a minimal reduction in *Sargassum* biomass (1.1 $\%.d^{-1}$) being recorded within their territories. In contrast, reductions in *Sargassum* biomass were high in areas adjacent to *D. prosopotaenia* territories (83.8 $\%.d^{-1}$), and within and adjacent to the territories of the five remaining damselfish species (76.2 - 92.5 $\%.d^{-1}$). Overall, only *D. prosopotaenia* provided a refuge for leathery brown macroalgae, and may facilitate the development of this macroalgae on mid-shelf reefs of the GBR.

Habitat patches that varied in the spatial arrangement and density of macroalgae (0.25-6.23 $kg.m^{-2}$) were created on an inshore reef in the central GBR using transplanted *Sargassum*. Feeding on the *Sargassum* was dominated by two species, *Kyphosus vaigiensis* and *N. unicornis*. Both species displayed a preference for the relatively open habitat patches with low cover and biomass of *Sargassum*; only switching to the higher density patches after much of the *Sargassum* biomass within the lower density patches had been consumed. Similarly, grazing on the algal turf covered substratum within the habitat patches displayed an exponential decline with increasing *Sargassum* biomass. These feeding preferences appeared not to be related to bottom-up factors as food availability was proportional to macroalgal density for browsers and broadly comparable among habitat patches for grazers. It appears more likely that the avoidance of the higher macroalgal density patches was related to an increase in the perceived risk of predation.

Overall, the consumption rates of *Sargassum* in the present study provided strong evidence for the potential role of browsing fishes in limiting the distribution of adult *Sargassum* on mid- and outer-shelf reefs of the GBR. Browsing intensity was, however, moderated by the presence of *D. prosopotaenia* and the density of the *Sargassum* presented. These negative interactors are important and provide the mechanistic bases through which *Sargassum* may colonize new locations, and expand and persist once established. Despite some evidence of latitudinal variation on inshore reefs, the reliance on a single species removing *Sargassum* across a range of habitats and reefs in the northern GBR was striking. This limited redundancy, both within and across local (0.1 – 40 km) scales, highlights the potential for single-species functional groups and emphasizes the importance of looking beyond biological diversity as a source of ecological stability.

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Chapter 1: General Introduction

Herbivory is widely acknowledged as a key process structuring plant communities in both terrestrial and aquatic ecosystems (Huntly 1991; Scheffer et al. 2001; Burkepile and Hay 2006). Whilst there are fundamental differences among ecosystems in the nature of herbivory and its importance relative to other processes (Shurin et al. 2006; Hillebrand et al. 2007; Gruner et al. 2008), areas of moderate to high grazing are often characterized by a low biomass of highly productive plants; a grazing lawn (sensu Bell 1971; McNaughton 1984). Within these systems a marked reduction in herbivory often leads to a shift to an alternate state dominated by a high biomass of larger, less productive and less palatable plants. Shifts between herbaceous and woody vegetation have been documented for a range of terrestrial systems, including tropical and subtropical savannas (Walker et al. 1981; Archer et al. 1988; Dublin et al. 1990), mesic grasslands (Dobson and Crawley 1994), and salt marshes (Bazely and Jeffries 1986). In marine systems, shifts to macroalgal, or seaweed, dominance have been documented on tropical and temperate reefs following reductions in herbivore populations (Hughes 1994; Steneck et al. 2002, 2004). The persistence of these shifts long after herbivore populations have been restored highlights the difficulty of reversing such shifts. In these cases, the dominant vegetation often reaches a size refuge from the majority of herbivores. Seedlings of woody plants and macroalgal propagules are easily eliminated by grazing herbivores (Lubchenco and Gaines 1981; Holmgren et al. 2006), however as they grow they become less susceptible to the same suite of herbivores. Quantifying the impact of different herbivore groups is fundamental to our understanding and management of these ecosystems.

Coral reefs are one of the worlds' most productive and biologically diverse ecosystems. On healthy coral-dominated reefs, with intact herbivore populations, the algal community is dominated by highly productive algal turfs (primarily filamentous algae, macroalgal propagules, and detritus) and grazing resistant crustose coralline algae. On coral reefs over ninety percent of the daily production of algal turfs is consumed by a diverse assemblage of grazing fishes and invertebrates (Hatcher 1983; Polunin and Klumpp 1992). Following large scale coral mortality the dead coral skeletons are rapidly colonized by algal turfs (Diaz-Pulido and McCook 2002), subsequently increasing algal abundance and production. On reefs with intact herbivore communities these algal communities are maintained in a cropped state (Arthur et al. 2005), suggesting that there is an innate capacity to compensate for the increased algal production. However, regional reductions in roving herbivorous fishes (namely Acanthuridae, Kyphosidae, Labridae (parrotfishes), and Siganidae) through overfishing have limited the ability of many reefs to meet algal production. This disequilibrium between algal production and consumption may release macroalgal propagules and cropped adult macroalgae from top-down control, and ultimately lead to a shift to dominance by leathery brown macroalgae (Hughes 1994; McClanahan et al. 2001; Graham et al. 2006). Once established, these shifts appear difficult to reverse as these macroalgae are unpalatable to the majority of herbivores (Bellwood et al. 2006) and have been shown to suppress the growth, survival, fecundity, and recruitment of corals (Jompa and McCook 2002a, b; Hughes et al. 2007; Mumby et al. 2007). Given the potential importance of macroalgae in coral reef phase-shifts, our ability to successfully manage coral reefs into the future will benefit from a clearer, quantitative understanding of the roles of individual herbivorous fish species and the locations in which these roles are exhibited.

Roving herbivorous fishes may be broadly classified into two functional groups (i.e., grazers and browsers) based on the algal material they target (Steneck 1988; Bellwood et al. 2004). Grazing taxa (including scraping and excavating parrotfishes) typically feed on the epilithic algal matrix, or algal turfs (EAM; sensu Wilson et al. 2003), and play an important role in preventing shifts to alternate states and reassemble following disturbances (Bellwood et al. 2004; Nyström 2006). Recent studies have shown, however, that grazing fishes have a limited capacity to remove leathery macroalgae and consequently reverse phase-shifts to macroalgal dominance (Bellwood et al. 2006; Fox and Bellwood 2008a). The removal of leathery macroalgae, in particular *Sargassum*, appears to represent a separate but critical process on coral reefs (Bellwood et al. 2006). On the Great Barrier Reef (GBR), one of the world's most intact coral reef systems, the majority of studies examining this process have been conducted on the Orpheus Island, an inshore island in the central GBR (see McCook 1996, 1997 for exceptions). Of these studies all were conducted on the leeward side of the island, with the majority restricted to a single bay and/or a single habitat (Bellwood et al. 2006; Mantyka and Bellwood 2007; Fox and Bellwood 2008a; Cvitanovic and Bellwood 2009; Lefèvre and Bellwood 2010). These studies have provided useful insights into the potential role of macroalgal browsers in structuring algal communities on this inshore reef system; however, little is known of this process across broader spatial scales.

Within the GBR, there are marked gradients in benthic composition, herbivore community structure, environmental parameters, and ecosystem processes both across the continental shelf and among habitats within a reef (McCook and Price 1997; Fabricius and De'ath 2001; Hoey and Bellwood 2008; Wismer et al. 2009). Erect brown macroalgae, in particular *Sargassum* spp. (Ochrophyta: Phaeophyceae), are a dominant feature of shallow coastal reefs where they form dense stands up to 3 m in height which can cover over fifty percent of the substratum (Bellwood et al. 2006; Wismer et al. 2009). In contrast, erect brown macroalgae are present in low densities on mid- and outer-shelf reefs (McCook et al. 1997, 2000). Quantifying the rates of removal of leathery macroalgae and identifying the species contributing to this function across a range of spatial scales is central to our understanding of this process and the resilience of the system as a whole.

Aims and thesis outline

Given the potential importance of macroalgae in coral reef degradation and the limited spatial extent of previous studies examining macroalgal removal, the main objective of this thesis was to investigate the role of fishes in structuring macroalgal communities across broader spatial scales. Using transplanted *Sargassum*, the largest coral reef macroalga, to directly quantify macroalgal removal the four primary aims of this study were to: (1) quantify variation in the rates of removal of adult macroalgae across two distinct spatial scales, (a) among mid-shelf reef habitats and (b) among reefs spanning the continental shelf; (2) identify the species responsible for removing macroalgal biomass across the same spatial scales; (3) investigate the role of a second group of herbivorous fishes, the territorial damselfishes, in influencing macroalgal removal rates and shaping macroalgal distributions; and (4) examine the influence of macroalgal density on habitat use and feeding behaviour by herbivorous fishes.

These aims are addressed in a series of five separate studies following the chapters outlined below, and correspond directly to the publications derived from this thesis (see Appendix F for full list). **Chapter 2** provides a quantitative assessment of the rate of removal of two species of *Sargassum* across eight habitats of varying depth and wave exposure on a mid-shelf reef in the northern GBR. These rates are compared to visual census estimates of the abundance and biomass of herbivorous fishes to test the assumption that the functional impact of a species is proportional to its density within a particular location. **Chapter 3** builds on this foundation by using stationary underwater video cameras to directly quantify the species responsible for removing the macroalgal biomass across six mid-shelf reef habitats. In doing so, the extent of functional redundancy within and among habitats is assessed. **Chapter 4** examines the process of macroalgal browsing across a broader, cross-shelf spatial scale. Rates and agents of macroalgal removal are directly quantified within two habitats on each of eight reefs spanning the continental shelf in the northern GBR. To determine the effect of the local environment in shaping patterns of browsing intensity, removal rates are compared to the distribution of both herbivorous fishes and benthic algal communities. **Chapter 5** investigates the role of six common territorial damselfishes in shaping macroalgal distributions on a mid-shelf reef. The composition of algae is quantified and the effect of resident damselfish on browsing intensity is evaluated. Finally, **Chapter 6** uses habitat patches of varying macroalgal density to examine the influence of the physical structure of macroalgal stands on the feeding behaviour of both grazing and browsing coral reef fishes.

Chapter 2: Among-habitat variation in herbivory on *Sargassum* spp. on a mid-shelf reef in the northern Great Barrier Reef

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2.1. Introduction

Herbivory has long been recognized as a key process structuring benthic communities on coral reefs (Stephenson and Searles 1960; Randall 1965). Variation in the intensity of herbivory has been cited as a significant factor determining the standing biomass (Lewis and Wainwright 1985; Albert et al. 2008), productivity (Russ 2003) and succession (Steneck 1988; Hixon and Brostoff 1996) of algal communities. On reefs with intact herbivore communities, in excess of ninety percent of the net daily production of the algal community is consumed by herbivorous fishes (Hatcher 1983; Polunin and Klumpp 1992). At reduced levels of herbivory, the balance between the production and consumption of algae is disrupted. Numerous studies have demonstrated that the exclusion of herbivores from small areas of reef leads to a proliferation of algal biomass and a shift to slower growing erect macroalgae such as *Sargassum* (e.g., McClanahan et al. 2003; Hughes et al. 2007). Over larger scales, regional reductions in herbivores through overfishing have compromised the resilience of these systems (Bellwood et al. 2004; Burkepile and Hay 2006; Mumby et al. 2006) and ultimately resulted in system-wide declines to macroalgal dominance (Hughes 1994; Hunter and Evans 1995; McClanahan et al. 2001). While such shifts to macroalgal dominance may only manifest following widespread coral mortality or ecosystem disruption (Hunter and Evans 1995; McClanahan et al. 2001), the inability of these reefs to recover from disturbances highlights the critical role of herbivory in maintaining a healthy balance between corals and algae. Reductions in herbivory have also been indirectly linked to reductions in the survival, fecundity and recruitment of corals (Jompa and McCook 2002a, b; Hughes et al. 2007), further limiting the capacity of these reefs to regenerate.

Large variations in the abundance and community structure of herbivorous fishes has been documented across latitudes (Floeter et al. 2005); between reefs from differing shelf locations (Hoey and Bellwood 2008) and levels of fishing (Hay 1984); and among habitats within a single reef (Russ 1984). This spatial variation has often been cited as a significant factor in the distribution of algal communities across similar scales, with fleshy or erect macroalgae being negatively related to herbivore densities (Williams and Polunin 2001) or biomass (Wismer et al. 2009). This correlative approach typically views herbivory as a uniform process, with all taxa having a similar impact on the system (cf., Choat 1991). There is, however, considerable variation in feeding behaviour among herbivorous taxa. This variation has been demonstrated to be functionally significant, influencing the standing crop and succession of algal communities (Carpenter 1986; Ceccarelli et al. 2005a; Burkepile and Hay 2008).

Acknowledging these differences, another suite of studies has adopted a modelling approach to indirectly quantify the impact of particular functional or taxonomic components of the herbivorous fauna (e.g., Mumby 2006; Hoey and Bellwood 2008). The population impact of individual taxa is estimated as the product of density estimates from visual census, feeding rates and bite size. This approach is based on the largely implicit assumption that species exert a functional impact that is proportional to their density within a particular location (i.e. individuals feed within the location they are recorded in visual surveys). The only study to have directly tested this assumption found that presence broadly corresponded to function for three species that grazed on the epilithic algal matrix (Fox and Bellwood 2008b). Remote underwater video observations indicate, however, that this relationship is not likely to hold for all functional groups, especially those that remove leathery macroalgae, or seaweed (Steneck 1983; Bellwood et al. 2006; Fox and Bellwood 2008a).

Given the importance of herbivory in maintaining the health and resilience of coral reefs there is a clear need for the direct quantification of herbivory across a range of scales. Whilst numerous experiments have used transplanted pieces of seagrass (primarily *Thalassia*) and macroalgae as a metric for the intensity of herbivory across reef gradients in the Caribbean (e.g., Hay 1981, 1984; Steneck 1983; Lewis 1985, 1986; Lewis and Wainwright 1985; Reinthal and MacIntyre 1994), few studies have directly quantified herbivory among habitats on the Great Barrier Reef (GBR) (for exceptions see McCook 1996, 1997; Fox and Bellwood 2008a).

Within the GBR, there are marked gradients in the relative abundance of turf-, coralline- and macro-algae both across the continental shelf and among habitats within a reef (McCook and Price 1997; Fabricius and De'ath 2001; Wismer et al. 2009). Leathery brown macroalgae, in particular *Sargassum* spp. (Ochrophyta: Phaeophyceae), are a dominant constituent of shallow habitats on inshore reefs on the GBR where they often forms dense stands with biomass exceeding 7 kg m^{-2} (wet weight) and covering over fifty percent of the substrata (McCook and Price 1997; Bellwood et al. 2006; Wismer et al. 2009). In contrast, leathery brown macroalgae is virtually absent (< 1% cover) from all mid- and outer-shelf reef habitats (McCook and Price 1997; Wismer et al. 2009). While short-term nutrient pulses have been demonstrated to increase the growth and net photosynthetic rate of *Sargassum* (Schaffelke and Klumpp 1998a,b), Fabricius et al. (2005) reported that the abundance of Phaeophyceae displayed no response along a water quality gradient on inshore reefs in the northern GBR. Variation in grazing intensity by herbivorous fishes appears to be the primary determinant of

Sargassum distribution within inshore reefs. Estimates of herbivore activity from both visual census (Fox and Bellwood 2007) and *Sargassum* bioassays (McCook 1997; Fox and Bellwood 2008a) have displayed strong negative relationships with the abundance of *Sargassum* among habitats on inshore reefs in the central GBR. Furthermore, the experimental exclusion of large herbivorous fishes following a widespread coral bleaching event induced a shift to macroalgal (primarily *Sargassum*) dominance, while in adjacent areas macroalgal abundance remained low (Hughes et al. 2007).

Despite the number of studies that have examined the processes that regulate macroalgal abundance on inshore reefs very few have examined these processes on reefs further offshore. This is surprising given the marked separation of inshore reefs from mid- and outer-shelf reefs in benthic composition, herbivore community structure, environmental parameters and ecosystem processes (Fabricius and De'ath 2001; Brodie et al. 2007; Hoey and Bellwood 2008; Wismer et al. 2009). The aim of this study, therefore, is to quantify variation in the rate of removal of two species of macroalgae (*Sargassum*) across multiple habitats on a mid-shelf reef in the northern Great Barrier Reef (GBR), and determine if the rates of removal displayed any relationship with the abundance or biomass of herbivorous fishes across those scales. Specifically, I tested the hypothesis that the removal of *Sargassum* displays variation among habitats of varying wave exposure and depth. Exclusion experiments were conducted to confirm that any observed losses of *Sargassum* biomass were due to herbivory.

2.2. Materials and Methods

This study was conducted between November 2006 and January 2007 on Lizard Island (14°40'S, 145°28'E) in the northern GBR. Seven habitats of varying wave exposure and depth were selected to examine among-habitat variation in both the rates of macroalgal removal and herbivorous fish communities (Fig. 2.1; see Depczynski and Bellwood 2005 for detailed habitat descriptions). The exposed reef slope, crest and flat were located on the south-east aspect of the island and directly exposed to the prevailing south-east trade winds. The exposed slope was at a depth of 10 – 14 m on the steeply inclined region of the reef. The exposed crest (2 – 4 m depth) was the region that marked the transition between the steeply inclined reef slope and the extensive shallow region of the reef. The exposed reef flat (1 – 2 m depth) was approximately 20 -25 m behind the reef crest, in the region immediately beyond the wave break. The back reef was at the leeward margin of the reef flat at a depth of 2 – 4 m and marked the transition from the reef flat to deeper lagoonal habitats dominated by sand. Three habitats were selected on the leeward or sheltered side of the island. The patch reef habitat (4 – 6 m depth) represented an isolated reef on the leeward side of the island. The sheltered reef flat (1 – 2 m) and sheltered reef base (6 – 8 m) were located on a fringing reef on the north-western side of the island (Fig. 2.1). These habitats are characteristic of Indo-Pacific coral reefs and have been used extensively to describe variation in both fish and benthic community composition (Done 1982; Russ 1984; Depczynski and Bellwood 2005).

Benthic surveys

To quantify the variation in the algal community and benthic community structure twelve replicate 10 m transects were censused within each habitat. Transects were haphazardly placed within each habitat and, where possible, laid parallel to the reef crest. The type of substratum immediately under the transect tape and one metre either side was recorded at one metre intervals along the transect, following Bellwood (1995), giving a total of 33 points per transect. Substratum categories were identified as macroalgae (> 10 mm in height, identified to species where possible), epilithic algal matrix (EAM; sensu Wilson et al. 2003, ≤ 10 mm in height), crustose coralline algae (CCA), cyanobacteria, live scleractinian coral, damselfish territory (marked by long epilithic algae defended by a damselfish), soft coral, sand, sand and rubble, and ‘other’. Any other species of macroalgae within each transect area (i.e., 10 m × 2 m) were also recorded.

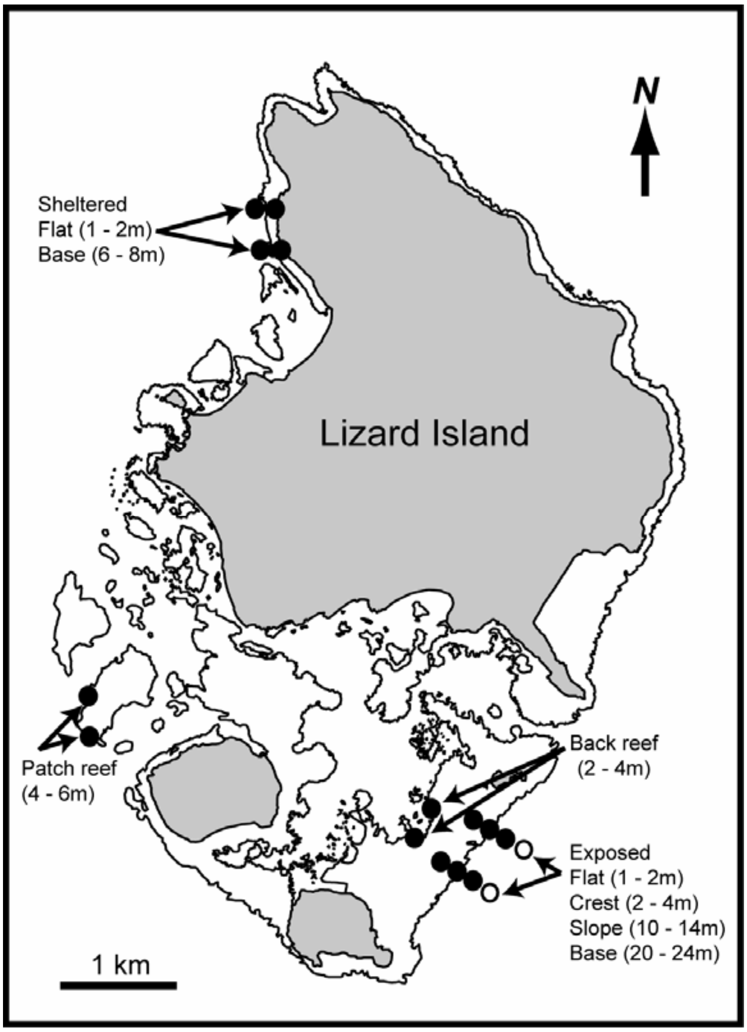

Fig. 2.1: Map of Lizard Island indicating the location of the seven habitats of varying water depth and wave exposure. Filled circles represent the approximate location of the two sites used for *Sargassum* bioassays within each habitat. Open circles represent the location of the two sites within the exposed reef base habitat, an additional habitat used for *S. swartzii* bioassays. The prevailing wind is from the southeast.

Macroalgal transplants

To quantify the variation in the removal of macroalgae amongst habitats a series of transplant experiments were conducted. Two species of *Sargassum* (*S. swartzii* and *S. cristaefolium*) were collected from the reef flat of two inshore reefs in the Turtle Island Group (14°43'S, 145°12'E), approximately 28 km west of Lizard Island. Individual *Sargassum* thalli were removed by cutting the holdfast as close to the point of attachment as possible. All *Sargassum* thalli were returned to Lizard Island and placed in a large (6000 L) aquarium with flow through seawater within 90 min of collection.

Individual *Sargassum* thalli were spun in a salad spinner for 30 s to remove excess water, and the wet weight and maximum height of the thallus recorded. The mean mass and height of each thallus was 451.3 ± 2.6 g (SE) and 460 ± 6 mm for *S. swartzii* and 283.8 ± 1.8 g and 484 ± 9 mm for *S. cristaefolium*. Haphazardly selected *Sargassum* thalli were transplanted to each of two sites within each of the seven habitats around Lizard Island. Adjacent sites within each habitat were separated by a minimum of 50 m. The *Sargassum* was attached to the reef using a rubber band and galvanized wire (0.5 mm diameter). Briefly, a knot was tied in a broad rubber band to produce two loops. One loop was wound around the base of the thallus, approximately 20 mm above the holdfast. A short length of wire was then placed through the remaining loop of the rubber band and attached directly to the reef substratum. Each *Sargassum* thallus was individually identified with a small plastic label that was attached to the reef approximately 1.5 m from the *Sargassum*. After 24 h the *Sargassum* was collected, spun in a salad spinner for 30 s, weighed and the maximum height of the thallus recorded.

At each of the two sites within each habitat ten *S. swartzii* thalli (n = 20 thalli per habitat) and six *S. cristaefolium* thalli (n = 12 thalli per habitat) were transplanted during the experimental period. A maximum of two thalli were transplanted within a site during any given 24-h period, with adjacent thalli being separated by a minimum of 5 m. A further six *S. swartzii* thalli were transplanted to each of two sites within an additional habitat, the exposed reef base (20 – 24 m depth; Fig. 2.1). Logistical constraints and the limited availability of *S. cristaefolium* at the time of the study contributed to the lower number of thalli used for this species, and precluded *S. cristaefolium* from being transplanted to the exposed reef base.

To quantify the removal rates over a longer period (7-days) four *S. swartzii* thalli were transplanted to each of two sites within the eight habitats (n = 8 thalli per habitat). Adjacent thalli were separated by a minimum of 5 m. The thalli were collected after a period of 7-days and processed as described previously.

Exclusion experiment

To determine if observed losses of *Sargassum* biomass were due to herbivory two exclusion experiments were conducted. Free standing cages (approximately 1000 × 600 × 600 mm) with 50 mm square polyethylene mesh were used to exclude large herbivorous fishes from transplanted *S. swartzii*. The 50 mm mesh was selected as it minimized the caging artifacts (i.e., shading and reduction in water flow) while excluding the size classes of herbivorous fishes that have been demonstrated to be important in the removal of erect macroalgae (Bellwood et al. 2006; Fox and Bellwood 2008a). The *Sargassum* was processed as previously described prior to transplanting to the reef. Six haphazardly selected *S. swartzii* thalli were transplanted to each of two habitats, the exposed reef crest and back reef. These two habitats were selected as they displayed the highest rates of algal removal, are located at similar depths but are subject to markedly different wave and current intensities (Fulton and Bellwood 2005). Within each habitat three *S. swartzii* thalli were left exposed to resident herbivores and three thalli were placed inside individual exclusion cages for a period of 24 h. After 24 h the *Sargassum* was collected and processed as described previously. This procedure was repeated over 6 days (n = 18 thalli per treatment per habitat).

To quantify the losses of *Sargassum* biomass that were attributable to handling and to confirm that the observed losses of *Sargassum* biomass over the 7-day period were due to herbivory a second exclusion experiment was conducted. Six haphazardly selected *S. swartzii* thalli were transplanted to each of two habitats, the exposed reef crest and back reef. Within each habitat three *S. swartzii* thalli were left exposed to resident herbivores and three thalli were placed inside individual exclusion cages for 7 days. This procedure was replicated over two 7-day periods (n = 6 thalli per treatment per habitat). Eight additional *S. swartzii* thalli were held in separate 60 L aquaria with flow through seawater for 7 days to quantify losses of *Sargassum* biomass that were attributable to handling.

Distribution of herbivorous fishes

To quantify the distribution of all roving nominally herbivorous fishes (i.e. Acanthuridae, Ephippidae, Kyphosidae, Labridae (parrotfishes), Pomacanthidae, and Siganidae) a series of timed swims was conducted in each of the seven habitats around Lizard Island. Four censuses were conducted within each habitat and included the areas adjacent to the sites used for the transplant experiments. Adjacent censuses were separated by a minimum of 20 m. Each census consisted of a diver swimming parallel to the reef crest for 10 min and recording all nominally herbivorous fishes greater than 10 cm total length (TL) within a 5 m wide transect that extended from the reef substratum to the surface of the water. A second diver recorded all individuals less than 10 cm TL in a 1 m wide transect. Individual fishes were identified and placed into 5 cm size categories for those greater than 10 cm TL, and in 2.5 cm size categories for those less than 10 cm TL. Care was taken not to re-census fish that left and subsequently re-entered the transect area. Numbers per unit effort were converted to densities per unit area by estimating the length of each transect (mean = 118 m, see Bellwood and Wainwright 2001). Density estimates were converted to biomass using length-weight relationships for each species (Kulbicki et al. 2005).

There is considerable variation in feeding behaviour of herbivorous fishes, both among and within families. This variation has been related to their ability to consume different algal functional groups and consequently their impact on ecosystem processes. The nominally herbivorous fishes recorded during the visual censuses were therefore placed into one of five functional groupings (macroalgal browsers, turf algal grazers, scrapers, excavators, and ‘other’) based on diet (Robertson and Gaines 1986; Randall et al. 1997; Choat et al. 2002) and direct video observations (Bellwood et al. 2006; Cvitanovic and Bellwood 2009). In particular, *Calotomus carolinus*, *Kyphosus vaigiensis*, *Naso lituratus*, *Naso unicornis,* and *Platax pinnatus* were identified as browsers of *Sargassum* and other erect brown macroalgae (namely Phaeophyceae: *Dictyota*, *Padina*, *Turbinaria*). Species within the four remaining functional groups (i.e., turf algal grazers, scrapers, excavators, and ‘other’) typically feed on crustose coralline algae and/or the epilithic algal matrix and are not likely to consume the transplanted *Sargassum*.

Statistical analyses

Variation in the rate of removal of *Sargassum* biomass among habitats and sites was analysed using three nested two-factor ANOVA’s. Habitat was fixed while site was random and nested within habitat. The analyses were based on the proportion of the initial, or transplanted, biomass removed from individual *Sargassum* thalli. A separate analysis was performed for each species of *Sargassum* over a 24 h period, and *S. swartzii* over a 7-day period. Assumptions of the ANOVA were examined by residual analysis. The proportion of biomass removed was arcsine-square root transformed for *S. swartzii* and $^4\sqrt{}$ transformed for *S. cristaefolium* to improve normality and homoscedasticity. Tukey's HSD tests were used to identify which means contributed to any significant differences detected.

The loss of *S. swartzii* biomass was compared amongst treatments (caged vs. open) and habitats using two orthogonal two-factor ANOVA's. The analyses were based on the proportion of the initial biomass lost from individual *S. swartzii* thalli over 24-h and 7-day periods. Assumptions of the ANOVA were examined by residual analysis. The proportion of biomass removed was arcsine-square root transformed to improve normality and homoscedasticity. The loss of biomass from *S. swartzii* held in aquaria was compared to those held in exclusion cages on the back reef and reef crest using a one-factor ANOVA. The analysis was based on the proportion of the initial biomass lost from individual *S. swartzii* thalli over a 7-day period. A Tukey's HSD test was used to identify which means contributed to any significant differences detected.

Among habitat variation in the density and biomass of (a) all roving herbivorous fishes and (b) browsers of erect brown macroalgae, hereafter referred to as macroalgal browsers, was analysed using a series of one-factor ANOVAs (n = 4 transects per habitat). Assumptions of the ANOVA were examined by residual analysis. Density and biomass of macroalgal browsers were subsequently $\log_{10}$ and square-root transformed respectively to improve normality and homoscedasticity. The relationship between the rate of removal of the two species of *Sargassum* and the abundance and biomass of all roving herbivorous fishes, macroalgal browsers, and each species within the macroalgal browser group was examined using correlations. Partial correlations controlling for the availability and relative susceptibility of the ambient macroalgal community within each habitat were also calculated (see Appendix A for details).

2.3. Results

The epilithic algal matrix (EAM), or algal turfs, dominated the benthic algal communities of the seven habitats around Lizard Island, ranging from 13.6 – 47.0 % (Table 2.1). With the exception of two calcified red alga, *Amphiroa* sp. and *Galaxaura* sp., the cover of macroalgae was low. *Galaxaura* was restricted to the sheltered and back reef habitats with the highest cover being recorded on the sheltered reef flat where it covered almost one-third of the substrata. *Amphiroa* also had the highest cover on the sheletered reef flat (12.1 %), with low cover in all other habitats (≤ 2.5 %). Erect brown macroalgae (Ochrophyta) was rare across all habitats (< 1 % cover), with only a single *Sargassum cristaefolium* and seven *Turbinaria ornata* thalli being recorded across all censuses. A thorough search of each habitat revealed another *S. cristaefolium* on the reef crest, and another species, *Sargassum* sp., present in the back reef, patch reef and sheltered reef base habitats. These thalli were too small (< 5 cm in height) to identify to species, and represented densities of less than one thallus per 100 m^2 of reef.

There were marked differences in the removal rates of *Sargassum* across the eight habitats, with both species displaying broadly similar patterns (Table 2.2a; Fig. 2.2). The shallow habitats on the exposed aspect of the reef (i.e. back reef, reef flat and crest) experienced the highest reductions in mass (81 – 92 %.d^{-1}) for both *S. swartzii* and *S. cristaefolium*, while the deeper exposed habitats (reef slope and base) displayed the lowest reductions (4 – 13 %.d^{-1}) over a 24-h period (Fig. 2.2). In contrast, the

Table 2.1: Summary of the benthic community composition at each of the seven habitats around Lizard Island. Mean percentage cover of each of the substrata categories (based on twelve 10 m transects within each habitat) are given. Values in parentheses are standard errors. + indicate macroalgae that were present within one transect but not recorded using the point intercept method, ++ indicate macroalgae that were present in two or more transects.

	Sheltered			Exposed			
	Base	Flat	Patch	Back	Flat	Crest	Slope
Epilithic algal matrix	47.0 (2.4)	13.6 (2.4)	35.1 (3.0)	22.0 (3.5)	34.8 (3.5)	19.7 (1.6)	23.0 (3.0)
Crustose coralline algae	0	2.5 (0.9)	0.7 (0.3)	4.8 (1.5)	14.9 (2.3)	9.6 (1.5)	3.0 (1.1)
CHLOROPHYTA							
Halimeda opuntia	+	0	+	2.7 (0.9)	0	0	+
Chlorodesmis fastigiata	0	0	+	+	0	++	0
RHODOPHYTA							
Amphiroa sp.	2.5 (0.5)	12.1 (1.8)	0.8 (0.4)	1.5 (0.6)	0.3 (0.3)	0.3 (0.3)	0.5 (0.5)
Galaxaura sp.	9.6 (3.1)	30.6 (2.8)	+	0.8 (0.5)	0	0	0
OCHROPHYTA (PHAEOPHYCEAE)							
Padina sp.	++	++	+	++	0	+	++
Sargassum cristaefolium	0	0	0	0	0.3 (0.3)	+	0
Sargassum sp.	+	0	+	+	0	0	0
Turbinaria ornata	0	0	0	0.5 (0.3)	0.8 (0.5)	0.5 (0.5)	0
Cyanobacteria	1.0 (0.6)	0.8 (0.4)	0	0.8 (0.4)	0	0	0.3 (0.3)
Damselfish territory	5.8 (1.6)	16.9 (1.8)	10.1 (2.0)	15.2 (4.8)	9.1 (1.0)	8.3 (1.2)	2.5 (1.1)
Sand	3.3 (0.9)	2.0 (0.7)	2.3 (1.1)	12.1 (4.9)	5.6 (1.7)	0	0.3 (0.3)
Sand & Rubble	8.1 (1.3)	6.8 (1.5)	5.8 (1.3)	12.9 (3.4)	0	6.8 (1.1)	3.0 (1.5)
Live coral	18.9 (1.7)	10.6 (1.0)	22.2 (2.2)	9.6 (2.4)	13.6 (1.7)	41.7 (2.2)	46.7 (4.1)
Soft coral	2.8 (1.1)	3.3 (0.8)	23.0 (2.5)	16.7 (2.8)	20.4 (1.6)	10.3 (1.6)	18.4 (2.0)
Other	1.0 (0.6)	0.8 (0.4)	0	0.5 (0.3)	0.3 (0.3)	2.8 (0.9)	2.3 (1.3)

reduction in mass within the three sheltered habitats varied between the two species. *S. swartzii* displayed relatively high rates of removal on the patch reef and sheltered reef base and flat (63 – 76 %.d^{-1}; Fig. 2.2a), while the reduction in mass was considerably lower for *S. cristaefolium* (38 – 64 %.d^{-1}; Fig. 2.2b) across the same habitats. Details of the variation among sites are given in Appendix A.

Over the 7-day period there was almost complete removal of *S. swartzii* biomass within all sheltered habitats and the shallow exposed habitats, ranging from 86.2 ± 10.0 % on the sheltered reef flat to 99.2 ± 0.5 % on the exposed reef crest (Fig. 2.3). The proportion of biomass removed decreased significantly on the exposed reef slope (57.9 ± 10.0 %) and base (10.6 ± 8.7 %; Table 2.2b).

There were significant interactions between habitat and treatment on the reduction in *S. swartzii* biomass for both the 24-h ($F_{1,68} = 22.610$, $p < 0.001$) and 7-day ($F_{1,20} = 15.051$, $p < 0.001$) exclusion experiments. *S. swartzii* transplanted within exclusion cages exhibited minimal reductions in biomass on both the reef crest (4.0 %) and back reef (1.1 %) over the 24-h period (Fig. 2.4). In contrast, *S. swartzii* exposed to reef herbivores exhibited significantly higher reductions in biomass; 73.1 % and 96.2 % on the back reef and reef crest, respectively.

Over the 7-day period there was almost complete removal of the *S. swartzii* biomass exposed to herbivores, ranging from 96.2 % on the back reef to 98.2 % on the reef crest (Fig. 2.4). Within the exclusion cages the biomass of *S. swartzii* decreased by 20.7 % on the reef crest and increased by 9.6 % on the back reef. The reduction in biomass of the *S. swartzii* thalli held in aquaria (1.1 %) was significantly lower than thalli held in exclusion cages on the reef crest over the 7-day period ($F_{2,17} = 15.447$, $p < 0.001$; Fig. 2.4).

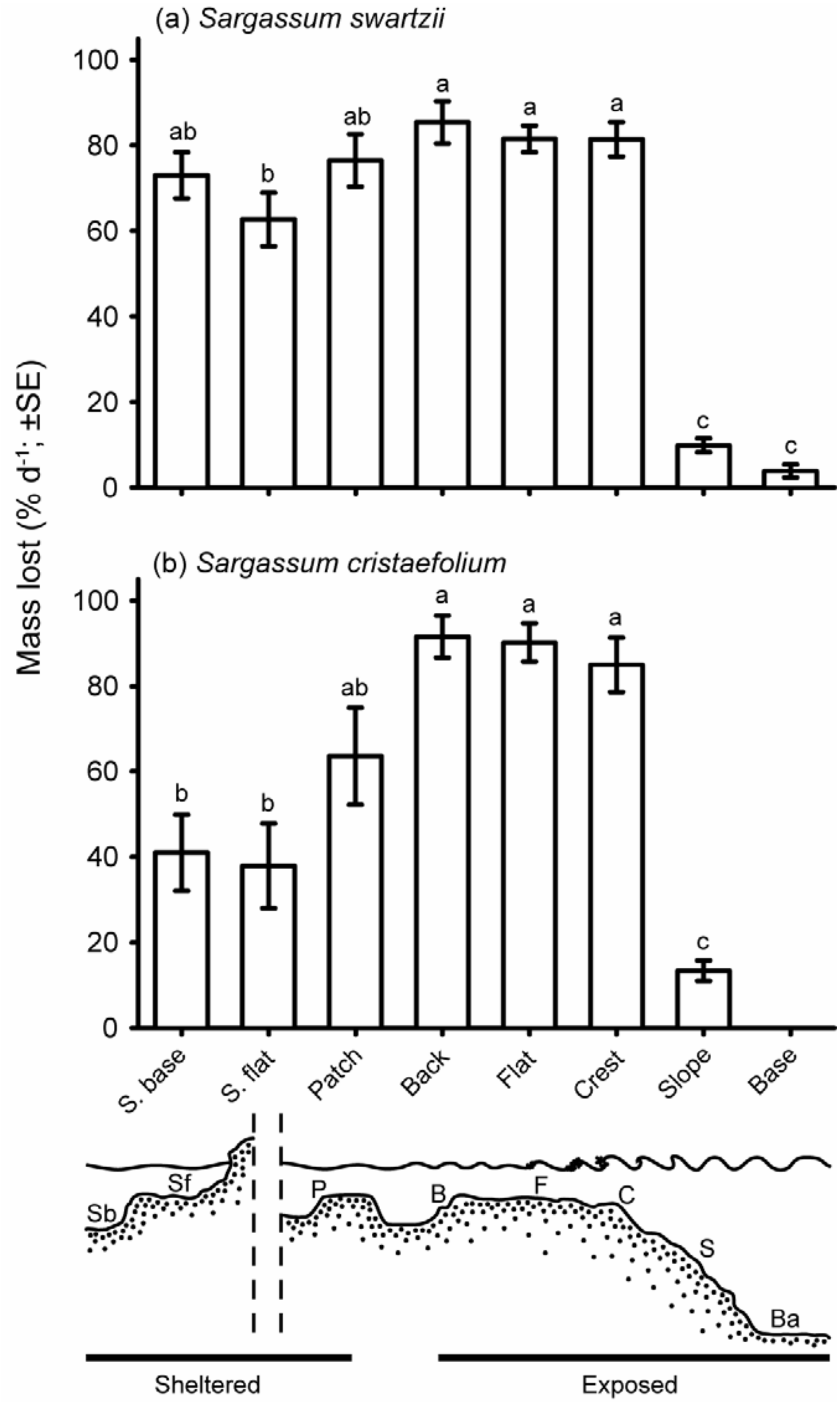

Fig. 2.2: Among habitat variation in the relative removal rates of (a) *Sargassum swartzii* and (b) *Sargassum cristaefolium* on Lizard Island. The means are based on twenty thalli transplanted for 24 hours within each habitat for *S. swartzii* and twelve thalli within each habitat for *S. cristaefolium*. The letters above each bar indicate homogenous groups identified by Tukey's HSD post-hoc analyses. *Sb* sheltered reef base, *Sf* sheltered reef flat, *P* patch reef, *B* back reef, *F* exposed reef flat, *C* exposed reef crest, *S* exposed reef slope, *Ba* exposed reef base.

Table 2.2: Summary of nested two-factor ANOVAs comparing the proportion of transplanted *Sargassum* biomass removed from two sites within each of seven (*S. cristaefolium*) or eight (*S. swartzii*) habitats around Lizard Island; (a) over 24 h, (b) 7 days. Analyses were based on individual *Sargassum* thalli transplanted within each site. The proportion of biomass removed was arcsine-square root transformed for *S. swartzii* and $\sqrt[4]{}$ transformed for *S. cristaefolium*.

	Source of variation	SS	df	MS	F	p
(a) 24 h						
S. swartzii	**Habitat**	**19.816**	**7**	**2.831**	**8.859**	**0.003**
	Site (Habitat)	**2.563**	**8**	**0.320**	**6.738**	**<0.001**
	Residual	6.465	136	0.048		
S. cristaefolium	**Habitat**	**1.633**	**6**	**0.272**	**3.897**	**0.049**
	Site (Habitat)	**0.489**	**7**	**0.070**	**5.962**	**<0.001**
	Residual	0.820	70	0.0117		
(b) 7 day						
S. swartzii	**Habitat**	**10.245**	**7**	**1.464**	**22.528**	**0.001**
	Site (Habitat)	0.520	8	0.065	1.794	0.102
	Residual	1.738	48	0.036		

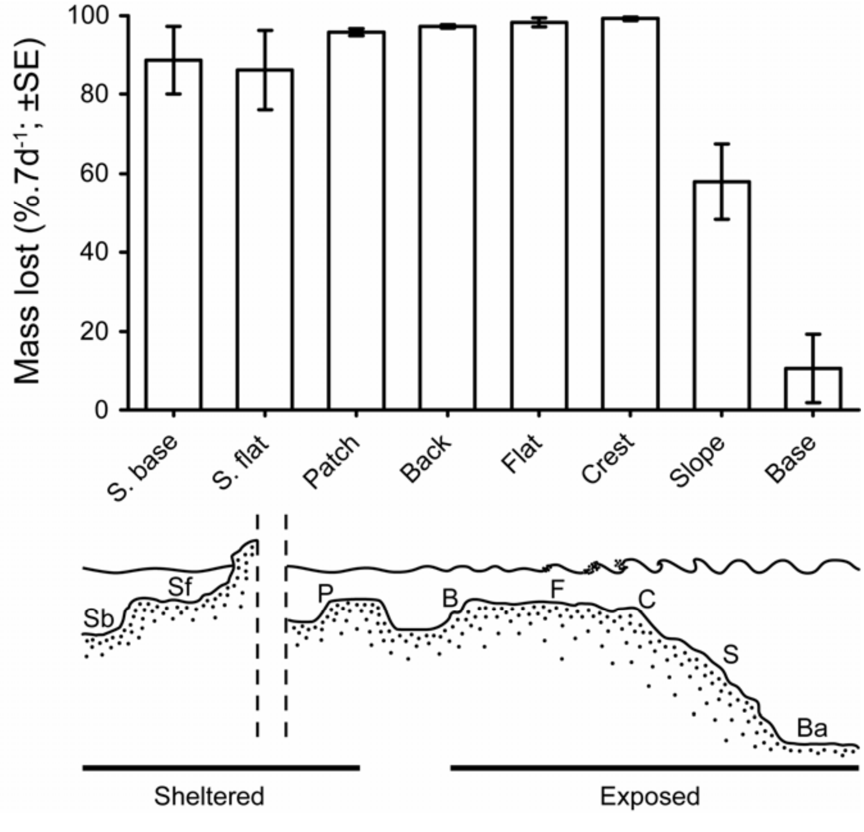

Fig. 2.3: Variation in the removal rates of *Sargassum swartzii* among eight habitats of varying exposure and depth on Lizard Island over a 7-day period. The means are based on four thalli transplanted into each of two sites within each habitat. Abbreviations defined in Fig. 2.2.

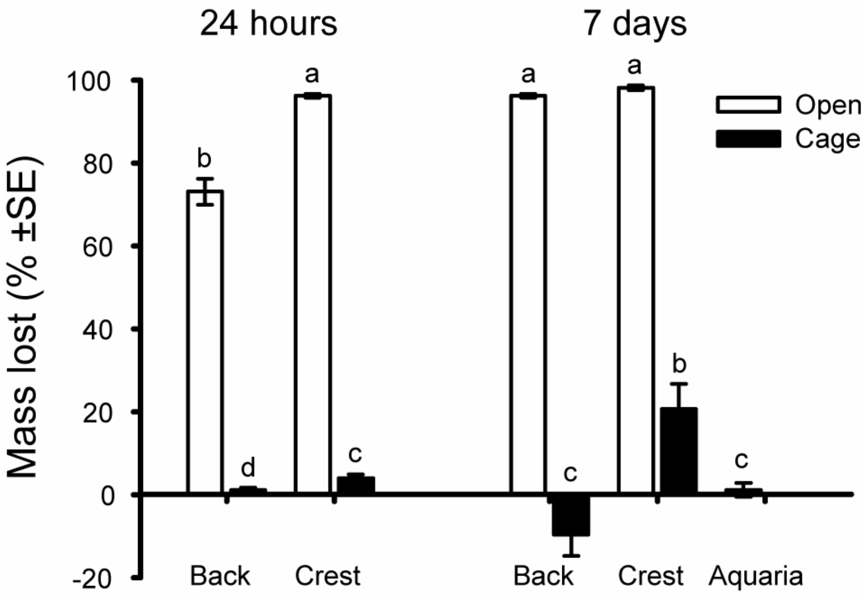

Fig. 2.4: Effect of excluding herbivores from *Sargassum swartzii* transplanted to the exposed reef crest and back reef on Lizard Island for periods of 24 hours and 7 days. Open bars represent thalli exposed to resident herbivores, closed bars represent thalli transplanted within exclusion cages. The letters above each bar indicate homogenous groups identified by Tukey's HSD post-hoc analyses.

The density and biomass of all roving herbivorous fishes (density: $F_{6,21} = 2.716$, $p = 0.04$; biomass: $F_{6,21} = 9.504$, $p < 0.001$) and macroalgal browsers (density: $F_{6,21} = 4.656$, $p = 0.004$; biomass: $F_{6,21} = 4.445$, $p = 0.005$) displayed significant variation amongst the seven habitats on Lizard Island. The density of roving herbivores was greatest on the reef crest (3753 ± 763 ind.ha^{-1}) and decreased significantly in the patch reef habitat (1434 ± 312 ind.ha^{-1}). In contrast, the biomass of roving herbivorous fishes was greatest on the back reef (681 ± 67 kg.ha^{-1}) and decreased significantly on the patch reef, slope and exposed flat (110 - 316 kg.ha^{-1}). The density and biomass of macroalgal browsers was lowest on the exposed reef flat, crest and slope (density: 8.5 – 12.7 ind.ha^{-1}; biomass: 0.7 – 11.7 kg.ha^{-1}) and increased on the sheltered flat, sheltered base and back reef (density: 76.6 – 85.1 ind.ha^{-1}; biomass: 84.5 – 156.0 kg.ha^{-1}). Variation in the herbivorous fish community composition is given in Appendix A.

There were no significant relationships between the density or biomass of all roving herbivorous fishes, macroalgal browsers, or the five species of macroalgal browsers independently (*Calotomus carolinus*, *Kyphosus vaigiensis*, *Naso lituratus*, *Naso unicornis*, and *Platax pinnatus*) with the proportion of biomass removed from either species of *Sargassum* across the seven habitats during a 24-h period (Table 2.3, Fig. 2.5). Incorporating the availability and relative susceptibility of the ambient macroalgal community within each habitat into the model had little effect on these relationships (see Appendix A).

Table 2.3: Correlations between the rate of removal of the two species of *Sargassum* and the density and biomass of all roving herbivorous fishes, macroalgal browsers, and five macroalgal browsing species independently across seven habitats around Lizard Island. Analyses are based on the mean proportion of biomass removed in a 24-h period within each habitat (*S. swartzii*: n = 20, *S. cristaefolium*: n =12). Density and biomass estimates are based on the mean of four 10-min timed swims within each habitat. Pearson's correlation coefficients are given.

		Sargassum swartzii		*Sargassum cristaefolium*	
		r	**p**	**r**	**p**
Roving herbivores	density	0.284	0.536	0.317	0.488
	biomass	0.183	0.695	-0.030	0.948
Macroalgal browsers	density	0.266	0.564	-0.090	0.848
	biomass	0.284	0.538	0.000	0.999
Calotomus carolinus	density	-0.667	0.101	-0.744	0.055
	biomass	-0.667	0.101	-0.744	0.055
Kyphosus vaigiensis	density	-0.010	0.982	-0.338	0.459
	biomass	0.002	0.997	-0.384	0.396
Naso lituratus	density	0.098	0.835	-0.281	0.542
	biomass	0.098	0.835	-0.281	0.542
Naso unicornis	density	0.346	0.448	0.341	0.454
	biomass	0.316	0.490	0.213	0.646
Platax pinnatus	density	0.091	0.847	-0.321	0.483
	biomass	0.091	0.847	-0.319	0.486

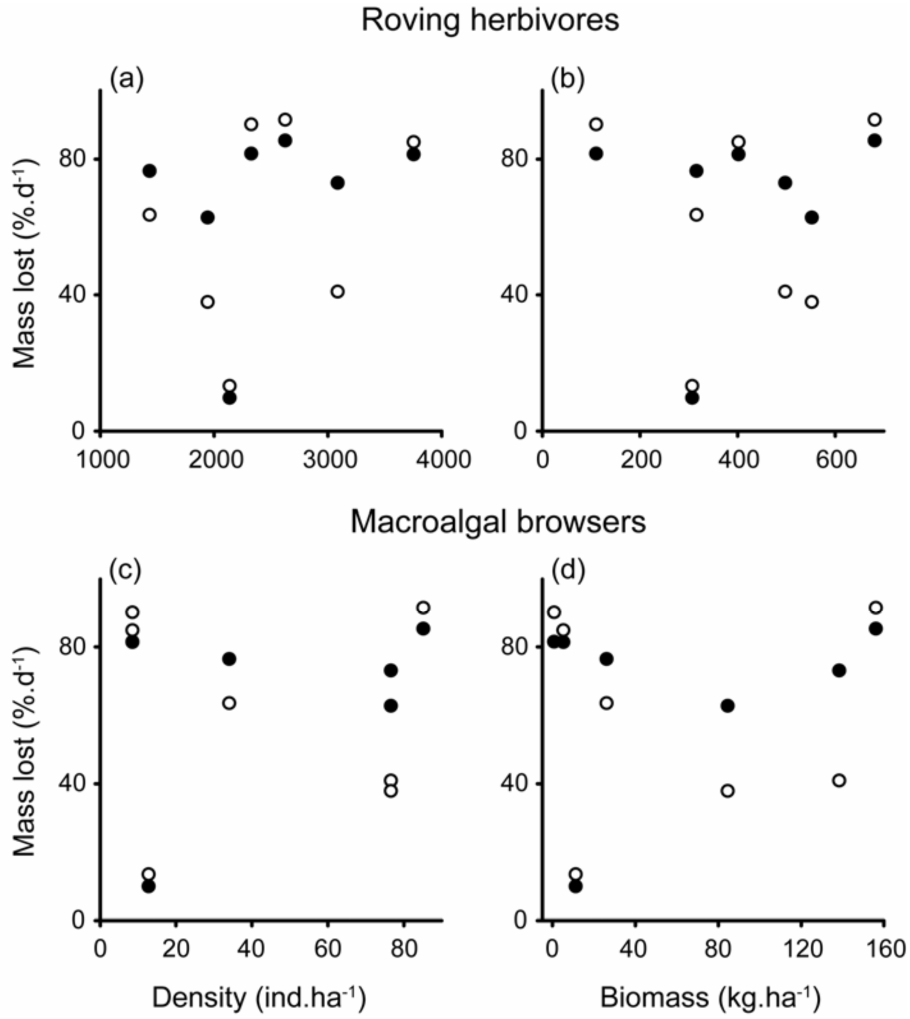

Fig. 2.5: Relationships between the rates of removal of *Sargassum* and the density and biomass of herbivorous fishes across seven habitats on Lizard Island; (a) density of roving herbivorous fishes (b) biomass of roving herbivorous fishes, (c) density of macroalgal browsers, (d) biomass of macroalgal browsers. Open circles, *Sargassum swartzii*; closed circles, *Sargassum cristaefolium*. Mass lost is the mean proportion of biomass removed in a 24-h period within each habitat (*S. swartzii*: n = 20, *S. cristaefolium*: n =12). Density and biomass estimates are based on the mean of four 10-min timed swims within each habitat.

2.4. Discussion

Variation in browsing intensity across a depth gradient has been documented on both Pacific and Caribbean reefs with the impact generally being greatest on the reef crest and decreasing both down the slope and across the reef flat (Hay 1981; Lewis and Wainwright 1985; Stimson et al. 2001). Consumption rates of *Sargassum* in the present study likewise displayed a marked decrease with depth within the exposed habitats, but little variation across the exposed reef flat or among depths on the sheltered reef. While only two habitats were examined across the exposed reef flat, the lack of variation was striking. Previous studies have reported reductions in browsing intensity of 50 - 80% across similar scales (i.e., reef crest to outer flat) on reefs of varying exposure (windward vs. leeward) and structure (barrier vs. fringing) (Reinthal and MacIntyre 1994; Stimson et al. 2001; Fox and Bellwood 2008a). The factors that have been hypothesized to influence this gradient on many reefs (e.g., structural complexity, predation risk and algal quality) may not be operating at Lizard Island (see Fox and Bellwood 2007 for a comprehensive discussion of these factors). Indeed, the exposed reef flat and crest habitats supported similar densities and biomass of macroalgal browsers indicating that access to the reef flat was not limited, at least for this functional group.

Traditionally, studies examining herbivory on coral reefs have inferred function from presence. This approach is based on the largely implicit assumption that fishes exert a functional impact that is proportional to their density within a particular location. This assumption is likely to hold for fishes that feed within the location that they are recorded in visual censuses and is supported by numerous studies that have documented a positive relationship between grazing rates and the density or biomass of herbivores, either collectively (Lewis and Wainwright 1985; Stimson et al. 2001; Williams and Polunin 2001; Wismer et al. 2009) or specific taxonomic or functional components (McClanahan et al. 1994; Sluka and Miller 2001). This relationship may breakdown if the species exhibit either positive or negative responses to diver presence (Bellwood et al. 2006), or undergo migrations between foraging and resting sites (Mazeroll and Montgomery 1998). In the present study, among habitat variation in the removal of *Sargassum* displayed no relationship with the estimated density or biomass of herbivorous fishes in total, or individually for those species that are known to consume *Sargassum* and other erect brown macroalgae. While the power of these analyses was low, the lack of a relationship, especially for macroalgal browsing species was surprising. Numerous studies have reported strong positive relationships between grazing intensity and fish biomass using comparable sampling designs (e.g., Lewis and Wainwright 1985; Fox and Bellwood 2007).

The technique used to quantify the distribution of herbivorous fishes in the present study (i.e., 10-min timed swims) was selected as it minimized potential observer effects and increased the likelihood of detecting larger roving species (Bellwood and Wainwright 2001). It may, however, have inherent and largely unavoidable biases associated with those species that exhibit a strong and rapid response to diver presence. Recent studies using remote underwater video have highlighted the potential dangers in using correlative approaches, especially for species that consume macroalgae. Fox and Bellwood (2008b) reported a distinct gradient in the removal of *Sargassum* assays across the fringing reef flat of an inshore island in the central GBR. While the gradient in grazing intensity was positively correlated to the biomass of herbivorous fishes, underwater video revealed that a species not observed during visual censuses (*Siganus canaliculatus*) was responsible for consuming the majority of the *Sargassum* assays (Fox and Bellwood 2008a). At the same location a single species of batfish *Platax pinnatus* was almost solely responsible for reversing an experimentally-induced phase shift dominated by *Sargassum*, while the local ‘herbivorous’ fish fauna had little impact

(Bellwood et al. 2006). It is therefore possible that removal rates at Lizard Island are driven by species that are underestimated in visual surveys.

Variation in the benthic algal community may have influenced the relative palatability of the *Sargassum* assays among habitats and subsequently the removal rates recorded in the present study. While this may directly affect the food or algal choice within the entire guild of herbivorous fishes, it appears unlikely to influence the food choice of those species that browse on erect brown macroalgae on Lizard Island. Of all the macroalgal species recorded within the seven habitats in the present study, all have been demonstrated to be less susceptible to fish grazing than *Sargassum* on the GBR (Mantyka and Bellwood 2007). *Galaxaura*, the most abundant macroalga on Lizard Island, and *Chlorodesmis* have been shown to be largely resistant to fish grazing (Paul and Hay 1986; Mantyka and Bellwood 2007). The calcified macroalgae, *Amphiroa* and *Halimeda*, while moderately susceptible to grazing are primarily consumed by scraping (*Hipposcarus longiceps* and *Scarus rivulatus*) and excavating (*Chlorurus microrhinos*) parrotfishes (Mantyka and Bellwood 2007). Although widely distributed, the cover of erect brown macroalgae was low across all habitats on Lizard Island. This, coupled with the lower susceptibility of other erect brown macroalgae species to grazing (*Turbinaria*: 79 %.3h^{-1}, *Padina*: 93.% 3h^{-1}; cf. *Sargassum* 96 %.3h^{-1}; Mantyka and Bellwood 2007) suggest that the grazing of *Sargassum* assays was unlikely to be influenced by among habitat variation in the benthic algal community.

The relatively high rates of removal of *Sargassum* across all shallow water habitats in the present study provide support for the overriding role of herbivory in limiting the abundance of *Sargassum* on mid-shelf reefs of the GBR (McCook 1996). Even on the deeper reef slope habitat over half the *Sargassum* mass was removed in 7 days. *Sargassum* is seasonally abundant on shallow inshore habitats and virtually absent on all mid- and outer-shelf reef habitats on the GBR (McCook and Price 1997). When protected from large herbivores the biomass of *S. swartzii* displayed varying responses, increasing on the back reef and decreasing on the reef crest over a 7-day period. This variation between habitats suggests that while water quality parameters may be sufficient for growth, physical properties such as wave action may limit the distribution of *Sargassum* from some areas, such as the exposed reef crest. Even with the limited spatial replication of the present study (i.e., one reef and two sites per habitat) that precludes generalizations across other mid-shelf reefs, among habitat differences were detected suggesting that the observed differences were related to habitat features, rather than purely spatial variation.

While the among habitat removal rates of the two species of *Sargassum* displayed broadly similar patterns, the reduction in biomass of *S. cristaefolium* was consistently lower than that of *S. swartzii* in the three sheltered habitats (i.e., sheltered reef base, sheltered reef flat and patch reef). These lower rates of removal may reflect the differential response of the herbivore communities in these habitats to variation in morphological and chemical defenses or nutritional quality of the algae. Interspecific variation in both the chemical and morphological defenses of marine algae has frequently been related to the relative susceptibility of algal species to grazing (e.g., Littler et al. 1983; Hay and Fenical 1988). Steinberg et al. (1991) reported high levels of variation in removal rates amongst seven tropical (ca 15 - 90 $\%.6h^{-1}$) and four temperate (ca 0 – 80 $\%.6h^{-1}$) species of *Sargassum* transplanted to the leeward reef slope of a mid-shelf reef in the central GBR. However, they reported that the variation in removal rates displayed no relationship with the concentration of phenolic compounds, the most common chemical defense in phaeophytes (Steinberg et al. 1991). In contrast, Pennings and Paul (1992) demonstrated that physical toughness in two species of *Sargassum* was directly related to herbivory by an opistobranch gastropod, with the force required to penetrate the thallus of *S. cristaefolium* being almost double that required for *Sargassum polycystum*. Although measures of physical toughness were not quantified in the present study, *S. cristaefolium* appeared to be more robust, possessing thick ovate blades with duplicate margins (Trono 1998). In contrast, *S. swartzii* had relatively thin lanceolate blades. Physical toughness may therefore be a significant factor in driving the variation in herbivory on the two species in the present study.

Macrophyte (seagrass and algae) assays have been used extensively to quantify variation in browsing intensity among locations (Hay 1984; Lewis 1985, 1986; Lewis and Wainwright 1985; McClanahan et al. 1994), to examine susceptibility of various algal species to herbivory (Steinberg et al. 1991; Mantyka and Bellwood 2007), to demonstrate the relative contribution of herbivory in shaping benthic community structure (Hay 1981; McCook 1996), or to examine ecosystem health (Littler and Littler 2007). Despite the widespread application of algal assays, large variations in methods make direct comparisons among studies difficult. While the duration of the assays and focal species may be tailored to specific questions, there is a pressing need to standardize the metric used to quantify the removal of assay material. Studies using *Sargassum* assays have reported losses based on the proportional change in length (Fox and Bellwood 2008a) or mass (Lewis 1985; McCook 1996, 1997; Mantyka and Bellwood 2007), and the proportion of assays completely removed (Hay 1981; Steinberg et al. 1991) or with feeding marks evident (McClanahan et al. 1994; Marques et al. 2006). Such methodological differences may have a significant influence on estimates of both absolute and relative rates of herbivory. For example, Bellwood et al. (2006) estimated a 50% reduction in the thallus surface area of a large stand of

Sargassum over a 5-day period, yet reported little change in height over the same period. A standard method would have great benefit for comparative purposes.

Direct quantification of grazing intensity using assays revealed a different pattern to that which may be inferred based on herbivore densities. While not providing a comprehensive assessment of all aspects of herbivory, the assays provided overwhelming support for the role of herbivory in limiting macroalgal abundance on mid-shelf reefs on the GBR. The capacity of a reef system to remove erect macroalgae is a key component in maintaining a healthy balance between corals and benthic algae following disturbances. The intense browsing across all shallow habitats not only suggests there is a high degree of resilience among these habitats, but also for the reef as a whole. While assays have been used to quantify herbivory on reefs with depleted herbivore faunas (i.e., Caribbean and east African reefs) their use on more intact systems such as the GBR has been limited. The use of assays in relatively intact systems may provide further insight into the mechanisms that not only shape algal distributions but also those that promote the resilience of coral reefs.

Chapter 3: Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs

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3.1. Introduction

The loss of biodiversity across local, regional, and global scales and the collapse of numerous terrestrial, freshwater and marine ecosystems (Scheffer et al. 2001; Folke et al. 2004) has intensified research into the relationship between biodiversity and ecological function (e.g., Cardinale et al. 2006). Biological diversity has long been argued to be a source of ecological stability, with increasing diversity providing a degree of insurance (or resilience) against natural and anthropogenic stressors (e.g., Holling 1973; Yachi and Loreau 1999; Folke et al. 2004). While the nature of this relationship is complex, increasing species richness is assumed to increase both the interspecific diversity of responses to environmental changes (i.e., response diversity: Elmqvist et al. 2003) and the number of species that contribute to any particular ecosystem function (i.e., functional redundancy: Walker 1992). The existence of such relationships is, however, dependent on the functional characteristics of the component species and the ecosystem process being considered.

Coral reefs are one of the world's most biologically diverse ecosystems, yet despite this diversity several coral reef systems have undergone phase shifts from coral- to macroalgal-dominance (Hughes 1994; McClanahan et al. 2001; Graham et al. 2006). Whilst such shifts have been triggered by a range of perturbations (including coral bleaching, hurricanes, eutrification and disease), regional reductions in herbivorous fishes through overfishing often underpins the degradation of these reefs (Hughes 1994;

Bellwood et al. 2004; Mumby et al. 2006). These changes have highlighted the importance of herbivores in maintaining a healthy balance between corals and algae, and the resilience of the system as a whole. Reduced grazing by herbivorous fishes has also been linked to reductions in the survival, fecundity and recruitment of corals (Jompa and McCook 2002a, b; Hughes et al. 2007; Mumby et al. 2007), further limiting the capacity of these reefs to regenerate.

Traditionally studies examining herbivory on coral reefs have adopted correlative approaches, relating spatial variation in the distribution of algal communities or the removal of macrophyte assays (i.e., transplanted pieces of seagrass or macroalgae) to the distribution of herbivorous fishes across similar scales (Sluka and Miller 2001; Newman et al. 2006). The problems with such approaches are twofold. Firstly, the majority of these studies have viewed herbivory as a uniform process, with all taxa having a similar impact on the system. There is, however, considerable variation in feeding behaviour in reef fishes, both among and within taxonomic groups. This variation has been demonstrated to be functionally significant, influencing the structure of algal communities (Ceccarelli et al. 2005a; Burkepile and Hay 2008). Secondly, correlative approaches infer function from presence. They are based on the implicit assumption that species exert a functional impact that is proportional to their density within a particular location. Whilst this assumption does appear to hold for some fishes, recent evidence using stationary underwater video cameras (first used by Steneck 1983) has demonstrated that this relationship is not likely to hold for all species, especially those that consume erect macroalgae (Bellwood et al. 2006; Fox and Bellwood 2008a). Given the potential importance of macroalgae in coral reef phase-shifts, our ability to successfully manage coral reefs into the future will benefit from a clearer, quantitative understanding of the roles of individual herbivorous fish species and the locations in which these roles are exhibited.

Herbivorous fishes may be broadly classified into four functional groups based on their roles in ecosystem processes: excavators, scrapers, grazers, and macroalgal browsers (Steneck 1988; Bellwood et al. 2004). Whilst excavating, scraping, and grazing taxa generally consume algal turfs, they perform different and complimentary roles in helping reefs to resist shifts to alternate states. In contrast, the removal of adult macroalgae by herbivorous fishes (i.e., macroalgal browsers) appears to represent a separate but critical process in the reversal of phase-shifts (Bellwood et al. 2006). Recent studies on the Great Barrier Reef (GBR), one of the world's most intact coral reef systems, have demonstrated that only a few species are responsible for the removal of erect brown macroalgae within this system (Bellwood et al. 2006; Mantyka and Bellwood 2007; Fox and Bellwood 2008a; Cvitanovic and Bellwood 2009). However, all of these studies were spatially restricted. All were conducted on the leeward side of a single inshore island, with the majority restricted to a single bay and/or a single habitat. Identifying the species contributing to this function across a range of spatial scales is central to our understanding of this process and the resilience of the system as a whole (Peterson et al. 1998; Nyström and Folke 2001).

Within the GBR, there is a marked separation of inshore reefs from mid- and outer-shelf reefs in benthic composition, herbivore community structure, environmental parameters and ecosystem processes (Fabricius and De'ath 2001; Hoey and Bellwood 2008; Wismer et al. 2009). Erect brown macroalgae, in particular *Sargassum* spp. (Ochrophyta: Phaeophyceae), are a dominant feature of shallow coastal reefs where they form dense stands up to 3 m in height which can cover over fifty percent of the substratum (Bellwood et al. 2006; Wismer et al. 2009). In contrast, erect brown macroalgae are present in low densities on mid- and outer-shelf reefs (McCook et al. 2000). Whilst variation in grazing intensity has been shown to be a primary determinant of *Sargassum* distributions on mid-shelf reefs of the GBR (McCook 1996), the identity of the species responsible for this process are not known. The aim of this study, therefore, was to identify the species responsible for removing erect brown macroalgae across multiple mid-shelf reef habitats on the GBR, and in doing so, to quantify the extent of functional redundancy within and amongst habitats. The identification of these species is an essential step to understanding the resilience of these habitats, and the reef as a whole.

3.2. Materials and Methods

Study location

The study was conducted during a three week period in November 2007 on Lizard Island (14°40’S, 145°28’E) in the northern GBR (Fig. 3.1). Six habitats of varying wave exposure and depth were selected to examine among-habitat variation in the rates of macroalgal removal and to identify the species responsible for consuming the macroalgal biomass (Fig. 3.1c). Three habitats were located on the south-east aspect of the reef and directly exposed to the prevailing south-east trade winds: the exposed reef crest (2 – 4 m depth), flat (1 – 2 m) and back reef (2 – 4 m). The remaining three habitats were located on the leeward or sheltered side of the island: a patch reef habitat (4 – 6 m depth), a sheltered reef flat (1 – 2 m) and sheltered reef base (6 – 8 m) on a fringing reef on the north-western side of the island (Fig. 3.1c).

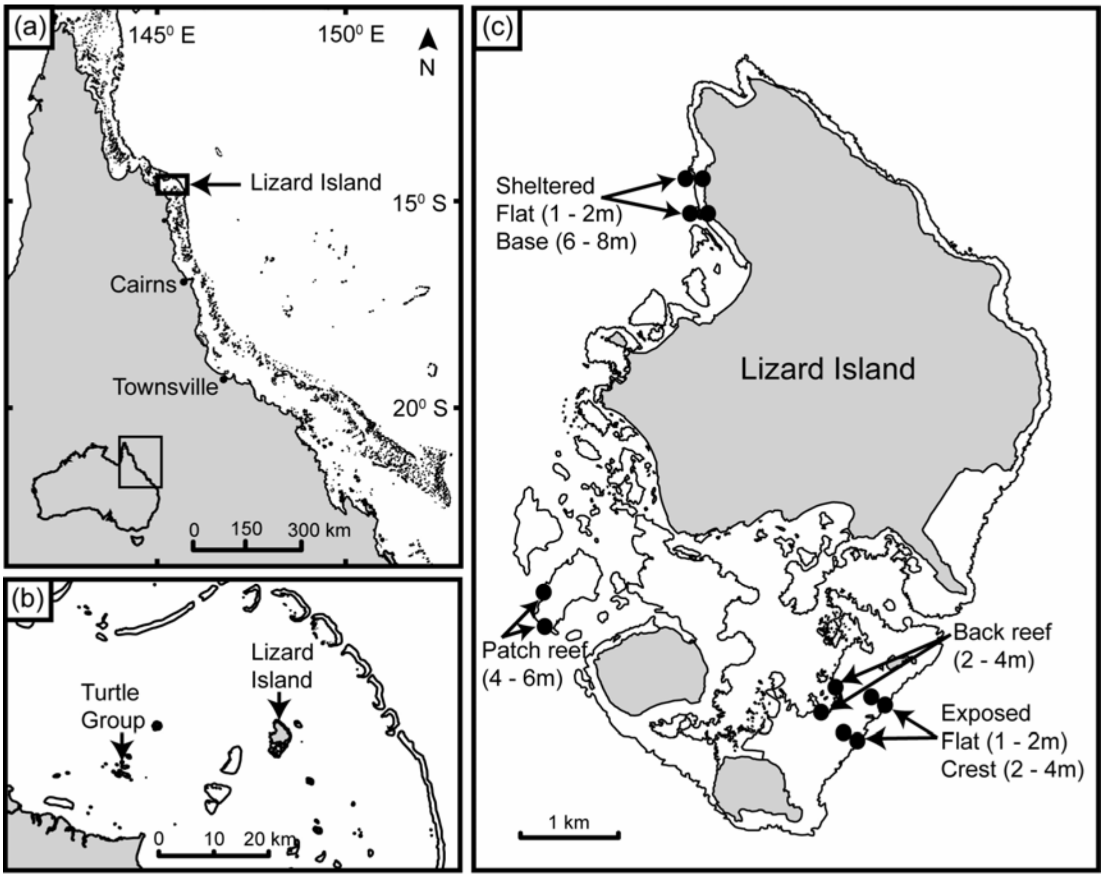

Fig 3.1: Map of the Great Barrier Reef (GBR) showing the location of the study sites. **(a)** Geographic location of Lizard Island. **(b)** Position of Lizard Island across the continental shelf in the northern GBR. The location of the Turtle Group, the site of collection of *Sargassum swartzii*, on the inner-shelf is also given. **(c)** Map of Lizard Island indicating the location of each of two sites within the six habitats of varying water depth and wave exposure. The prevailing wind is from the southeast.

Benthic surveys

To quantify the variation in the algal community and benthic community structure twelve replicate 10 m transects were censused within each habitat (see Chapter 2 for detailed description). Substratum categories follow those defined in Chapter 2. To detect less abundant macroalgal taxa each transect area (i.e., 10 m × 2 m) was systematically searched and the presence of all macroalgal species recorded. Finally, a thorough search of benthic community was also conducted during two 60-80 min surveys within each habitat. Each survey consisted of a diver swimming along a meandering path and examining all non-coral substrata for the presence of any macroalgal taxa.

Macroalgal assays

To quantify variation in the removal of macroalgae amongst habitats a series of macroalgal assays were conducted. *Sargassum swartzii* (Ochrophyta: Phaeophyceae) was collected from the windward reef flat of an inshore reef in the Turtle Island Group (14°43’S, 145°12’E), approximately 28 km west of Lizard Island and 11 km from the mainland (Fig. 3.1b). Individual *S. swartzii* thalli were removed by cutting the holdfast as close to the point of attachment as possible. All *S. swartzii* thalli were returned to Lizard Island and placed in a large (6000 L) aquarium with flow through seawater within 90 min of collection. All thalli were transplanted to the reef within 3 days of collection.

Individual *S. swartzii* thalli were spun, weighed and measured as previously described (Chapter 2). The mean mass of each thallus was 363.6 ± 4.7 g (SE). Five haphazardly selected *S. swartzii* thalli were transplanted to each of two sites within each of the six habitats around Lizard Island for a period of eight hours. Adjacent sites within each habitat were separated by a minimum of 50 m. All assays were deployed between 07:00 and 08:00 h and collected between 15:00 and 16:00 h, encompassing most of the herbivore feeding day. Within each site, one *S. swartzii* thallus was placed inside a free standing exclusion cage (approximately 1000 × 600 × 600 mm; 50 mm square polyethylene mesh) to control for the effects of handling and translocation. The four remaining *S. swartzii* thalli were left exposed to resident herbivores, with adjacent thalli being separated by a minimum of 5 m. All *S. swartzii* thalli were haphazardly placed within each site and attached to the reef using a rubber band and a short length of galvanized wire (0.5 mm diameter). Each *S. swartzii* thallus was individually identified with a small plastic label that was attached to the reef approximately 1.5 m from transplanted *S. swartzii*. After eight hours, all *S. swartzii* thalli were collected and spun and measured as described above. This procedure was replicated three times within each habitat (180 thalli in total), with individual deployments being randomly allocated among sites and habitats over the three-week experimental period.

Video analysis

To identify the fish species removing the macroalgae, stationary underwater digital video cameras (Sony DCR-SR100 HDD cameras in Ikelite housings) were used to record feeding activity on the transplanted *S. swartzii* within each habitat. A camera, mounted on a concrete block, was positioned approximately 2 m from one of the four *S. swartzii* thalli exposed to herbivores at each site within each habitat. Filming commenced immediately after the *S. swartzii* was attached to the reef, with a small scale bar being placed adjacent to each thallus for approximately 10 s to allow calibration of fish sizes on the video footage. Video recording was continuous for the eight hour experimental period, with only a brief (2 – 4 min) interval after four hours to allow for an obligatory battery change. This procedure was replicated three times within each site resulting in 48 hours of video observations for each habitat (288 h in total).

All video footage was viewed and the number of bites taken from the *S. swartzii* by each species and size (total length, TL) of fish was recorded. 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. The biomass of each fish was estimated from published length-weight relationships (Kulbicki et al. 2005).

Diurnal versus nocturnal assays

To quantify variation in the removal of *S. swartzii* between diurnal and nocturnal periods a series of assays were conducted within the exposed reef crest and back reef habitats. *S. swartzii* was collected and processed as previously described prior to transplanting to the reef. The mean mass of each thallus was 373.5 ± 6.9 g (SE). Three haphazardly selected *S. swartzii* thalli were transplanted to each of two sites within the two habitats. Diurnal assays were transplanted to the reef at dawn (~ 05:30) and collected at dusk (~ 18:30). Conversely, nocturnal assays were transplanted at dusk and collected at dawn. This procedure was replicated three times within each habitat.

Distribution of herbivorous fishes

To quantify the abundance of roving herbivores in the study areas, a series of timed swims were conducted in each of the six habitats around Lizard Island. Roving herbivorous fishes were the nominally herbivorous members of the families Acanthuridae, Ephippidae, Kyphosidae, Labridae (parrotfishes), Pomacanthidae, and Siganidae (Choat et al. 2002). Four censuses were conducted within each habitat, with adjacent censuses being separated by a minimum of 20 m. Each census consisted of a diver swimming at a constant depth and parallel to the reef crest, where possible, for 10-min and recording all nominally herbivorous fishes greater than 10 cm TL within a 5 m wide transect that extended from the reef substratum to the surface of the water. A second diver recorded all individuals less than 10 cm TL in a 1 m wide transect. Individual fishes were identified and placed into 5 cm size categories. Care was taken not to re-census fish that left and subsequently re-entered the transect area. Timed swims were selected to minimize observer effects and increase the likelihood of detecting larger roving species. The transect width was selected to maximize the area censused while minimising potential biases associated with variation in underwater visibility among habitats. Numbers per unit effort were converted to densities per unit area by estimating the length of each transect (mean = 118 m, see Bellwood and Wainwright 2001). Density estimates were converted to biomass using length-weight relationships for each species. All censuses were performed between 09:00 and 14:00 h on days that macroalgal assays were not being conducted within those habitats.

Within the guild of herbivorous fishes there is considerable variation in feeding behaviour, which is related to the ability of individual species to consume different algal functional groups. Of those species recorded, *Calotomus carolinus*, *Kyphosus vaigiensis*, *Naso lituratus*, *Naso unicornis*, *Platax pinnatus* and *Siganus canaliculatus* were identified as browsers of erect brown macroalgae (namely Phaeophyceae: *Dictyota*, *Padina*, *Sargassum*, *Turbinaria*) based on diet (Robertson and Gaines 1986; Choat et al. 2002) and direct video observations (Bellwood et al. 2006; Cvitanovic and Bellwood 2009).

Statistical analyses

A three-factor nested ANOVA was used to determine if the rate of removal of *S. swartzii* biomass varied among habitats, sites, or in the presence of a video camera. Two factors, habitat and camera presence, were fixed, with site random and nested within habitat. The analysis was based on the proportion of the initial, or transplanted, biomass removed during eight hours on the reef. Assumptions of the ANOVA were examined by residual analysis and subsequently the proportion of biomass removed was arcsine-square root transformed. The reduction of *S. swartzii* biomass within the exclusion cages was compared among habitats and sites using a two-factor nested ANOVA. A three-factor nested ANOVA was used to determine if the rate of removal of *S. swartzii* biomass varied among time periods (diurnal vs. nocturnal), habitats or sites. The proportion of biomass removed was arcsine-square root transformed to improve normality and homoscedasticity.

Relationships between the rates of removal of the *S. swartzii* and the abundance and biomass of macroalgal browsing species, both collectively and independently, were examined using a series of correlations (with Bonferroni correction). The removal of *S. swartzii* may be dependent on the availability and relative palatability of algae in the vicinity. I therefore calculated a grazing preference index (GPI) for each habitat;

$$\mathrm{GPI} = \Sigma\, p_i .\, c_i ,$$

where p_i is the proportion of biomass removed from the *i*th macroalgal species in a 3-h period (from Mantyka and Bellwood 2007), and c_i is the proportional cover of the *i*th macroalgal species within each habitat (Table 3.1). For the less abundant macroalgal taxa, their cover was estimated to be 0.1 % if they were recorded during the systematic search of each transect area, and 0.05 % if they were identified during extensive searches of the habitat. The GPI was incorporated into the correlation model and partial correlation coefficients calculated to examine the relationships between the grazing intensity of *S. swartzii* and the abundance and biomass of macroalgal browsers.

A simultaneous multiple regression analysis was conducted to determine the impact of each species recorded during video observations on the removal of *S. swartzii* biomass. The number of mass standardized bites for each species was regressed against the reduction in biomass of *S. swartzii*. To increase the power of the analysis all non-macroalgal browsing species that were estimated to have taken less than 0.1 % of the total mass standardized bites were pooled into higher taxonomic groupings.

3.3. Results

The epilithic algal matrix (EAM), or algal turfs, dominated the benthic algal communities of the six habitats around Lizard Island, ranging from 6.6 – 47.0 % (Table 3.1). With the exception of two calcified red alga, *Amphiroa* sp. and *Galaxaura* sp., the cover of macroalgae was low across all habitats. Erect brown macroalgae were rare across all habitats, with the highest cover (5.6 %) being recorded on the exposed reef flat (Table 3.1). Thorough searches of all habitats revealed at least three species of *Sargassum* were present, albeit it in very low densities, on the reefs surrounding Lizard Island. *Sargassum swartzii* was the most widespread species being recorded in four of the six habitats, while *S. polycystum* was restricted to the three sheltered habitats and *S. cristaefolium* was restricted to the exposed reef crest and flat (Table 3.1). Another potential species, *Sargassum* sp. was recorded in the sheltered reef base and back reef habitats, however these thalli were too small (< 5 cm in height) to identify to species.

There were marked differences in the removal rates of *S. swartzii* among habitats ($F_{5,6} = 6.88$, $p = 0.016$) and sites within each habitat ($F_{6,126} = 11.15$, $p < 0.001$). No significant variation was detected in response to the presence of a video camera ($F_{1,126} = 2.29$, $p = 0.13$). There was a clear separation of habitats based on wave exposure, with the three exposed habitats displaying significantly higher reductions in biomass (82 – 87 $\%.8h^{-1}$) than the three sheltered habitats (21 – 31 $\%.8h^{-1}$; Fig. 3.2a). The reduction in biomass of *S. swartzii* held within exclusion cages was consistently low (overall mean = 3.9 $\%.8h^{-1}$) and displayed little variation among habitats ($F_{5,6} = 0.66$, $p = 0.67$) or sites ($F_{6,24} = 0.90$, $p = 0.51$). There was a marked difference between diurnal and nocturnal removal rates of *S. swartzii* ($F_{1,2} = 7628.6$, $p < 0.001$), with diurnal removal rates (94.4 ± 0.4 %) being significantly higher than nocturnal removal

Table 3.1: Summary of the benthic community composition within the six habitats around Lizard Island. Mean percent cover of each of the substrata categories (based on twelve 10 m transects within each habitat) within each habitat are given. Values in parentheses are standard errors. + indicate macroalgae that were present within a transect but not recorded using the point intercept method, * indicate macroalgae that were recorded during an extensive search of each habitat.

	Sheltered			Exposed		
	Base	Flat	Patch	Back	Flat	Crest
Epilithic algal matrix	47.0 (2.7)	18.2 (2.7)	35.4 (2.9)	6.6 (2.4)	35.1 (3.6)	18.7 (1.4)
Crustose coralline algae	+	1.0 (0.6)	0.3 (0.3)	6.8 (2.5)	14.9 (2.3)	13.4 (1.4)
CHLOROPHYTA						
Halimeda spp.	*	+	0.5 (0.5)	2.5 (0.7)	0	0
Chlorodesmis fastigiata	*	*	+	0.3 (0.3)	0	0.5 (0.3)
RHODOPHYTA						
Acanthophora spicifera	*	0	*	0.3 (0.3)	0	0
Asparagopsis taxiformis	0	*	*	0	0	0
Amphiroa sp.	1.7 (0.7)	9.3 (2.0)	1.5 (0.6)	3.5 (1.5)	+	0.8 (0.5)
Galaxaura sp.	8.3 (2.1)	33.3 (3.0)	*	*	0	0
OCHROPHYTA (PHAEOPHYCEAE)						
Dictyota spp.	*	*	0	+	0	0
Padina sp.	+	*	1.0 (0.6)	0.3 (0.3)	0	0
Sargassum cristaefolium	0	0	0	0	1.0 (0.6)	+
Sargassum polycystum	+	*	*	0	0	0
Sargassum swartzii	*	0	+	+	0	+
Sargassum sp.	*	0	0	*	0	0
Turbinaria ornata	0	0	*	0.3 (0.3)	4.6 (1.0)	0.3 (0.3)
Cyanobacteria	0.3 (0.3)	+	+	0.5 (0.3)	*	+
Damselfish territory	12.4 (1.7)	13.9 (1.8)	14.1 (2.6)	16.7 (2.9)	4.3 (0.9)	12.4 (1.7)
Sand & Rubble	9.6 (1.6)	5.1 (1.3)	8.8 (2.5)	25.5 (3.7)	5.8 (1.7)	3.0 (1.0)
Live coral	14.1 (2.0)	11.6 (2.4)	20.5 (3.7)	23.2 (4.3)	13.6 (1.7)	42.2 (2.9)
Soft coral	5.8 (1.8)	7.1 (1.6)	17.9 (3.8)	12.6 (2.1)	20.5 (2.0)	8.8 (2.2)
Other	0.8 (0.4)	0.5 (0.3)	0	1.0 (0.4)	0.3 (0.3)	0

rates (3.2 ± 0.3 %). There was no difference among habitats ($F_{1,2} = 1.63$, $p = 0.33$) or sites ($F_{2,2} = 0.54$, $p = 0.65$).

In contrast to the removal rates of *S. swartzii*, the biomass of macroalgal browsers was generally greater within the three sheltered habitats (72.6 – 106.5 kg.ha^{-1}) than within the three exposed habitats (3.8 – 60.0 kg.ha^{-1}; Fig. 3.2b). Two species, *N. unicornis* and *K. vaigiensis*, dominated the macroalgal browser community, accounting for 51 % and 37 % of the total biomass across all habitats, respectively. With the exception of the exposed reef flat habitat, in which *S. canaliculatus* accounted for 87 % of the macroalgal browser biomass, *N. unicornis* and *K. vaigiensis* collectively accounted for 68 – 100 % of the macroalgal browser biomass within each habitat. Surprisingly, the reduction in *S. swartzii* biomass displayed no relationship to the abundance or biomass of macroalgal browsing species, either collectively or independently, across the six habitats (Table 3.2). Incorporating the grazing preference index into the correlation model and subsequently controlling for the relative availability and susceptibility of the ambient macroalgal community within each habitat had no detectable effect on these relationships (Table 3.2).

Analysis of the video footage revealed that a single species, *N. unicornis*, was almost solely responsible for removing the *S. swartzii* biomass from all six habitats (Fig. 3.2c), with up to eighteen individuals observed feeding at any one time. In total, 42,246 bites from 38 fish species were recorded on the transplanted *S. swartzii* across the six habitats, with *N. unicornis* accounting for 89.8 % of the total bites, and 94.6 % of the total mass standardized bites (Table 3.3). The only other species to take a substantial number of bites from the *S. swartzii* was *K. vaigiensis*, accounting for 4.7 % of the total mass standardized bites, which were largely restricted to the sheltered reef flat (Fig. 3.2c). Each of the remaining 36 species, including the macroalgal browsing *C. carolinus*

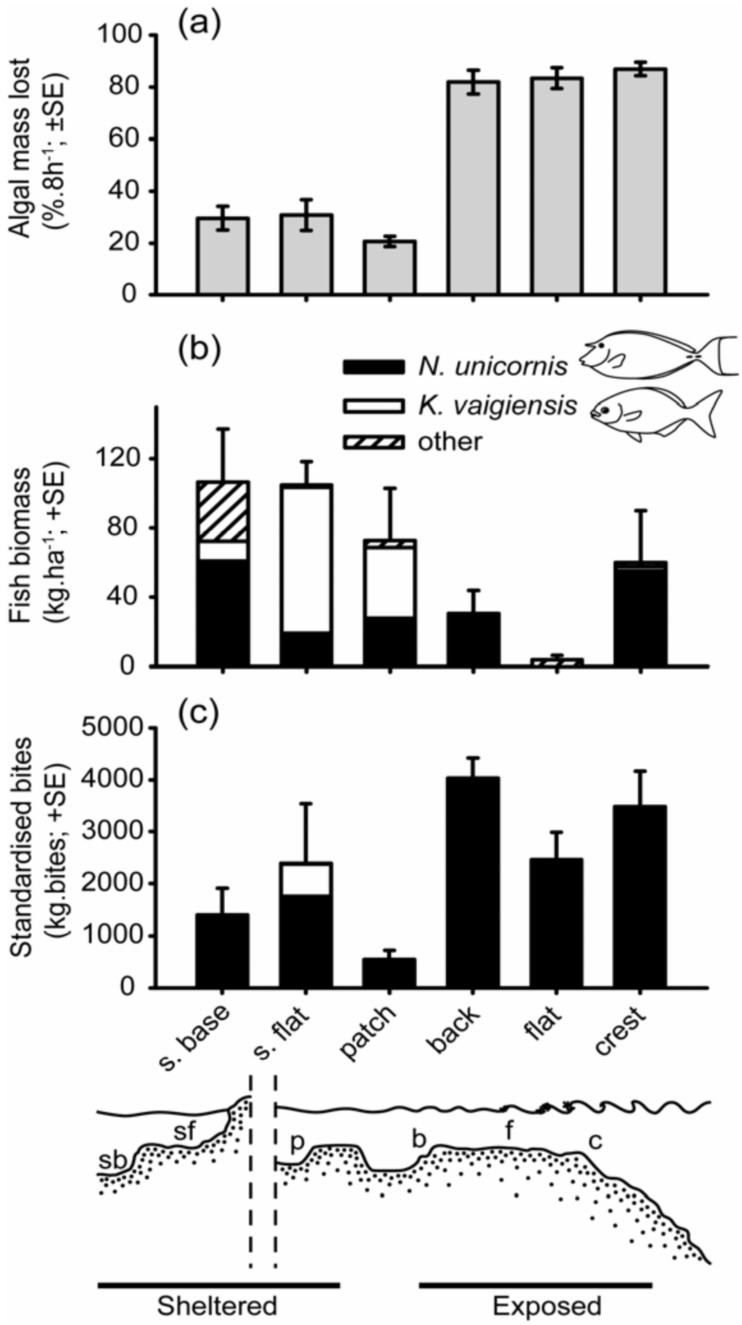

Fig. 3.2: **(a)** Variation in browsing intensity on *Sargassum swartzii* across six habitats of varying exposure on Lizard Island. The means are based on four thalli transplanted for 8 hours into each of two sites within each habitat and replicated over 3 days. **(b)** Mean biomass of browsers of brown macroalgae per hectare estimated from four 10-min underwater visual censuses within each habitat. *Naso unicornis* (filled bar), *Kyphosus vaigiensis* (open bar), and other macroalgal browsers, namely *Calotomus carolinus*, *Naso lituratus*, *Platax pinnatus* and *Siganus canaliculatus* (hatched bar). **(c)** Mean number of mass standardized bites (total bites × body mass in kg) taken by all species from *Sargassum swartzii* within each of six habitats. Sb sheltered reef base, Sf sheltered reef flat, P patch reef, B back reef, F exposed reef flat, C exposed reef crest.

and *S. canaliculatus*, accounted for less than 0.3 % of the total mass standardized bites. No bites were observed for the two remaining macroalgal browsing species, *N. lituratus* and *P. pinnatus*, recorded during the visual surveys. The results of the simultaneous multiple regression analysis showed that only bites taken by *N. unicornis* had a significant influence in explaining the reduction in *S. swartzii* biomass with the overall model explaining 89 % of the variation in the reduction in biomass (Table 3.3).

Table 3.2: Relationship between consumption rates of *Sargassum swartzii* and herbivorous fishes. Correlations are based on the mean proportion of *Sargassum swartzii* biomass removed over an 8h period within each of the six habitats around Lizard Island. Density and biomass estimates are based on the mean of four 10-min timed swims within each habitat. Bonferroni corrected α = 0.006. Partial correlations were calculated controlling for the availability and relative palatability of resident macroalgae within each habitat.

		Bivariate correlation		Partial correlation	
		r	**p**	***ρ***	**p**
All roving herbivores	density	0.698	0.123	0.690	0.197
	biomass	0.471	0.346	0.489	0.404
Macroalgal browsers	density	-0.729	0.100	-0.754	0.141
	biomass	-0.815	0.048	-0.807	0.099
Calotomus carolinus	density	-0.190	0.346	-0.541	0.346
	biomass	-0.525	0.284	-0.898	0.039
Kyphosus vaigiensis	density	-0.618	0.191	-0.712	0.178
	biomass	-0.705	0.118	-0.822	0.088
Naso lituratus	density	-0.662	0.152	-0.837	0.077
	biomass	-0.595	0.213	-0.745	0.149
Naso unicornis	density	0.256	0.625	0.189	0.761
	biomass	-0.158	0.766	-0.338	0.579
Platax pinnatus	density	-0.414	0.415	-0.507	0.383
	biomass	-0.414	0.415	-0.507	0.383
Siganus canaliculatus	density	0.259	0.620	0.387	0.520
	biomass	0.291	0.576	0.398	0.507

Table 3.3: Relationship between herbivore feeding rates and consumption of *Sargassum swartzii*. Results of simultaneous multiple regression analysis examining the relationship between the mass removed from transplanted *Sargassum swartzii* and the number of mass standardized bites taken by each fish species. Overall model $r^2 = 0.893$, $F_{13,22} = 14.172$, $p < 0.0001$. Significant results are highlighted in bold. Total number of bites and mass standardized bites recorded across all habitats are given. *Acanthurus* spp.: *A. blochii*, *A. dussumieri*, *A. nigricauda*, *A. nigrofuscus*, *A. olivaceus*; *Naso* spp.: *N. annulatus*, *N. brevirostris*, *N. tonganus*; Other acanthurids: *Ctenochaetus striatus*, *Zebrasoma scopas*, *Z. velliferum*; *Pomacanthus* spp.: *P. semicirculatus*, *P. sexstriatus*; *Siganus* spp.: *S. argenteus*, *S. corallinus*, *S. puellus*, *S. punctatissimus*, *S. puntatus*; Reef parrotfishes (sensu Streelman et al. 2002): *Chlorurus microrhinos*, *C. sordidus*, *Scarus flavipectoralis*, *S. ghobban*, *S. niger*, *S. rivulatus*, *S. schlegeli*, *S. spinus*; Other taxa: *Chaetodon auriga*, *Chaetodon citrinellus*, *Coris batuensis*, *Hemigymnus melapterus*, *Thalassoma jansenii*, *Sufflamen chrysopterus*.

	Bites	Mass std bites (kg.bites)	β	S.E. of β	t_{22}	p
Macroalgal browsers						
Calotomus carolinus	101	61.3	0.101	0.083	1.221	0.235
Kyphosus vaigiensis	2077	4026.0	0.028	0.159	0.179	0.860
Naso unicornis	37992	81214.4	**0.898**	**0.105**	**8.581**	**< 0.001**
Siganus canaliculatus	17	3.0	0.088	0.078	1.139	0.267
Other herbivores						
Acanthurus spp.	474	156.2	0.165	0.090	1.821	0.082
Naso spp.	99	96.8	-0.009	0.180	-0.050	0.960
Other acanthurids	27	4.8	-0.087	0.129	-0.672	0.508
Kyphosus cinerescens	5	5.5	-0.146	0.182	-0.801	0.431
Pomacanthus spp.	23	6.2	-0.018	0.076	-0.244	0.810
Siganus doliatus	1210	202.6	0.133	0.094	1.424	0.169
Siganus spp.	160	18.5	0.143	0.150	0.953	0.351
Reef parrotfishes	28	8.7	-0.0436	0.097	-0.449	0.657
Other taxa	33	1.9	0.118	0.078	1.515	0.144

3.4. Discussion

Despite the reefs around Lizard Island supporting over fifty roving herbivorous fish species and six macroalgal browsing species, a single species, *Naso unicornis*, was almost solely responsible for performing a key ecological process; the removal of erect brown macroalgae. Traditionally, species diversity within a functional group is assumed to confer a degree of redundancy within group members (Holling 1973; Chapin et al. 1997; Folke et al. 2004; but see Bellwood et al. 2003). Our results, however, highlight the potential for single-species functional groups, even in exceptionally species-rich ecosystems. The reliance on a single species across a range of habitats not only emphasizes the apparent lack of functional equivalents within each habitat, but also among habitats separated by several kilometres. This limited redundancy, both within and across local (1 – 10 km) scales, underscores the need to assess the functional roles of individual species when formulating strategies to maintain the resilience of these ecosystems.

Consumption rates of adult *S. swartzii* in the present study were broadly comparable to those previously recorded on both inner- and mid-shelf reefs on the GBR (McCook 1996; Cvitanovic and Bellwood 2009) and provide additional support for the role of herbivory in structuring the distribution of *Sargassum* within these reefs. However, it is the identity of the species responsible for the macroalgal removal that is central to our understanding of this process and the management of the resilience of coral reefs. *N. unicornis* was the dominant consumer of adult *Sargassum* across all habitats in the present study, despite considerable among-habitat variation in the community structure of macroalgal browsing fishes. Although the diversity of macroalgal browsing fishes is low when compared to other functional groups of reef fish (Bellwood et al. 2004; Nyström 2006), the apparent lack of redundancy both within and among habitats was striking. The rapid and almost complete consumption of the bioassays by *N. unicornis* within the three exposed habitats (82 – 87 %.8h^{-1}) could be argued to have precluded other macroalgal browsing species access to this resource. However, the lower consumption rates within the three sheltered habitats (21 – 31 %.8h^{-1}), together with the estimated greater biomass of other macroalgal browsing species within these habitats, suggest that these species may have a limited capacity to compensate for the loss of *N. unicornis*.

Several studies on inshore GBR reefs have reported the removal of *Sargassum* to be dominated by a single species (Bellwood et al. 2006; Mantyka and Bellwood 2007; Fox and Bellwood 2008a); however, all of these studies have been conducted over small spatial scales (10 – 100 m). The only study to have examined this process over a larger scale (1 -10 km) reported significant variation among three adjacent bays, with a single species dominating the removal of *Sargassum* from the reef crest in each bay (Cvitanovic and Bellwood 2009). Surprisingly, the three species that have been reported to dominate this process on inshore reefs, *K. vaigiensis*, *S. canaliculatus*, and *P. pinnatus*, had little impact on the consumption of *S. swartzii* in the present study, despite visual estimates suggesting they were among the most abundant macroalgal browsing species within three of the six habitats examined. Conversely, none of these studies on inner-shelf reefs have reported any significant feeding by *N. unicornis*, despite being regularly observed in visual censuses of the study sites. These differences among locations and studies highlights the extent of variability in herbivory on coral reefs. These studies share a common pattern (i.e., dominance by one species) yet the species differ markedly among sites. Why these species differ is hard to explain but may include the density or biomass of the *Sargassum* presented, relative palatability or susceptibility of transplanted algae, and the relative densities of the macroalgal browsing species. Each of these issues is considered below.

The majority of previous studies have used methods that are broadly comparable to the present study, and have reported feeding on individual *Sargassum* thalli ranging in mass from 45.7 g (Mantyka and Bellwood 2007) to over 300 g (Fox and Bellwood 2008a). These studies were all conducted, at least in part, within the same location on an inshore island in the central GBR; the reef crest of a fringing reef in Pioneer Bay, Orpheus Island. Collectively, they have reported *S. canaliculatus* or *K. vaigiensis* to be the dominant browsers of *Sargassum*, with no variation in relation to the biomass of individual thalli. In contrast, Bellwood et al. (2006) reported a batfish, *P. pinnatus*, was responsible for removing most of the *Sargassum* biomass from large (25 m^2) previously caged areas in the same location. These areas represented a much greater biomass of *Sargassum* (5.3 – 8.1 $kg.m^{-2}$), and suggest that the three dimensional structure provided by the 3 m high canopy of *Sargassum* may influence the species that forage in these areas. Similar findings have been reported for African savannahs, where elephants favored areas with high tree density, while smaller herbivores favored areas with low tree density (Riginos and Grace 2008).

Variation in the palatability or susceptibility of transplanted *Sargassum* may also have contributed to the differences in the dominant macroalgal browser among studies. Whilst the *Sargassum* used in the experiments on Orpheus Island were not identified to species, it may be reasonable to assume that they differed from the present study as *S. polycystum* and *S. baccularia* are the most abundant species on those reefs (A. Hoey pers. obs.). Interspecific variation in both the chemical and morphological defenses of terrestrial and marine plants has frequently been related to their relative susceptibility to grazers (Hay 1991; Coley and Barone 1996). However, such relationships appear not to hold among *Sargassum* species. Steinberg et al. (1991) found no relationship between the browsing susceptibility and secondary metabolite concentrations or physical toughness for seven tropical and four temperate species of *Sargassum* on a mid-shelf reef on the GBR. Chemical extracts from several species of *Sargassum* have also been shown to have no effect on feeding by fishes (Steinberg and Paul 1990) or urchins (Bolser and Hay 1996). Furthermore, Cvitanovic and Bellwood (2009) reported variation in the dominant browser of *Sargassum* sp. among adjacent bays, suggesting that interspecific variation in the susceptibility of *Sargassum* may not be a primary factor determining the dominant browser in this system.

The susceptibility of a species to herbivores is not, however, simply a function of its absolute palatability, but rather its palatability relative to those of co-occurring species (Atsatt and O'Dowd 1976). Therefore, the feeding response of macroalgal browsers may be influenced by the availability and relative palatability of algal communities within each location, or by the presence of epiphytic algae on the *Sargassum* itself. The present study was the first to examine the influence of resident algal communities on the removal rates of *Sargassum*. Although this did not explain the among-habitat variation the removal of *S. swartzii* in the present study, the densities of macroalgae were generally low across all habitats. In contrast, macroalgal cover is typically high on inshore reefs of the GBR (Done et al. 2007; Wismer et al. 2009), and may influence the relative attractiveness of the transplanted algae. In previous studies on inshore reefs, macroalgal densities are greatest on the reef flat (Fox and Bellwood 2007) with large stands of *Padina* and *Sargassum* often occurring within 20 – 40 m of the reef crest. This algal resource has been hypothesized to be largely unavailable to herbivorous fishes due to various factors that limit access to the reef flat (for example, predation risk and structural complexity: Fox and Bellwood 2008a). In the present study, *N. unicornis* fed intensively on both the exposed and sheltered reef flats, suggesting that access to the reef flat may not be limiting for this species. The presentation of *Sargassum* on the crest of inshore reefs may, therefore, not have represented an attractive or novel food item to the resident *N. unicornis*, and may explain the lack of feeding by *N. unicornis* despite being present in these locations.

Variation in the epiphytic algal community may also influence the relative palatability of *Sargassum*. For example, the presence of epiphytic algae has been demonstrated to induce urchin grazing on a temperate *Sargassum*, a species that was otherwise avoided by the urchins (Wahl and Hay 1995). Whilst epiphyte communities were not quantified, *Sargassum* growing on fringing reef flats on the leeward side of Orpheus Island has relatively high loads of epiphytes and associated fine sediments/detritus (Lefèvre and Bellwood 2010). In contrast, the *Sargassum* used in the present study was collected from the windward reef flat and had a very low load of epiphytes. These differences may be reflected in the relative proportion of bites taken by non-macroalgal browsing fishes among studies. Feeding by these fishes, in particular *Siganus doliatus*, accounted for approximately half of all bites taken from studies at Orpheus Island (Fox and Bellwood 2008a; Cvitanovic and Bellwood 2009), but collectively these fishes accounted for less than 5 % of the bites in the present study. Feeding by these species, however, had little impact on the reduction of *Sargassum* biomass in the present study suggesting that they were selectively cropping the epiphytes and not removing underlying *Sargassum*.

Seasonal variation in herbivore preferences have been documented in response to varying prey availability and quality across a range of terrestrial and aquatic ecosystems (Owen-Smith 1994; Shepherd and Hawkes 2005). Although this is potentially important as macroalgal display strong seasonal patterns on coral reefs

(Martin-Smith 1993), the timing of previous studies are broadly comparable and all have coincided with the peak in *Sargassum* biomass (Nov – Mar). Variation within this period appears to be minimal with *S. canaliculatus* being identified as the dominant browser on inshore reefs in both December (Fox and Bellwood 2008a) and March (Mantyka and Bellwood 2007). Furthermore, *N. unicornis* was observed feeding on *Sargassum* during initial trials on the exposed reef crest and back reef habitats at Lizard Island from September to mid-January.

Perhaps the most intuitive explanation for the variation among studies is the relative densities of the macroalgal browsing species. However, the among-habitat variation in consumption rates of *S. swartzii* in the present study displayed no relation to visual estimates of density or biomass of *N. unicornis*, or all macroalgal browsing fishes collectively. This lack of relationship between visual estimates and functional impact appears to be a common occurrence for macroalgal browsing fishes on the GBR, with the dominant species often not being recorded within the study sites (Bellwood et al. 2006; Fox and Bellwood 2008a; Cvitanovic and Bellwood 2009). Whilst *N. unicornis* was recorded in visual censuses in five of the six habitats examined in the present study, the density estimates did not reflect their functional impact in each habitat. For example, only one individual was recorded during visual censuses of the exposed reef flat, yet groups of up to fourteen individuals were frequently recorded feeding on *S. swartzii* within that habitat. Such disparity may reflect the 'wary' nature of *N. unicornis* (Myers 1991) resulting in negative responses to diver presence (Kulbicki 1998), or be related to their relatively large home ranges (Meyer and Holland 2005). Irrespective of the mechanism, these results highlight the potential difficulties when using correlative approaches and the inherent dangers of evaluating ecosystem processes and resilience based on visual census data alone.

Invertebrate grazers, in particular urchins, are often viewed as key components of the herbivorous fauna on some coral reefs, especially those subject to overharvesting of herbivorous fishes (Hughes 1994). Many of these grazing macroinvertebrates are nocturnally active (Carpenter 1997) and would not have been captured by the video observations in the present study. However, the limited reductions in algal biomass from both nocturnal and caged diurnal transplants suggest that invertebrates were not important browsers of adult S*argassum* in this system. This is supported by studies that have found urchins and other grazing invertebrates have a low preference for *Sargassum* (Cruz-Rivera and Paul 2006; Coppard and Campbell 2007).

The results of the present study highlight the potential importance of *N. unicornis* on mid-shelf reefs of the GBR, and may have implications for other Indo-Pacific reefs. *Naso unicornis* is a widespread species, ranging from the Red Sea to French Polynesia, and from Japan to Lord Howe Island (Myers 1991), where it is a common member of herbivorous fish communities. Throughout much of its range erect brown macroalgae (namely *Sargassum*, *Turbinaria* and *Dictyota*) have been reported to be the dominant food items (GBR: Choat et al. 2002; Hawaii: Jones 1968; Micronesia: Myers 1991; Seychelles: Robertson and Gaines 1986). Even on mid- and outer-shelf reefs on the GBR, where macroalgal cover has been reported to be low (< 1 %: Wismer et al. 2009), fleshy brown macroalgae accounted for approximately two-thirds of the stomach content volume (Choat et al. 2002). Whilst the generality of the role of *N. unicornis* on other Indo-Pacific reefs cannot be assumed without further investigation, the predominance of erect brown macroalgae in the diet coupled with the widespread distribution suggests that such generalities may be expected.

The reliance on a single species performing a key ecological role across a range of habitats highlights the potential vulnerability of these reefs to disturbance. The importance of this role may only be realized on reefs facing increased macroalgal abundance, such as the preliminary stages of a phase-shift (Hughes et al. 2007). On 'healthy' coral-dominated reefs the majority of the algal production is consumed by a diverse assemblage of grazing fishes and invertebrates (Polunin and Klumpp 1992). However, once established the removal of macroalgae is dependent on a smaller suite of species, a critical functional group, which, if overharvested, may be incapable of reversing this condition (cf., Ledlie et al. 2007).

Naso unicornis is a large (up to 700 mm TL) and long-lived species (up to 30 years: Choat and Axe 1996) making it extremely susceptible to fishing pressure. Given the potential importance of *N. unicornis* in the regenerative capacity of reefs, it is a sobering fact that this species is targeted by commercial, recreational, and artisanal fisheries throughout much of its range (Fig. 3.3), often forming a large proportion of the total catch (Dalzell et al. 1996; Rhodes et al. 2008; Appendix B). The limited available evidence suggests that this fishing pressure has already reduced the abundance and size

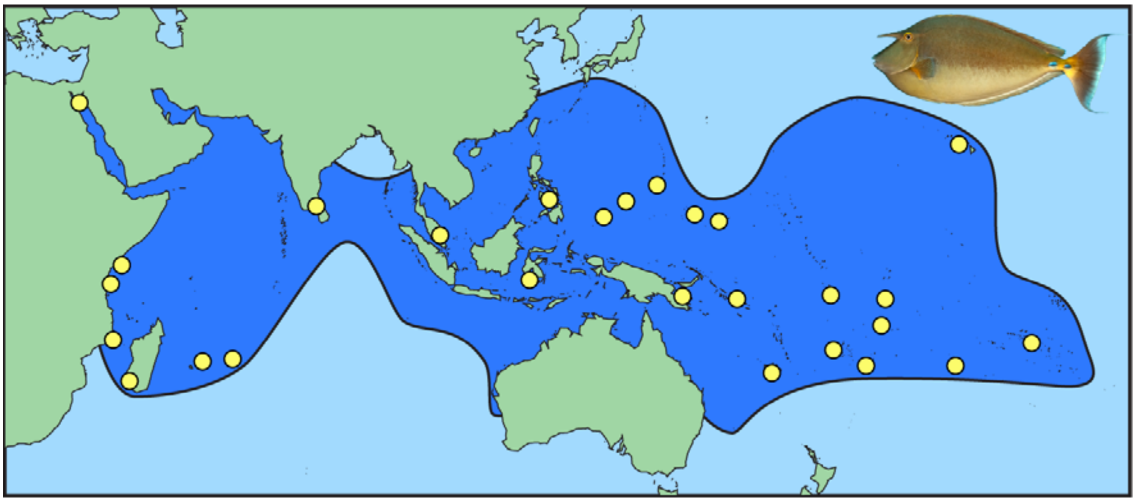

Fig. 3.3: Geographic range and spatial extent of fishing pressure for the bluespine unicornfish, *Naso unicornis*. Locations where it is targeted by commercial, artisanal, or recreational fishers are indicated by yellow circles. The sources of the fisheries data are given in Appendix B.

structure of several of these populations (Wantiez et al. 1997; Rhodes et al. 2008). Whilst the consequences of such exploitation to reef health may not be readily apparent, this change in population structure could combine with other events to bring around a shift in the control of macroalgae. Given the importance of this single species, management and conservation strategies may need to look beyond the preservation of species diversity and focus on the maintenance of ecological processes and the protection of key species in critical functional groups.

Chapter 4: Cross-shelf variation in browsing intensity on the Great Barrier Reef

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4.1. Introduction

Herbivory is widely accepted as a key process determining the structure and resilience of both terrestrial and aquatic ecosystems (McNaughton 1984; Burkepile and Hay 2006). Within coral reef ecosystems, the removal of roving herbivorous fishes through overfishing has underpinned shifts from coral- to macroalgal-dominance on several Caribbean and east African reefs (Hughes 1994; McClanahan et al. 2001; Graham et al. 2006). The degradation of these reefs has highlighted the importance of herbivores in structuring algal communities and maintaining a healthy balance between corals and macroalgae (Bellwood et al. 2004; Mumby et al. 2006). The collective loss of all roving herbivorous species and the subsequent degradation of those reefs may imply that herbivory is a uniform process, or that each species has a similar impact on the system. There is, however, considerable variation in feeding behaviour among herbivorous taxa.

Roving herbivorous fishes may be broadly classified into two functional groups (i.e., grazers and browsers) based on the algal material they target (Steneck 1988; Bellwood et al. 2004). Grazing taxa (including scraping and excavating parrotfishes) typically feed on the epilithic algal matrix, or algal turfs (EAM; sensu Wilson et al. 2003), and play an important role in helping reefs to resist shifts to alternate states and reassemble following disturbances (Bellwood et al. 2004; Nyström 2006). Recent studies have shown, however, that these fishes have a limited capacity to remove erect brown, or leathery, macroalgae from the reef (Bellwood et al. 2006; Chapter 3). The removal of leathery macroalgae, in particular *Sargassum*, appears to be restricted to a small suite of species (hereafter referred to as browsers) and represents a separate but critical process on coral reefs (Bellwood et al. 2006). Quantifying the impact of these different herbivore groups is, therefore, will greatly benefit our understanding and management of these ecosystems. Inferences from visual census estimates have been used to successfully model the functional impact of grazing taxa across a range of spatial scales (e.g., Mumby 2006; Hoey and Bellwood 2008); however such approaches appear problematic for browsing taxa (Bellwood et al. 2006; Chapter 3). One of the most useful methods to quantify browsing intensity on coral reefs has been bioassays.

Macrophyte assays (i.e., transplanted pieces of seagrass and macroalgae) have been used extensively to directly quantify herbivory across a range of scales on Caribbean reefs; from local (Hay 1981; Lewis 1985, 1986) to regional (Hay 1984; Paul and Hay 1986) scales. In contrast, macrophyte assays have only been used over relatively small, within-reef, spatial scales on Indo-Pacific reefs (e.g., McClanahan et al. 1999; Sluka and Miller 2001; see McCook 1996 for exception). On the Great Barrier Reef (GBR), the world's largest coral reef system, the vast majority of these studies have been conducted on a single inshore island, Orpheus Island, in the central GBR (Mantyka and Bellwood 2007; Fox and Bellwood 2008a; Cvitanovic and Bellwood 2009). These studies have provided useful insight into the potential role of macroalgal browsers in structuring algal communities on this inshore reef system; however little is known of this process across broader spatial scales. Quantifying the removal of macroalgae and identifying those species responsible for removing the algal biomass across a range of scales is fundamental to our understanding of the processes that structure these systems.

Within the GBR, there is a marked separation of inshore reefs (approximately 5 – 20 km offshore) from mid- (30 – 60 km offshore) and outer-shelf (50 – 100 km offshore) reefs in benthic composition, herbivore community structure, environmental parameters and ecosystem processes (Fabricius and De'ath 2001; Hoey and Bellwood 2008; Wismer et al. 2009). Leathery macroalgae, in particular *Sargassum* spp. (Ochrophyta: Phaeophyceae), is a dominant feature of inshore reefs on the GBR where it often forms dense stands up to 3 m in height and can cover in excess of fifty percent of the substratum (McCook at al. 1997; Wismer et al. 2009). Leathery macroalgae is less abundant on mid-shelf reefs (< 5% cover; Chapter 2, 3), and has been recorded but usually uncommon on outer-shelf reefs (McCook et al. 2000). This variation in macroalgal cover has been shown to be negatively related to the biomass of roving herbivorous fishes collectively, but not to that of macroalgal browsers (Wismer et al. 2009).

To date, all studies that have identified the species responsible for removing adult *Sargassum* have been restricted spatially, being conducted on a single island or reef. Several recent studies on Orpheus Island, an inshore reef in the central GBR, have demonstrated that the removal of *Sargassum* bioassays is dominated by two species, *Kyphosus vaigiensis* and *Siganus canaliculatus* (Mantyka and Bellwood 2007; Fox and Bellwood 2008a; Cvitanovic and Bellwood 2009). In contrast, the only study to have examined this process beyond inshore GBR reefs, found that *Naso unicornis* was almost solely responsible for removing adult *Sargassum* from multiple habitats surrounding Lizard Island, a mid-shelf reef in the northern GBR (Chapter 3). Whilst temporal and latitudinal variation among studies precludes any direct comparisons, collectively these studies suggest that the relative importance of individual browsing species may change across the continental shelf. Quantifying the rates and agents of macroalgal browsing, and how they vary across the continental shelf is important if we are to understand the processes that structure algal communities.

The aims of this study were to: 1) directly quantify variation in intensity of browsing on *Sargassum* assays across several reefs spanning the continental shelf in the northern GBR; 2) examine the relationship between browsing intensity, the biomass of macroalgal browsing fishes and distribution of macroalgal communities across the same scale; 3) identify the species responsible for removing *Sargassum* biomass from these reefs. In doing so this study will, for the first time, quantify rates of macroalgal browsing across the entire continental shelf and determine the extent of functional redundancy within this process across multiple reefs.

4.2. Materials and Methods

Rates of macroalgal removal

Study sites

This study was conducted during January – February 2007 on six reefs spanning the continental shelf in the northern section of the GBR (approx. 14°40’S; Fig. 4.1). Two reefs were selected from each of three cross-shelf locations: inner-, mid-, and outer-shelf. Two reefs within the Turtle Island Group (11 – 15 km from the mainland) were selected as inner-shelf reefs, MacGillivray Reef and Lizard Island (28 – 35 km) as mid-shelf reefs, and Day Reef and Hicks Reef (48 – 53 km) as outer-shelf reefs (Fig. 4.1). Within each of these reefs two habitats, the reef crest and back reef, were selected to examine cross-shelf variation in the distribution of macroalgae and herbivorous fishes, and the intensity of macroalgal browsing. The reef crest was located on the south-east aspect of each reef and directly exposed to the prevailing south-east trade winds. The reef crest (2 – 4 m depth) was the region that marked the transition between the steeply inclined seaward reef slope and the extensive shallow region of the reef. The two inner-shelf reefs lacked a clearly defined reef crest with the reef gently sloping from a sand base at a depth of 6 – 12 m to a reef flat (0.5 – 2 m depth). The reef crest on the inner-shelf reefs was, therefore, defined as the region on the south-eastern aspect of the reef at a depth of 2 - 4 m, depending on tidal height. The back reef was at the leeward margin of the reef flat at a depth of 2 – 4 m and marked the transition from the reef flat to deeper habitats dominated by sand. These two habitats were selected as they are located in similar water depth but are subject to markedly different wave and current intensities (Fulton and Bellwood 2005).

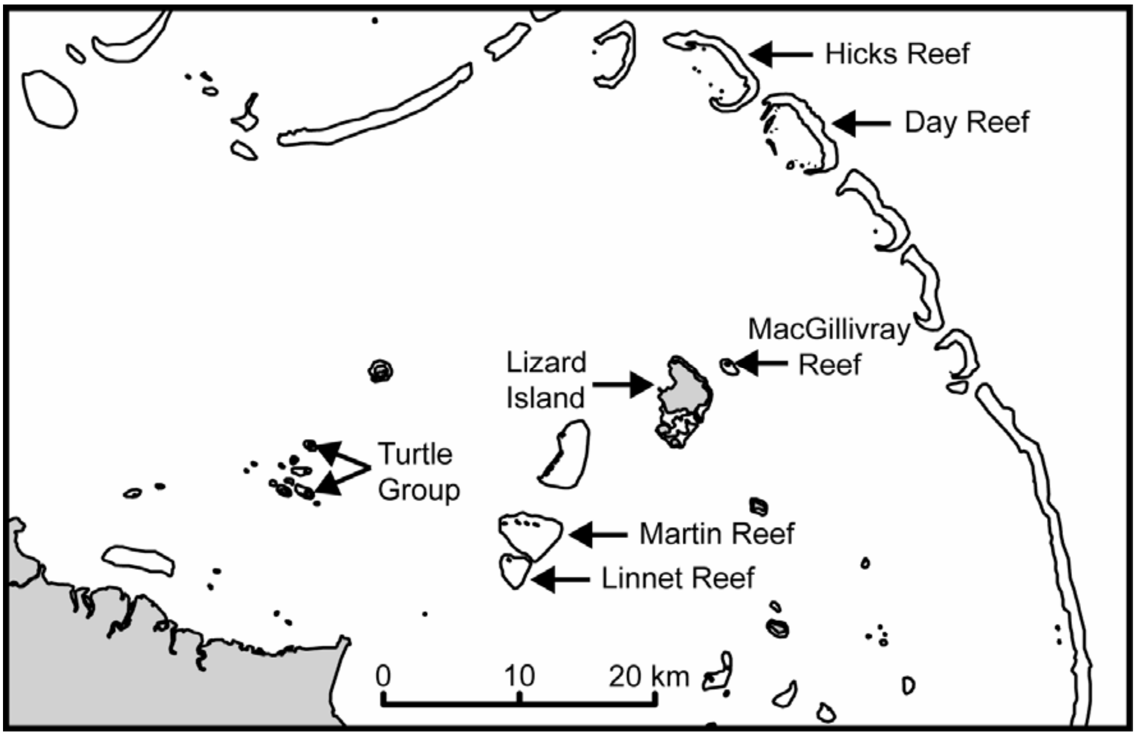

Fig. 4.1: Map of the northern Great Barrier Reef (GBR) showing the position of the eight study reefs across the continental shelf. The two reefs in the Turtle Group were the inner-shelf reefs, Martin and Linnet Reefs were the intermediate inner/mid-shelf reefs, Lizard Island and MacGillivray Reef the mid-shelf reefs, and Day and Hicks Reefs the outer-shelf reefs. Rates of macroalgal removal were quantified across six reefs: two reefs within each of the inner-, mid-, and outer-shelf positions. Agents of macroalgal removal were quantified across all eight reefs.

Distribution of macroalgae and herbivorous fishes

The distribution of macroalgae was quantified across the six reefs using a series of point intercept transects. Six replicate 10 m transects were censused at two sites in each of two habitats (i.e., reef crest and back reef) on each reef. Adjacent sites within each habitat were separated by a minimum of 200 m. Transects were haphazardly placed within each site and, where possible, laid parallel to the reef crest. The substratum immediately under the transect tape and one metre either side was recorded at one metre intervals along the transect, following Chapter 2. Substratum categories follow those defined in Chapter 2. Macroalgae (>10 mm in height) were identified to genus where possible and placed into functional groups (i.e., filamentous, corticated, foliose, leathery, and jointed calcareous) following Steneck and Dethier (1994).

To quantify the distribution of all roving nominally herbivorous fishes (i.e., Acanthuridae, Ephippidae, Kyphosidae, Labridae (parrotfishes), Pomacanthidae, and Siganidae) a series of timed swims was conducted on the reef crest and back reef of the six reefs. Four censuses were conducted within each habitat on each reef, and encompassed the sites used for the macroalgal surveys and transplant experiment (details below). Adjacent censuses were separated by a minimum of 50 m. Each census consisted of a diver swimming parallel to the reef crest for 10-min and recording all nominally herbivorous fishes greater than 10 cm total length (TL) within a 5 m wide transect that extended from the reef substratum to the surface of the water. A second diver recorded all individuals less than 10 cm TL in a 1 m wide transect. Individual fishes were identified and placed into 5 cm size categories. Numbers per unit effort were converted to densities per unit area by estimating the length of each transect (following Bellwood and Wainwright 2001). Density estimates were converted to biomass using length-weight relationships for each species (Kulbicki et al. 2005).

There is considerable variation in feeding behaviour of herbivorous fishes. This variation has been related to their ability to consume different algal functional groups and consequently their impact on ecosystem processes. *Calotomus carolinus*, *Kyphosus vaigiensis*, *Naso brachycentron, Naso lituratus*, *Naso unicornis, Platax pinnatus* and *Siganus canaliculatus* were identified as browsers of *Sargassum* and other fleshy brown macroalgae (namely Phaeophyceae: *Dictyota*, *Padina*, *Turbinaria*) based on gut content and behavioural evidence (Robertson and Gaines 1986; Choat et al. 2002; Bellwood et al. 2006; Cvitanovic and Bellwood 2009). The remaining taxa (i.e., grazers) typically feed on the EAM and/or crustose coralline algae.

Macroalgal transplants

To quantify the variation in the removal of leathery macroalgae among shelf locations and habitats a transplant experiment was conducted. *Sargassum* was selected for the assays as it has been used extensively in previous studies on the GBR (e.g., McCook 1996, 1997; Fox and Bellwood 2008a; Cvitanovic and Bellwood 2009) and is often viewed as a sign of reef degradation. *Sargassum* was the dominant alga following phase-shifts to macroalgal dominance on east African reefs (McClanahan et al. 2001; Graham et al. 2006) and in an experimentally-induced phase-shift on an inshore reef in the central GBR (Hughes et al. 2007). *Sargassum swartzii* (Ochrophyta: Phaeophyceae) was collected from the reef flat of an inshore reef in the Turtle Island Group (Fig. 4.1). Individual *S. swartzii* thalli were removed by cutting the holdfast as close to the point of attachment as possible. Algae were returned to Lizard Island and placed in a large (6000 L) aquarium with flow through seawater within 90 min of collection.

Individual *S. swartzii* thalli were spun, weighed and measured as previously described (Chapter 2). Three haphazardly selected thalli were transplanted to each of two sites within the two habitats (i.e., reef crest and back reef) on each of the six reefs. The sites were the same as those used for the macroalgal censuses, with adjacent sites within each habitat being separated by a minimum of 200 m. The mean initial mass and height of each *S. swartzii* thallus was 426.7 ± 1.5 g (SE) and 474 ± 5 mm, respectively. The *Sargassum* bioassay was attached directly to the reef using a rubber band and galvanized wire (see Chapter 2 for details), with a minimum of 5 m separating adjacent assays within each site. Each assay was individually identified with a small plastic label that was attached to the reef approximately 1.5 m from the algae. After a period of 24 hours all *S. swartzii* thalli were collected, spun and measured as previously described (Chapter 2). This procedure was replicated three times at each site within each habitat on each of the six reefs (n = 216 thalli).

To control for the effects of handling and to determine if observed losses of *Sargassum* biomass were due to herbivory, an exclusion experiment was conducted. Free standing cages (approximately 1000 × 600 × 600 mm) with 50 mm square polyethylene mesh were used to exclude large herbivorous fishes from transplanted *S. swartzii*. The 50 mm mesh was selected as it minimized the caging artifacts (i.e., shading and reduction in water flow) while excluding the size classes of herbivorous fishes that have been demonstrated to be important in the removal of fleshy macroalgae (Bellwood et al. 2006; Chapter 3). The *Sargassum* was processed as previously described prior to transplanting to the reef. Haphazardly selected thalli were transplanted to each of two sites within the reef crest and back reef habitats on the two mid-shelf reefs. These two reefs were selected as they displayed the highest rates of macroalgal removal. Within each site one thallus was left exposed to resident herbivores and one thallus was placed inside an exclusion cage for a period of 24-hours. After 24 hours the *Sargassum* was collected and processed as described previously. This procedure was replicated six times at each site (n = 96 thalli).

Statistical analyses

Variation in the distribution of macroalgae and the rate of removal of *S. swartzii* biomass among shelf positions, reefs, habitats and sites were analysed using two four-factor mixed model ANOVA's. The distribution of roving herbivores and macroalgal browsers were compared among shelf positions, reefs, and habitats using three-factor mixed model ANOVA's. Sites were pooled for the herbivore analyses as only four replicate timed swims were conducted within each habitat on each reef. Shelf position and habitat were fixed and orthogonal factors, and reef and site were random and nested factors in the models. The analyses were based on the proportional cover of macroalgae, the proportion of the initial, or transplanted, *Sargassum* biomass removed over a 24-hour period, and the biomass of roving herbivores and macroalgal browsers, respectively. Assumptions of the ANOVA's were examined by residual analysis. Subsequently, macroalgal cover and macroalgal browser biomass were √ transformed, the proportion of *S. swartzii* biomass removed was $^4\surd$ transformed, and the biomass of roving herbivores log transformed to improve normality and homoscedasticity.

To determine if the observed losses of *S. swartzii* biomass were due to herbivory the change in *S. swartzii* biomass was compared amongst treatments (caged vs. open), reefs, habitats and sites using a mixed model four-factor ANOVA. The analysis was based on the proportion of the initial biomass lost from individual *S. swartzii* thalli over a 24-h period. The proportion of *S. swartzii* biomass removed was √ transformed to improve normality and homoscedasticity.

Directional, or one-tailed, correlations were performed to determine if there was a positive relationship between the rates of removal of the *S. swartzii* and the biomass of macroalgal browsing species, both collectively and independently. The extremely low densities of *C. carolinus*, *N. brachycentron*, and *P. pinnatus* recorded across all visual censuses (< 5 individuals per species) precluded any meaningful comparisons. Therefore, correlations were not examined for these species. The susceptibility of an algal species to herbivores is not, however, simply a function of its absolute palatability, but rather its palatability relative to those of co-occurring species (Atsatt and O'Dowd 1976). The feeding response of macroalgal browsers to the *Sargassum* assays may, therefore, be influenced by the availability and relative palatability of the algal community within the vicinity of the transplanted *Sargassum*. We therefore calculated a grazing preference index (GPI) for each site (following Chapter 3);

$$\mathrm{GPI} = \Sigma\, p_i .\, c_i \,,$$

where p_i is the proportion of biomass removed from the ith macroalgal species in a 3-h period (from Mantyka and Bellwood 2007), and c_i is the proportional cover of the ith macroalgal species within each site. The GPI was incorporated into the correlation model and partial correlation coefficients calculated to examine the relationships between the rate of removal of *S. swartzii* and the biomass of macroalgal browsers. The reduction in *S. swartzii* biomass and the GPI were log transformed to improve linearity. As *Sargassum* is uncommon on outer-shelf reefs it may be reasonable to assume that it represents a novel food item to macroalgal browsers on these reefs. Subsequently, the correlations were performed for (a) all reefs simultaneously, and (b) inner- and mid-shelf reefs only (i.e., excluding outer-shelf reefs).

Agents of macroalgal removal

To identify the species responsible for removing the macroalgal biomass a second series of *Sargassum* assays was deployed during October – December 2008 on eight reefs spanning the continental shelf (Fig. 4.1). These reefs included the six reefs used previously to quantify the rates of macroalgal removal and two additional reefs, Martin Reef and Linnet Reef. These two reefs were included to determine if there was any transition in the rates or agents of macroalgal removal between the inner- (Turtle Island Group) and mid-shelf reefs (Lizard Island and MacGillivray Reef). Based on their position, Martin Reef and Linnet Reef (13 – 18 km from the mainland) are often classified as inner-shelf reefs (e.g., Bay et al. 2008; Farnsworth et al. 2010), however, in many aspects (e.g., reef geomorphology and fish community composition) they appear more typical of mid-shelf reefs. They have clearly defined reef crests, reduced turbidity compared to reefs within the Turtle Island Group and lack the large *Sargassum* beds characteristics of other inshore reefs in the region (A. Hoey pers. obs.). Martin and Linnet reefs, therefore, are referred to as transitional or inner/mid-shelf reefs,

Macroalgal assays

Sargassum swartzii was collected from the reef flat of an inshore reef in the Turtle Island Group and processed as described above. Prior to the start of the experiment an individual *S. swartzii* thallus was transplanted to each site within the two habitats on each reef. These thalli were left in place for five days to allow the resident fishes time to familiarize themselves with a potentially novel food item, especially on the outer-shelf reefs (see discussion for further details). Following this, five haphazardly selected *S. swartzii* thalli were transplanted to each of two sites within the two habitats (i.e., reef crest and back reef) on each of the eight reefs. Adjacent sites within each habitat were separated by a minimum of 200 m. The mean initial mass and height of each *S. swartzii* thallus was 360.5 ± 5.6 g (SE) and 563 ± 5 mm, respectively. All assays were deployed between 08:30 and 09:30 and collected after five hours, between 13:30 and 14:30. Within each site one assay was placed inside a free standing exclusion cage (approximately 1000 × 600 × 600 mm; 50-mm square polyethylene mesh) to control for the effects of handling and translocation. The four remaining assays were left exposed to resident herbivores, with adjacent assays being separated by a minimum of 5 m. This procedure was replicated three times within each site (480 thalli in total), with individual deployments being randomly allocated among shelf positions over the three-month experimental period.

To quantify feeding activity on the *S. swartzii* assays, remote underwater video cameras (Sony DCR-SR100 HDD cameras in Ikelite housings) were used. A camera, mounted on a concrete block, was positioned approximately 2 m from one of the assays exposed to herbivores at each site within each habitat. Filming commenced immediately after the assays were attached to the reef and was continuous, without interruption, for the 5-h experimental period. To allow calibration of fish sizes on the video footage a small scale bar was placed adjacent to each assay for the first 10 s of filming. This procedure was replicated three times within each site, resulting in 30 h of video observations for each habitat on each reef (480 h in total). All video footage was viewed and the number of bites taken from the assays by each species and size (TL) of fish was recorded. To account for body size related variation in the impact of individual bites, a mass standardized bite impact was calculated (see Chapter 3 for details).

Statistical analyses

The rate of removal of *S. swartzii* biomass and feeding on the assays by herbivorous fishes was compared among shelf positions, reefs, habitats and sites using two four-factor mixed model ANOVAs. Shelf position and habitat were fixed and orthogonal factors, and reef and site were random and nested factors in the models. The analyses were based on the proportion of the initial, or transplanted, *Sargassum* biomass removed over a 5-hour period, and the total mass standardized bites taken from each assay, respectively. Similarly, to determine if the effects of handling and transplantation varied among shelf positions, reefs, habitats and sites a four-factor mixed model ANOVA was used. Assumptions of the ANOVA's were examined by residual analysis. The proportion of *S. swartzii* biomass removed was $\sqrt[4]{}$ transformed, and the mass standardized bites were log transformed to improve normality and homoscedasticity.

A forward stepwise multiple regression analysis was conducted to determine the impact of each species recorded during video observations on the removal of *S. swartzii* biomass. The number of mass standardized bites for each species was regressed against the reduction in biomass of *S. swartzii*. To increase the power of the analysis all non-macroalgal browsing species that were estimated to have taken less than 0.2 % of the total mass standardized bites were pooled into higher taxonomic groupings.

4.3. Results

Distribution of macroalgae and herbivorous fishes

There were clear cross-shelf patterns in the distribution of macroalgae, roving herbivorous fishes and macroalgal browsing fishes (Fig. 4.2). Macroalgal cover was greatest on the inner-shelf reefs and decreased markedly on both mid- and outer-shelf reefs (Fig. 4.2a). However, variation among habitats resulted in a significant interaction between shelf position and habitat ($F_{2,3} = 25.85$, $p = 0.012$). Within the inner-shelf reefs macroalgal cover was greatest on the reef crest (48.7 %) and decreased significantly on the back reef (12.8 %). Leathery macroalgae (primarily *Sargassum* spp. and *Turbinaria* spp.) accounted for 64.0 % and 39.6 % of the macroalgae censused on the inner-shelf reef crest and back reef, respectively. On mid- and outer-shelf reefs macroalgal cover was greatest on the back reef (2.8 – 3.5 %) and decreased on the reef crest (0.4 – 0.5 %). Jointed calcareous macroalgae (primarily *Halimeda* and *Amphiroa*) accounted for 73.7 % of all macroalgae recorded on mid- and outer-shelf reefs.

The biomass of all roving herbivorous fishes displayed a general increase across the continental shelf, from 296.9 $kg.ha^{-1}$ on the inner-shelf back reef to 2654.8 $kg.ha^{-1}$ on the outer-shelf reef crest (Fig. 4.2b), but any trend was overshadowed by a shelf position by habitat interaction ($F_{2,39} = 4.25$, $p = 0.021$). The interaction was driven by the marked increase in herbivorous fish biomass on the outer-shelf reef crest.

Across all shelf positions the biomass of macroalgal browsers was highly variable but consistently greater on the reef crest than the back reef ($F_{1,39} = 17.79$, $p < 0.001$; Fig. 4.2c). There was an approximate two- to five-fold increase in the biomass of macroalgal browsers from the back reef (54.8 - 95.3 $kg.ha^{-1}$) to the reef crest (163.5 - 335.2 $kg.ha^{-1}$) across the three shelf positions (Fig. 4.2c). Further details of the ANOVA results are given in Appendix C. Of the seven macroalgal browsing species recorded during the visual censuses, *Naso unicornis* was the most widespread species being recorded in 44 of the 48 visual censuses and accounting for 70.5 % of the total macroalgal browser biomass recorded across all censuses. *Kyphosus vaigiensis*, despite

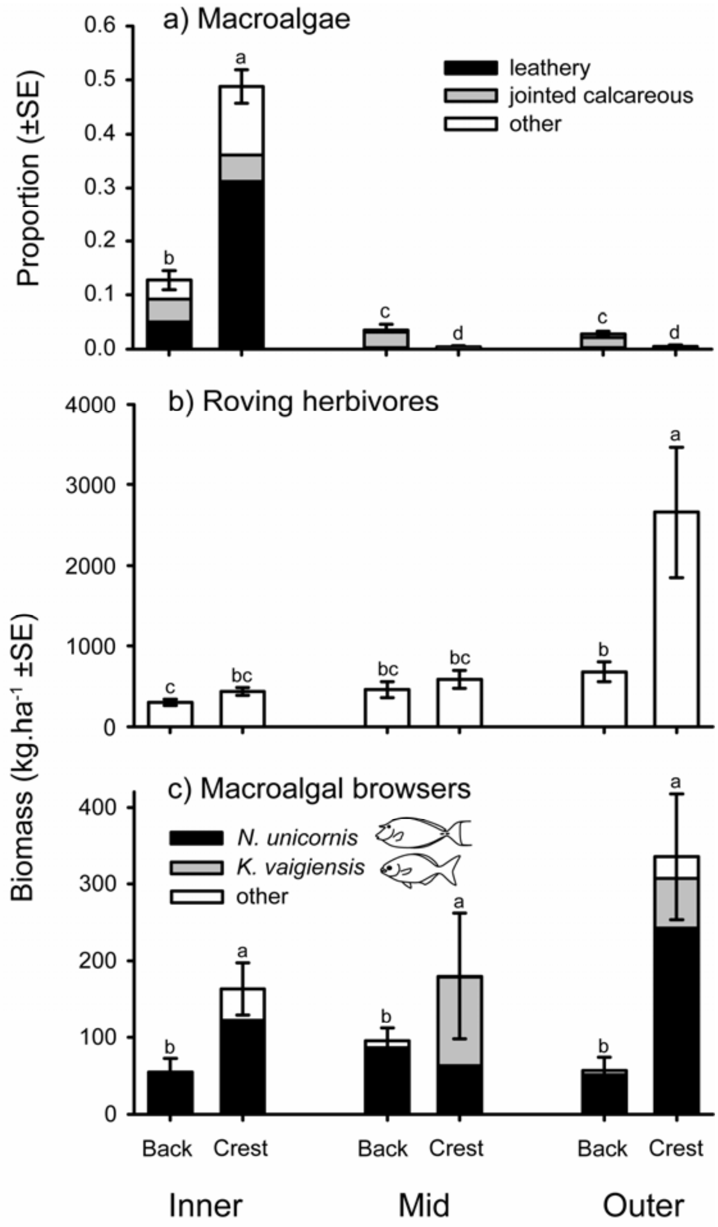

Fig. 4.2: Cross-shelf variation in the distribution of (a) macroalgae, (b) all roving herbivorous fishes, and (c) macroalgal browsing fishes in the northern Great Barrier Reef. The mean macroalgal cover is based on twelve point intercept transects within each of two reefs (n = 24). The mean macroalgal cover is divided into the relative contribution of functional forms. Black, leathery macroalgae (primarily *Sargassum* and *Turbinaria*); grey, jointed calcareous (primarily *Amphiroa*, *Galaxaura* and *Halimeda*); open, other (corticated and foliose). The mean biomass of roving herbivores and macroalgal browsers is based on four timed swims within each of two reefs (n = 8). The mean biomass of macroalgal browsers is divided into the relative contribution of the most abundant taxa. Black, *Naso unicornis*; grey, *Kyphosus vaigiensis*; open, other. The letters above each bar indicate homogenous groups identified by Tukey's HSD post-hoc analyses.

being only recorded on two of the six reefs surveyed accounted for 20.1 % of the total macroalgal browser biomass.

Rates of macroalgal removal

There were marked differences in the removal rates of *S. swartzii* among shelf positions ($F_{2,3} = 32.11$, $p = 0.009$) and sites nested within habitat, reef and shelf position ($F_{12,192} = 1.86$, $p = 0.041$). No significant variation was detected among habitats ($F_{1,3} = 0.18$, $p = 0.698$) or reefs within each shelf position ($F_{3,3} = 1.94$, $p = 0.300$). Further details of the ANOVA results are given in Appendix C. *S. swartzii* transplanted to the mid-shelf reef crest and back reef habitats experienced the highest reductions in biomass over the 24-h period, 79.9 %.d^{-1} and 55.2 %.d^{-1} respectively (Fig. 4.3). The reduction in *S. swartzii* biomass was markedly reduced on both the inner- (reef crest: 10.8 %.d^{-1}; back reef: 17.0 %.d^{-1}) and outer-shelf reefs (reef crest: 10.4 %.d^{-1}; back reef: 10.1 %.d^{-1}).

The results of the exclusion experiment indicated that treatment (i.e., caged vs. open; $F_{1,4} = 1012.35$, $p < 0.001$), and habitat ($F_{1,4} = 9.77$, $p = 0.035$) influenced the reduction of *Sargassum* biomass. *S. swartzii* transplanted within exclusion cages exhibited minimal reductions in biomass across all sites, ranging from 3.6 ± 0.7 (SE) % on the reef crest to 1.8 ± 0.6 % on the back reef. In contrast, *S. swartzii* exposed to reef herbivores exhibited significantly higher reductions in biomass; 81.6 ± 4.0 % and 59.1 ± 4.5 % on the reef crest and back reef, respectively.

No relationship was detected between the biomass of *S. swartzii* removed and the grazing preference index (GPI), the biomass of all macroalgal browsing species collectively, or the four macroalgal browsing species independently (Table 4.1a). Incorporating the grazing preference index into the correlation model and subsequently controlling for the relative availability and susceptibility of the ambient macroalgal community within each habitat had no detectable effect on these relationships. However, removing the outer-shelf sites from the analyses revealed markedly different results (Table 4.1b). The GPI was strongly negatively correlated with the removal of *S. swartzii* biomass across the 16 inner- and mid-shelf reef sites. Incorporating the GPI into the correlation revealed a significant positive relationship between the biomass of *N. unicornis* and the reduction in *S. swartzii* biomass (Table 4.1b).

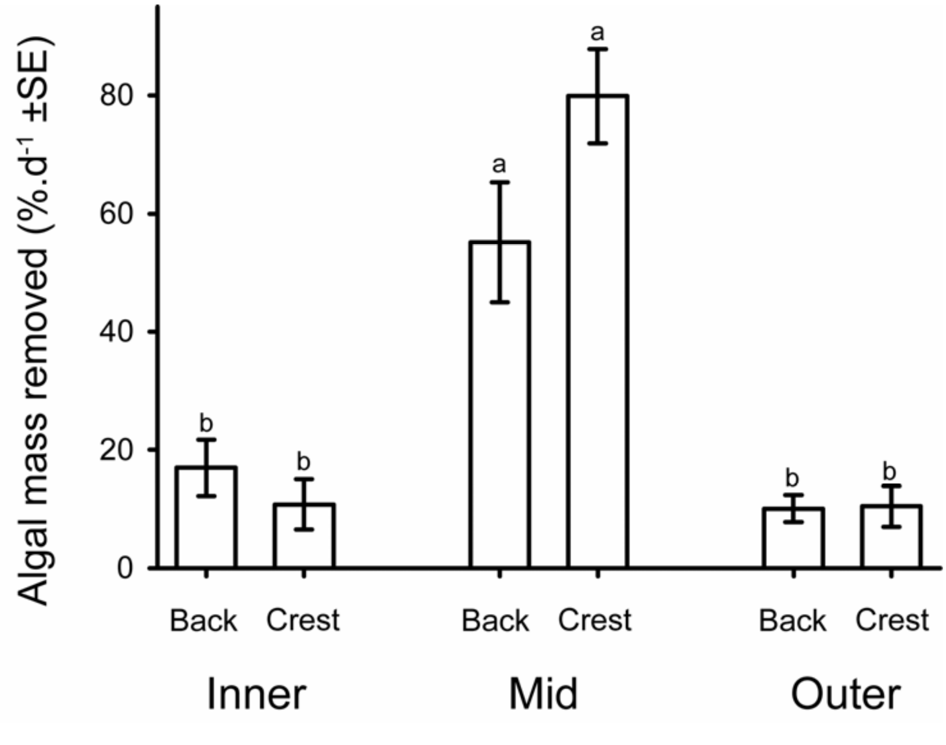

Fig. 4.3: Variation in the removal rates of transplanted *Sargassum swartzii* across the continental shelf in the northern Great Barrier Reef. The mass removed was calculated as the proportion of the initial, or transplanted, biomass removed. The means are based on 36 thalli transplanted for 24 hours within each habitat at each shelf position. The letters above each bar indicate homogenous groups identified by Tukey's HSD post-hoc analyses.

Table 4.1: Correlations between the reduction in *Sargassum swartzii* biomass over a 24-h period, the grazing preference index (GPI) and the biomass of macroalgal browsing fishes across (a) all shelf positions, and (b) inner- and mid-shelf only (i.e., excluding outer-shelf locations). The GPI incorporates the availability and relative palatability of the resident algal community. The reduction in *S. swartzii* biomass and the GPI were log-transformed. Bivariate and partial correlation coefficients (controlling for the GPI) are given. Significant relationships are shown in bold.

	Bivariate correlation		Partial correlation	
	r	**p**	***ρ***	**p**
(a) All shelf positions				
Grazing preference index (GPI)	-0.356	0.088		
Macroalgal browsers	-0.054	0.599	-0.183	0.798
Kyphosus vaigiensis	0.320	0.064	0.196	0.185
Naso lituratus	-0.383	0.968	-0.722	1.000
Naso unicornis	-0.285	0.911	-0.350	0.949
Siganus canaliculatus	-0.321	0.937	-0.076	0.635
(b) Inner- and mid-shelf reefs only				
Grazing preference index (GPI)	**-0.876**	**< 0.001**		
Macroalgal browsers	0.176	0.257	0.254	0.180
Kyphosus vaigiensis	0.382	0.072	-0.105	0.645
Naso lituratus	0.184	0.248	-0.419	0..940
Naso unicornis	-0.162	0.726	**0.607**	**0.008**
Siganus canaliculatus	-0.657	0.997	0.054	0.424

Agents of macroalgal removal

Over the 5-h period the reduction in *S. swartzii* biomass was influenced by an interaction between shelf position and habitat ($F_{3,4} = 7.14$, $p = 0.044$) and site ($F_{16,352} =$

6.04, $p < 0.001$). The significant effect of site was driven by differences among back reef sites on the two outer-shelf reefs, where removal rates ranged from 9.3 ± 1.6 (SE) to 84.8 ± 6.2 %.5h^{-1}. No significant variation was detected among reefs within each shelf position ($F_{4,4} = 2.65$, $p = 0.184$; see Appendix C for full ANOVA table). With the exception of the inner-shelf reefs where removal rates displayed no variation among habitats, the reduction in *S. swartzii* biomass was greater on the reef crest than the back reef (Fig. 4.4a). *S. swartzii* transplanted to the mid-shelf reefs experienced the greatest reductions in biomass (reef crest: 92.0 ± 1.6 %.5h^{-1}; back reef: 70.3 ± 3.9 %.5h^{-1}). The reduction in *S. swartzii* biomass was reduced on the outer-shelf reefs (reef crest: 73.4 ± 4.4 %.5h^{-1}; back reef: 32.1 ± 5.1 %.5h^{-1}), and lowest on the intermediate (reef crest: 9.3 ± 1.8 %.5h^{-1}; back reef: 3.1 ± 0.1 %.5h^{-1}) and inner-shelf reefs (reef crest: 1.9 ± 0.0 %.5h^{-1}; back reef: 3.4 ± 1.3 %.5h^{-1}; Fig. 4.4a). The reduction in biomass of *S. swartzii* held within exclusion cages was consistently low (overall mean = 2.4 ± 0.3 %.5h^{-1}) and displayed no significant variation among shelf positions, habitats, reefs, or sites (see Appendix C for full ANOVA table).

Not surprisingly feeding on the *S. swartzii* displayed a similar pattern to that of the reduction in algal biomass (Fig. 4.4), with the total mass standardized bites recorded being influenced by site ($F_{16,64} = 6.86$, $p < 0.001$) and an interaction between shelf position and habitat ($F_{3,4} = 7.52$, $p = 0.040$; see Appendix C for further details). Analysis of the video footage revealed that in total 82,621 bites from 42 fish species were recorded on the transplanted *S. swartzii* across all sites, with *N. unicornis* accounting for 82.0 % of all mass standardized bites (Table 4.2). The only other species to take a substantial number of bites from the *S. swartzii* were *K. vaigiensis* and *Siganus doliatus* accounting for 5.8 and 5.0 % of the total mass standardized bites, respectively (Table 4.2). Each of the remaining 39 species, including the macroalgal browsing *C.*

carolinus, *N. brachycentron*, *N. lituratus* and *S. canaliculatus*, accounted for less than 1.8 % of the total mass standardized bites. Results of the multiple regression indicated that feeding by *N. unicornis*, *K. vaigiensis*, *S. doliatus*, and *N. brevirostris* were all significantly related to the reduction in *S. swartzii* biomass (Table 4.2). Overall the model explained 93.2 % of the variation in the reduction in algal biomass, with *N. unicornis* alone accounting for 80.9 % of the total variation. Of the remaining species *K. vaigiensis* accounted for 8.8 %, while *S. doliatus* and *N. brevirostris* accounted for 2.5 % and 1.0% of the total variation, respectively.

Table 4.2: Results of forward stepwise multiple regression analysis examining the relationship between herbivore feeding rates and the reduction in *Sargassum swartzii* biomass over a 5-h period. Herbivore feeding rates are based on the number of mass standardized bites taken by each fish species. Reef parrotfish refer to the reef parrotfish clade (sensu Streelman et al. 2002) and include the genera *Bolbometopon*, *Chlorurus*, *Cetoscarus*, *Hipposcarus* and *Scarus*. Significant results are highlighted in bold.

	Bites	Mass standardized bites (kg.bites)	Multiple R^2	ΔR^2	P
Naso unicornis	**41,171**	**59,012.6**	**0.809**	**0.809**	**< 0.001**
Kyphosus vaigiensis	**8,176**	**4,175.6**	**0.897**	**0.088**	**< 0.001**
Siganus doliatus	**22,374**	**3,551.1**	**0.922**	**0.025**	**< 0.001**
Naso brevirostris	**1,719**	**1,076.0**	**0.932**	**0.010**	**< 0.001**
Calotomus carolinus	496	327.4	0.934	0.003	0.068
Naso brachycentron	6	4.7	0.940	0.000	0.858
Naso lituratus	1,871	1168.0	0.940	0.000	0.999
Siganus canaliculatus	823	237.5	0.940	0.000	0.518
Siganus corallinus	3,182	1241.6	0.938	0.002	0.099
Siganus spp.	146	73.2	0.936	0.002	0.100
Reef parrotfish	539	260.4	0.939	0.001	0.225
Other acanthurids	1,961	689.0	0.939	0.000	0.415

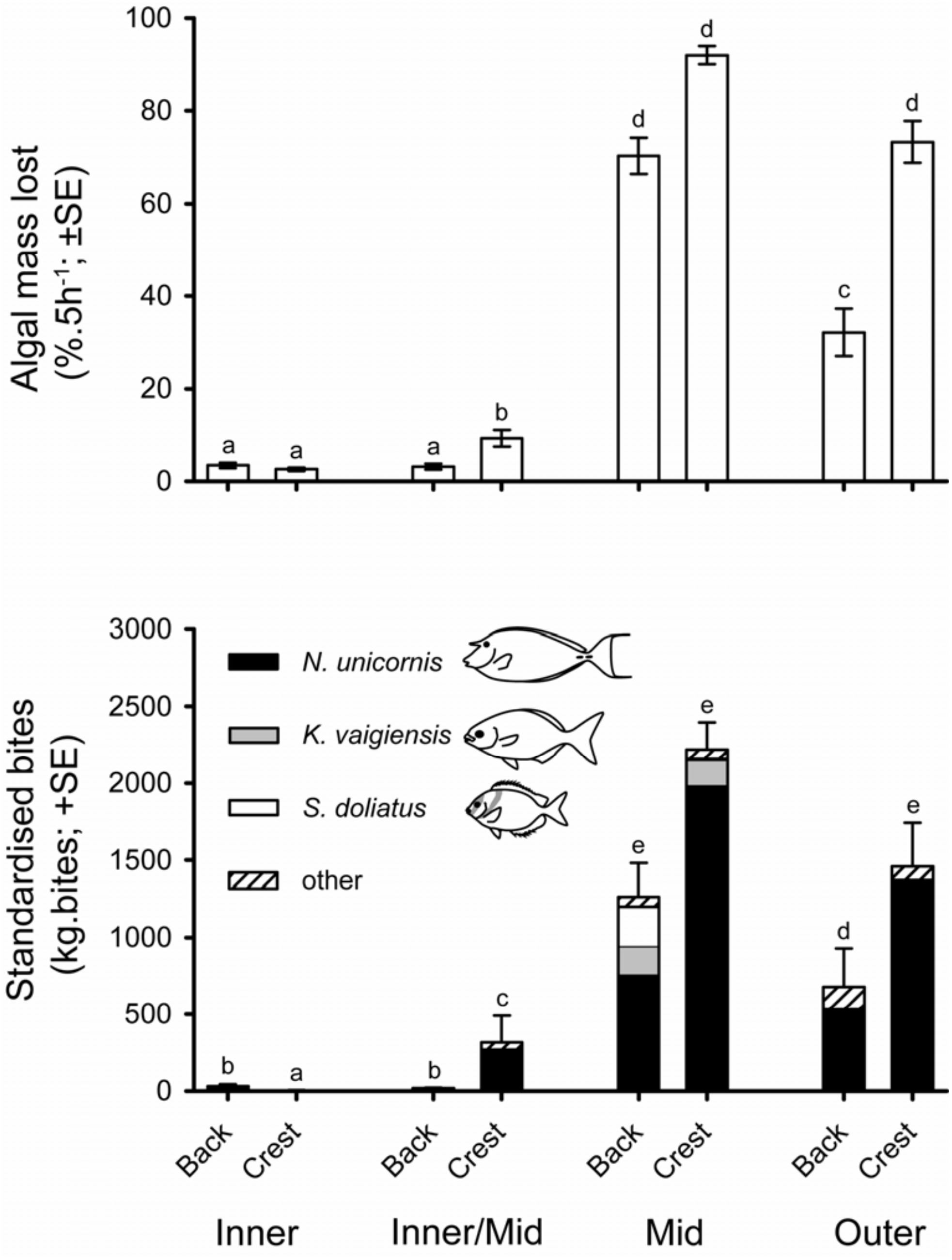

Fig. 4.4: Cross-shelf variation in browsing intensity in the northern Great Barrier Reef. a) Variation in the removal rates of transplanted *Sargassum swartzii* across two habitats and eight reefs spanning the continental shelf in the northern Great Barrier Reef. The mass removed was calculated as the proportion of the initial, or transplanted, biomass removed. The means are based on 48 thalli transplanted for 5 hours within each habitat at each shelf position. b) Mean number of mass standardized bites (total bites × body mass in kg) taken by all species from transplanted *S. swartzii* within two habitats within each of two habitats within each shelf position. *Naso unicornis* (black), *Kyphosus vaigiensis* (grey), *Siganus doliatus* (white), other taxa (hatched). The letters above each bar indicate homogenous groups identified by Tukey’s HSD post-hoc analyses.

4.4. Discussion

Rates of macroalgal removal

The direct quantification of browsing intensity using *Sargassum* assays revealed a distinct pattern across the continental shelf, with the highest rates being recorded within the two mid-shelf habitats and declining significantly across all inner- and outer-shelf habitats, at least for the initial 24-h deployments. Traditionally, studies examining herbivory on coral reefs have related variation in grazing and/or browsing intensity to the distribution of herbivores, either collectively (Lewis and Wainwright 1985; Reinthal and MacIntyre 1994) or to specific taxonomic or functional components (McClanahan et al. 1999; Sluka and Miller 2001). In the present study, however, patterns of browsing intensity could not be explained by variation in the distribution of macroalgal browsing fishes alone; rather they appeared to be influenced by several factors operating over different spatial scales. The attractiveness, or palatability, of the transplanted *S. swartzii* relative to the resident algal community, together with the biomass of a single macroalgal browsing species, *N. unicornis*, were significantly related to browsing intensity, but only across the inner- and mid-shelf reefs. In contrast, the initially low rates of browsing on the outer-shelf reefs (i.e., the 24-h assays) displayed no relationship to the biomass of macroalgal browsing fishes or the relative attractiveness of the *S. swartzii* assays. The factors influencing these low rates on outer shelf reefs are unclear but may be related to an initial reluctance to consume an unfamiliar, or novel, food resource (i.e., dietary conservatism; sensu Marples et al. 1998) by the resident fishes.

Cross-shelf variation in browsing intensity, as proxied by the *S. swartzii* assays, displayed no direct relationship to the distribution of macroalgal communities or the biomass of macroalgal browsing fishes across the three shelf positions. Variation in removal rates of *S. swartzii* among the inner- and mid-shelf reefs, however, appeared to be primarily determined by the resident algal community within each site, with removal rates being negatively related to the abundance and relative palatability of resident algal community (i.e., the GPI). In terrestrial systems the susceptibility of a plant to herbivores has long been known to be a function of its palatability relative to those of co-occurring species, rather than its absolute palatability (Atsatt and O'Dowd 1976). In tropical marine systems, however, this relationship has rarely been investigated (but see Poore and Hill 2005; Levenbach 2009 for temperate examples). The low removal rates of *S. swartzii* in areas of high cover of macroalgal cover (i.e., inner-shelf reefs) and the high removal rates in areas of low macroalgal cover (i.e., mid-shelf reefs) suggest that the resident algal community was influencing the relative attractiveness of the transplanted *S. swartzii*. McClanahan et al. (1999) reported a similar increase in feeding on transplanted *Sargassum latifolium* following the experimental removal of macroalgae. In contrast, resident algal communities have been shown to have no influence on among-habitat variation in the removal of *Sargassum cristaefolium* or *S. swartzii* on Lizard Island (Chapter 2, 3). The absence of a relationship may reflect the spatial scale examined, or the relatively low cover and limited among-habitat variation in macroalgal communities on Lizard Island.

After controlling for the influence of the resident algal communities, the residual variation in the removal rates of *S. swartzii* on inner- and mid-shelf reefs displayed a positive relationship with the biomass of *N. unicornis*. Recent studies using stationary underwater video cameras have highlighted the potential problems of using such correlative approaches, especially for browsers of *Sargassum* (Bellwood et al. 2006; Fox and Bellwood 2008a; Cvitanovic and Bellwood 2009; Chapter 2, 3). However, given the abundance of *N. unicornis*, and its dominant role in removing transplanted *S. swartzii* from multiple habitats on Lizard Island (Chapter 3), it is likely that this species contributes significantly to the observed patterns in the present study. Indeed, analysis of the video footage revealed that *N. unicornis* was primarily responsible for removing the transplanted *S. swartzii* across all reefs (see below for detailed discussion).

Within the GBR, herbivory has been hypothesized to be greatest on the reef crest of outer-shelf reefs, with this habitat supporting the highest densities and/or biomass of herbivorous fishes (e.g., Russ 1984; Wismer et al. 2009). While this does not hold for all herbivore functional groups (e.g., scraping parrotfishes: Hoey and Bellwood 2008), the highest biomass of macroalgal browsers, including *N. unicornis*, was recorded on the outer-shelf reef crest in the present study. These biomass estimates, together with the low cover of macroalgae on the outer-shelf reef crests, may lead to the expectation that browsing intensity would be greatest within this habitat. There was, however, an approximate five- to eight-fold reduction in the 24-h removal rates of *S. swartzii* transplanted to the outer-shelf reef crest and back reef habitats, when compared to the corresponding mid-shelf habitats. This apparent lack of feeding by *N. unicornis*, and other macroalgal browsing species, within this habitat may be related to within-habitat variation in the distribution of these fishes, the presence of a preferred food resource, and/or an aversion to an unfamiliar food type, or alga. These potential mechanisms are discussed below.

Within-habitat variation in the distribution of macroalgal browsers may have reduced the likelihood of these fishes encountering or locating the transplanted *S. swartzii*. On numerous occasions, however, several *N. unicornis* (2 – 7 individuals) and *N. lituratus* (1 – 2 individuals) were observed in the immediate vicinity of the transplanted *S. swartzii*. These fishes often approached and appeared to inspect the alga almost immediately after it was attached to the reef. Furthermore, the low cover of macroalgae (< 1% cover; primarily *Halimeda*) within this habitat, and our inability to detect a relationship between browsing intensity and the GPI suggest that alternate, or preferred food resources were not locally abundant. The dominance of fleshy brown macroalgae (namely *Dictyota* and *Turbinaria*) in the gut content of *N. unicornis* and *K. vaigiensis* collected from the same outer-shelf reefs (i.e., Day and Hicks Reefs: Choat et al. 2002), whilst raising questions regarding the source of these algae, suggest that these species are not shifting to alternate, non algal, food resources. Given the low abundance of *Sargassum* and other fleshy brown macroalgae across all outer-shelf habitats on the GBR (McCook et al. 1997, 2000; Wismer et al. 2009), it appears that these fishes may be extremely efficient at locating and consuming cryptic macroalgae (i.e., small thalli and/or thalli contained within crevices and caves), or accessing algae in off-reef habitats.

Perhaps the most plausible explanation for the lack of feeding by macroalgal browsers on the outer-shelf reef crests is that the transplanted *S. swartzii* represented an unfamiliar, or novel, food item to the resident fishes. Whilst many foraging decisions by animals are based on innate behaviour (Smith 1975), others appear to be related to the prior experience, or learning, of individuals (Marples et al. 1998; Martin and Fitzgerald 2005). When an animal encounters, or is presented with, an unfamiliar food item they often display a hesitation or aversion to approaching it (i.e., neophobia: Galef 1993). This aversion to approach is generally short-lived, however, there is often a longer-lived reluctance to consume the novel food (i.e., dietary conservatism: Marples et al. 1998; Marples and Kelly 1999). Whilst the majority of studies examining neophobia and dietary conservatism (collectively termed dietary wariness) have been conducted on rats or birds, the principles could apply equally to fish. The low densities of fleshy brown macroalgae, in particular *Sargassum* spp., on outer shelf reefs (McCook et al. 2000), and the lack of *Sargassum* in the gut content of *K. vaigiensis* and *N. unicornis* collected from these reefs (Choat et al. 2002), suggest that these fishes may not have initially recognized the transplanted *S. swartzii* as a safe or palatable food item. In contrast, *Sargassum* spp. are abundant on inner-shelf reefs, and relatively common on mid-shelf reefs (including *S. swartzii*), especially within damselfish territories (see Chapter 5). Subsequently the assays were likely to represent a familiar food for fishes on these reefs. This dietary conservatism appears to be relatively short-lived with direct observations of *N. unicornis* and *N. lituratus* inspecting the 24-h assays soon after they were transplanted to the outer-shelf reef crest indicating these fishes were not neophobic; and the placement of a single *S. swartzii* assay for several days at each site appeared sufficient for the resident fishes to sample and accept the transplanted *Sargassum* as a palatable food item, with removal rates increasing from 10.4 %.d^{-1} to 73.4 %.5h^{-1}.

The high browsing intensity on the two mid-shelf reefs was broadly comparable to those of previous studies and provides additional support for the role of herbivory in limiting the density of adult *Sargassum* on mid-shelf reefs of the GBR (McCook 1996; Chapter 2, 3). Browsing intensity on inner-shelf reefs of the GBR displays greater variation. Recent studies have reported relatively high rates of browsing on *Sargassum* assays on inshore reefs in the central GBR, with 30 – 95 % of the algal biomass being removed in a 3 h period (Mantyka and Bellwood 2007; Cvitanovic and Bellwood 2009). The present study was the first to examine this process on the inner-shelf of the northern GBR, and the low removal rates recorded on these reefs (10.8 – 17.0 %.d^{-1}) may suggest browsing intensity is suppressed at lower latitudes. McCook (1997), however, reported similar variation among two inshore reefs in the central GBR, with transplanted

Sargassum (primarily *Sargassum oligocystum* and *Sargassum tenerrimum*) being almost completely removed from the fringing reef of Great Palm Island, but persisting for several weeks on nearby Brooke Island. Although the local algal communities were not quantified, the proximity of the assays to large stands of *Sargassum* may have influenced the removal rates in these locations (ca. 20 m: Brooke Island; 60 m: Great Palm Island). This variation among studies, while precluding any generalizations regarding browsing intensity on inshore reefs of the GBR, highlights the need to consider the influence of both algal and herbivore communities, and adds to the growing body of literature that emphasizes the extent of spatial variability in browsing on coral reefs (e.g., Hay 1984; Cvitanovic and Bellwood 2009; Chapter 3).

Agents of macroalgal removal

Despite considerable cross-shelf variation in the rates of removal of *Sargassum*, there was little variation in the agents of macroalgal removal across the eight reefs. Feeding on the transplanted *S. swartzii* was dominated by a single browsing species, *N. unicornis*. *N. unicornis* accounted for 82 % of all standardized bites and explained over 80 % of the total variation in the reduction in *Sargassum* biomass across all reefs and habitats. Although the majority of this feeding activity was recorded on the mid- and outer-shelf reefs, *N. unicornis* accounted for over 72 % of the recorded feeding on the transitional inner/mid- and inner-shelf reefs. Feeding by *K. vaigiensis*, *S. doliatus*, and *N. brevirostris* were also significantly related to the reduction in *S. swartzii* biomass, however the relative contributions of these species were minor; collectively explaining only 12.2 % of the reduction in *Sargassum* biomass. The dependence on a single species performing a key ecological process across the continental shelf of the GBR is striking, and not only emphasizes the apparent lack of functional equivalents within each reef, but also among reefs separated by tens of kilometres.

With the exception of the two outer-shelf habitats, consumption rates of *S. swartzii* exposed to herbivores for 5 hours were broadly comparable to those obtained from assays exposed to herbivores for 24 hours at the same sites. It may, therefore, be reasonable to assume that the shorter duration was sufficient to capture the majority of the browsing activity on these reefs. The limited reduction in biomass of *S. swartzii* placed within exclusion cages (2.4 %.5h^{-1}) indicates that the losses were primarily related to the actions of herbivores. Interestingly, removal rates displayed limited variation among the inner/mid- and inner-shelfs, with only a small but significant increase on the inner/mid-shelf reef crest. These relatively low rates may have been related to the high cover of other fleshy brown macroalgae (primarily *Dictyota* spp. and *Hydroclathrus clathratus*) on the inner/mid-shelf reefs at the time of the study (A. Hoey pers. obs.).

Removal rates within the outer-shelf reef habitats increased markedly (from 10.8–17.0 %.d^{-1} to 32.1-73.4 %.5h^{-1}) following the placement of a *S. swartzii* assay for several days at each site prior to the start of the experiment. This relatively short timeframe appeared sufficient for the resident fishes to overcome their initial reluctance and recognize the transplanted *Sargassum* as a safe and palatable food item. Similar learning behaviour in response to novel food items has been reported for birds (Greenberg 1990; Marples et al. 1998), rats (Mitchell 1976; Galef 1993) and humans (Pilner et al. 1993). The present study appears to be the first to demonstrate such effects for coral reef fishes. Littler and Littler (2007) acknowledged the potential for novelty effects to influence the removal of macroalgal assays, suggesting a cosmopolitan alga be used to avoid such effects. Placing assay material at study sites for several days prior to the start of an experiment may provide a useful technique to overcome dietary wariness in future bioassay studies.

The present study is the first to report a significant relationship between the rate of removal of *Sargassum* and visual estimates of the biomass of the species responsible for consuming the *Sargassum* (i.e., *N. unicornis*). All previous studies using remote underwater video cameras to directly quantify feeding on *Sargassum* on the GBR have reported that the species responsible for removing the algal biomass have either not been recorded (Bellwood et al. 2006; Fox and Bellwood 2008a; Cvitanovic and Bellwood 2009) or underestimated (Chapter 3) during visual censuses at the study sites. This significant relationship may simply be a reflection of the larger spatial scale (10 – 40 km) in the present study, compared to those of previous studies (0.01 – 5 km). The ability to detect a relationship over smaller, within reef, spatial scales is likely to be hampered by the 'wary' nature of these fishes (Myers 1991; Kulbicki 1998), daily movements between adjacent habitats and sites (Meyer and Holland 2005) and the relative variation in fish densities and biomass among habitats/sites. Herbivorous fish communities on the GBR have been shown to exhibit greater variation in abundance, biomass, structure and function among reefs from different shelf positions than among reefs from the same shelf position or among habitats within a reef (e.g., Russ 1984; Hoey and Bellwood 2008). The larger spatial scale of the present study probably allowed relative differences in fish biomass among reefs to be detected. Nevertheless, the censuses may have underestimated the true densities of these fishes. For example, groups of up to 14 *N. unicornis* individuals were frequently recorded feeding on the transplanted *S. swartzii* on the reef crest of Lizard Island using remote videos, yet a maximum of 7 individuals were recorded within each visual census in that habitat.

Previous studies using *Sargassum* assays to examine the impact of browsing species on the GBR have revealed high local variability in the role of individual species both within and among studies (Mantyka and Bellwood 2007; Fox and Bellwood 2008a; Cvitanovic and Bellwood 2009). Collectively, these studies have reported the removal of *Sargassum* to be dominated by *K. vaigiensis* and *Siganus canaliculatus*, however; there was an almost complete shift in the relative importance of these species among adjacent bays, and among studies conducted at the same sites within a single bay. In contrast, the lack of variability in the dominant browser of *Sargassum* among habitats, reefs, shelf position, and studies in the northern GBR is remarkable (Chapter 3, present study), and highlights the apparent lack of functional equivalents performing this key ecological process. The importance of *N. unicornis* on other Indo-Pacific reefs cannot be assumed, however, its widespread distribution (Myers 1991) and the predominance of *Sargassum* and other fleshy brown macroalgae in the diet (Hiatt and Strasburg 1960; Jones 1968; Robertson and Gaines 1986; Choat et al. 2002) suggest that such generalities may be expected.

N. unicornis is targeted by fishers throughout much of its range (see Chapter 3; Appendix C), and has experienced marked declines in population structure in some locations (Wantiez et al. 1997; Bunce et al. 2008; Rhodes et al. 2008). The exploitation of this single species, while not appearing to have immediate consequences for coral reefs, may have set the stage for future ecological surprises (Scheffer et al. 2001; Folke et al. 2004). There is little doubt that coral reefs are under increasing pressure from environmental change and biotic exploitation (Bellwood et al. 2004; Newton et al. 2007). Many of the worlds' coral reefs have already undergone dramatic shifts to degraded states dominated by fleshy macroalgae (Hughes 1994; Graham et al. 2006), while other seemingly healthy reefs may be rapidly approaching thresholds which make such shifts seem inevitable. Coral cover on Indo-Pacific reefs has declined at an average annual rate of 1 % over the past two decades (Bruno and Selig 2007) with future predictions painting an even bleaker picture (Hoegh-Guldberg et al. 2007). With concomitant increases in macroalgae likely, the capacity to remove macroalgae may be critical to the future of coral reefs.

The present study is the most comprehensive assessment of macroalgal browsing on the GBR to date, and emphasizes the importance of examining reef processes across broad spatial scales. The direct quantification of browsing intensity using assays revealed marked variation across the continental shelf that could not be explained by herbivore densities alone. The high browsing intensity on mid-shelf reefs provides strong support for the potential of herbivory to limit macroalgal abundances on these reefs by removing adult algae. However, browsing on adult *Sargassum* appeared to be less critical on inner- and outer-shelf reefs. The limited browsing on inner-shelf reefs suggest that as macroalgal cover increases the algal communities are released from top-down control, even in systems with intact herbivore populations. The initially low rates of browsing on outer-shelf reefs suggest that macroalgal communities on these reefs may be limited by the supply of propagules or grazing of early developmental stages (Diaz-Pulido and McCook 2003). The reliance on a single species performing a key ecological function across the continental shelf of the GBR emphasizes the importance of looking beyond biological diversity as a source of ecological stability. The loss of a single species may severely erode the capacity of reefs to deal with change. The local extinction of the bumphead parrotfish, *Bolbometopon muricatum*, on many central Pacific reefs has undermined a major ecosystem process; external bioerosion (Bellwood et al. 2003). Understanding the role of individual species in ecosystem processes and identifying those species that may mitigate risks is paramount to the future sustainability of coral reefs, and ecosystems in general.

Chapter 5: Damselfish territories as a refuge for macroalgae on coral reefs

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5.1. Introduction

Herbivory is widely accepted as a key process determining the benthic community structure and resilience of coral reefs (Hughes 1994; Mumby et al. 2006), with roving herbivorous fishes (namely Acanthuridae, Kyphosidae, Labridae (parrotfishes), and Siganidae) playing a predominant role. On reefs with intact herbivore communities, grazing by herbivorous fishes maintains the benthic algal community in a cropped state dominated by highly productive algal turfs and grazing resistant coralline algae (Polunin and Klumpp 1992; Bellwood et al. 2004). However, at reduced levels of grazing, algal production may exceed consumption and ultimately lead to a shift to slower growing fleshy macroalgae, such as *Sargassum* (e.g., Steneck 1988; Hughes et al. 2007). Indeed, the regional loss of roving herbivorous fishes through overfishing has underpinned system-wide shifts to macroalgal dominance on reefs in the Atlantic (Hughes 1994), Pacific (Hunter and Evans 1995) and western Indian Oceans (McClanahan et al. 2001; Graham et al 2006). While such shifts may only be realized following widespread coral mortality, the hysteresis in ecosystems and the difficulty of reversing such shifts highlights the importance of herbivory in maintaining a healthy balance between corals and algae (Scheffer et al. 2001; Mumby and Steneck 2008).

The importance of roving herbivorous fishes in ecosystem processes, particularly in the context of reef degradation, is well established, and is directly related to the consumption of algal biomass. The role of territorial herbivorous fishes (primarily Pomacentridae) in structuring benthic communities has received considerable attention over the past three decades (reviewed by Ceccarelli et al. 2001). However, the majority of these studies have been conducted over small spatial scales, with relatively few examining their role in larger scale ecosystem processes and reef degradation (e.g., Ceccarelli et al. 2006; Ceccarelli 2007). This has presumably stemmed from their relatively small size (most < 20 cm maximum total length, TL: Randall et al. 1997) and restricted foraging ranges (0.2 – 6.3 m^2 territory size: Hata and Kato 2004; Ceccarelli 2005b). Indeed, the role of territorial damselfish in reef processes is not likely to manifest through the direct consumption of algae, but rather through the exclusion of other herbivorous taxa from their territories (e.g., Brawley and Adey 1977) and/or farming activities (i.e., the selective removal of undesirable algae, active site selection, and fertilization; Hata and Kato 2004; Jones et al. 2006). Through these activities territorial damselfish have been reported to maintain algal communities that differ in taxonomic composition (Hixon and Brostoff 1996; Ceccarelli 2007), have greater biomass (50 – 3500 % increase: Klumpp et al. 1987; Hata and Kato 2004) and greater productivity (74 – 405 % increase: Klumpp et al. 1987; Russ 1987) than those on adjacent substrata (reviewed by Ceccarelli et al. 2001). Whilst the majority of studies have been unable to distinguish between the effects of territory defense and farming, the rapid reduction in algal biomass following the removal of the resident damselfish (Brawley and Adey 1977; Mahoney 1981; Hourigan 1986; see Ceccarelli et al. 2005a for exception) suggests that territory defense is an important mechanism, at least for some species.

The majority of studies on coral reefs divide algae into three broad groups; algal turfs, or the epilithic algal matrix (EAM; sensu Wilson et al. 2003), macroalgae, and crustose algae. The division between algal turfs and macroalgae is typically related to the size, or height, of the algae. Algal turfs refer to short (< 10 mm in height), multispecific algal assemblages that are dominated by filamentous species, but may also include smaller forms, or developmental stages, of larger algal species that are maintained in cropped state by grazing (Steneck 1988). In contrast, macroalgae refer to larger (> 10 mm in height), and often more complex algal forms, such as articulated calcareous (e.g., *Halimeda*, *Amphiroa*), corticated terete (e.g., *Hypnea*, *Laurencia*), corticated foliose (e.g., *Dictyota*, *Padina*), and leathery macroalgae (e.g., *Sargassum*, *Turbinaria*; sensu Steneck 1988). Territorial damselfish are interesting in that they allow species within algal turfs to develop into larger macroalgal sizes, and at least some species appear to support fleshy macroalgae (i.e., corticated foliose and leathery macroalgae; sensu Ceccarelli et al. 2005b) within their territories (Hata and Kato 2004). As the transition between algal turfs and fleshy macroalgae is a critical issue in reef ecosystems the abundance and widespread distribution of territorial damselfishes (Ceccarelli et al. 2001) may place them in an important position in shaping the structure of benthic communities on reefs.

Macrophyte assays (transplanted pieces of seagrass or macroalgae) have been used extensively as a metric for the intensity of herbivory across reef gradients on both Caribbean (Hay 1981; Lewis 1985; Reinthal and MacIntyre 1994) and Indo-Pacific reefs (McCook 1996, 1997; Sluka and Miller 2001; Fox and Bellwood 2008a). However, only one study has considered the role of territorial damselfish in influencing the observed patterns (Lassuy 1980). This is surprising given that collectively damselfish territories can occupy over 50 % of the substrata across a reef, and up to 87 % of the substrata within individual reef habitats (Ceccarelli 2007). The aims of this study, therefore, were to quantify the territory composition of six species of territorial damselfish, and to determine if the rate of removal of fleshy macroalgae (*Sargassum swartzii*: Phaeophyceae) is influenced by the presence of any of these six species of territorial damselfish. *Sargassum* was selected for the macrophyte assays as it has been used extensively in previous studies (e.g., Lewis 1985; McCook 1996; Fox and Bellwood 2008a) and is often viewed as a sign of reef degradation. *Sargassum* was the dominant alga following phase-shifts to macroalgal dominance on east African reefs (McClanahan et al. 2001; Graham et al 2006) and in an experimentally-induced phase-shift on an inshore reef in the central Great Barrier Reef (Hughes et al. 2007).

5.2. Materials and Methods

Study site

This study was conducted between November 2006 and January 2007 on Lizard Island (14°40'S, 145°28'E), a mid-shelf granitic island in the northern Great Barrier Reef (GBR). Four sites were selected to examine variation in benthic community structure and composition of damsel territories (Mermaid Cove, Watsons Bay, Osprey Islet, Lagoon; Fig. 5.1). These sites were selected as they are sheltered from the prevailing south-easterly swell and supported higher densities of damselfish with visually apparent territories than exposed habitats (Meekan et al. 1995). Mermaid Cove, Watsons Bay, and Osprey Islet sites were located within sheltered bays on the northwest aspect of the island, while the Lagoon site was located on the leeward margin of an extensive reef flat on the south-eastern aspect of the island.

Benthic community structure and damselfish densities

To quantify the variation in the benthic community structure among the four sheltered sites a series of point intercept transects were censused. Twelve 10 m transects were haphazardly placed and censuses within each site (see Chapter 2 for detailed description). Substratum categories follow those defined in Chapter 2. Macroalgae were identified to genus where possible and placed into functional groups following Steneck (1988). For each point censused it was determined if that point was located within a damselfish territory, and the species of damselfish recorded.

The densities of territorial damselfish were quantified at each of the four sites using six 30 m transects. The transects were haphazardly placed within each site and all territorial damselfish within a 2 m wide belt were recorded.

Damselfish territory composition

The benthic composition of the territories of six damselfish species were quantified *in situ* using point intercept quadrats. The damselfish species selected were *Dischistodus perspicillatus*, *Dischistodus prosopotaenia*, *Dischistodus pseudochrysopoecilus*, *Hemiglyphidodon plagiometopon*, *Plectroglyphidodon lacrymatus*, and *Stegastes nigricans*. All of these species are relatively large (≥ 11 cm maximum TL; Randall et al. 1997) and maintain visually conspicuous territories. Ten haphazardly selected territories of the common species at each of the four sheltered sites (Table 5.1) were censused by placing a 0.55 × 0.55 m quadrat over the approximate centre of the territory. The quadrat was divided into a 10 ×10 grid using strings positioned at 5 cm intervals along the vertical and horizontal axes. The type of substratum under each of 100 points was recorded, providing an estimate of percent cover. Substratum categories were classified as previously described. An additional ten territories of *D. prosopotaenia* were censused at Coconut Beach, an exposed site on the south-eastern aspect of Lizard Island (Fig. 5.1).

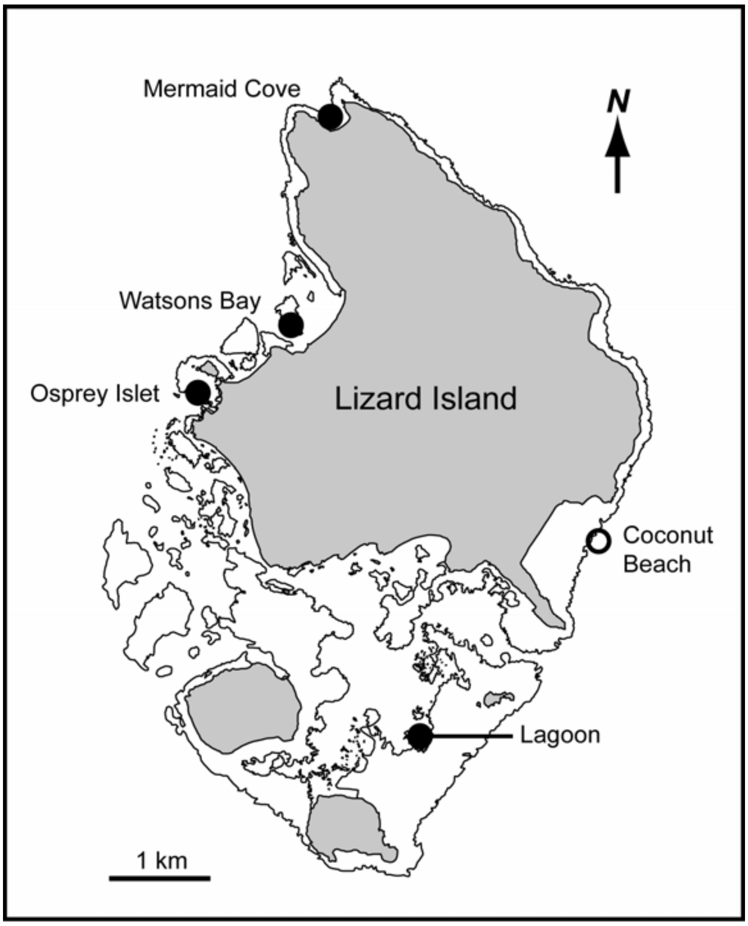


Fig 5.1: Map of Lizard Island indicating the location of the four sheltered sites (filled circles) used to quantify the benthic community structure, the territory composition of six common damselfish species, and the effect of territorial damselfish on the removal of *Sargassum*. The location of an additional site used to quantify the effect of *Dischistodus prosopotaenia* on the removal of *Sargassum* is also indicated (open circle). The prevailing wind is from the south-east.

Macroalgal transplants

To quantify the influence of territorial damselfish on the removal of *Sargassum* a series of transplant experiments were conducted at the two sites that supported the highest species richness of territorial damselfishes; Mermaid Cove and Lagoon. *S. swartzii* was selected for the transplant experiment as it was one of four *Sargassum* species recorded within damselfish territories on Lizard Island (this Chapter) and is the dominant species on the inshore reefs in the region (A.Hoey pers. obs.). *S. swartzii* was collected from the reef flat of an inshore reef in the Turtle Island Group (14°43'S, 145°12’E), approximately 28 km west of Lizard Island. Individual *Sargassum* thalli were removed by cutting the holdfast as close to the point of attachment as possible. All *Sargassum* thalli were returned to Lizard Island and placed in a large (6000 L) aquarium with flow through seawater within 90 min of collection.

Individual *S. swartzii* thalli were spun, weighed and measured as previously described (Chapter 2). The mean wet weight and height of each thallus was 51.2 ± 4.7g (SE) and 265 ± 2 mm, respectively. Two haphazardly selected *S. swartzii* thalli were allocated to an individual territory of one of the six damselfish species. One *S. swartzii* thallus was transplanted to the centre of the territory, and the remaining thallus was transplanted outside the territory; approximately 1.5 m from the perimeter of the territory. Each *S. swartzii* thallus was attached to an individually numbered small lead weight (approx. 40 g) using a rubber band and a cable tie. The lead weights allowed the *Sargassum* to be transplanted with minimum disturbance and enabled any displacement of the *Sargassum* by the resident damselfish to be quantified. After a period of 24 hours the *Sargassum* was collected, spun, weighed and the percentage mass lost calculated. Transplants were conducted within the territories of six damselfish species at Mermaid Cove, and five damselfish species at the Lagoon site due to a lack of *H. plagiometopon*. Within each site, a minimum of sixteen territories of each of the damselfish species were used for the transplant experiment (Table 5.1). To examine the generality of the effects of *D. prosopotaenia* on the removal of *Sargassum* additional transplants were conducted within 20 territories at two additional sites; Watsons Bay and Coconut Beach. Structured observations of the species responsible for removing the *Sargassum* assays were not performed as diver presence has been shown to influence the feeding behaviour of macroalgal browsing fishes (Fox and Bellwood 2008a; Chapter 3).

Table 5.1: Summary of the species and sample sizes within each site used for quantifying the territory composition and effect of resident damselfish on the removal of transplanted *Sargassum*. Maximum length refers to the maximum total length from Randall et al. (1997). The mean depth of territories of each species within each site is given.

	Dischistodus perspillatus	*Dischistodus prosopotaenia*	*Dischistodus pseudochrysopoecilus*	*Hemiglyphidodon plagiometopon*	*Plectroglyphidodon lacrymatus*	*Stegastes nigricans*
Maximum length (cm)	20	19	18	20	11	15
Mermaid Cove						
Depth (m)	6.0	5.7	4.5	4.1	2.7	2.7
Territory composition (n)	10	10	10	10	10	10
Sargassum transplants (n)	22	30	21	21	23	21
Lagoon						
Depth	3.5	3.4	1.3		1.6	2.2
Territory composition (n)	10	10	10		10	10
Sargassum transplants (n)	20	20	16		20	20
Watsons Bay						
Depth	2.7	2.1		3.2		
Territory composition (n)	10	10		10		
Sargassum transplants (n)		20				
Osprey Islet						
Depth	5.9	6.0		4.8		
Territory composition (n)	10	10		10		
Coconut Beach						
Depth		6.7				
Territory composition (n)		10				
Sargassum transplants (n)		20				

Statistical analyses

Variation in damselfish territory composition among species and sites was analysed using a one-factor multivariate analysis of variance (MANOVA). A composite of damselfish species and site was used as a factor in the analysis due to variability in the presence of each of the focal damselfish species within each site. Assumptions of the MANOVA were examined by residual analysis. The damselfish territory composition data was $\log_{10}(x + 1)$ transformed to improve multivariate normality. A canonical discriminant analysis (CDA) was then used to examine how species by site combinations differed in territory composition. Ninety-five percent confidence ellipses were plotted around the group centroids (Seber 1984).

A three-factor repeated measures ANOVA was used to determine if the rate of removal of *Sargassum* biomass varied among sites, damselfish species, or position relative to territory (i.e., within or outside territory). A repeated measures ANOVA was used to account for the non-independence of the paired thalli allocated to each damselfish territory. Type IV sums of squares were used to adjust for the missing data for *H. plagiometopon* at the Lagoon site. A two-factor repeated measures ANOVA was used to determine if the rate of removal of *Sargassum* biomass varied among sites, or position relative to the territories of *D. prosopotaenia*. The analyses were based on the proportion of the initial, or transplanted, biomass removed during 24 hours on the reef. Assumptions of the ANOVA were examined by residual analysis and subsequently the proportion of biomass removed was arcsine-square root transformed to improve normality and homoscedasticity. Tukey's HSD tests were used to identify which means contributed to any significant differences detected.

5.3. Results

Collectively, algae covered 41.5 ± 1.9 (SE) % of the substratum across the four sites, and was composed primarily of short and long algal turfs (21.0 %) and macroalgae (17.6 %; Fig. 5.2). The algal community outside damselfish territories was composed almost solely of short algal turfs (14.6 %) and crustose coralline algae (2.0 %). Within damselfish territories the algal community was composed of long turfs (5.9 %), short turfs (0.4 %), cyanobacteria (0.6 %), and a diversity of macroalgal species and functional groups (collectively 17.3 %; Fig. 5.2). Of all the macroalgae censused across all sites, 98.2 % were recorded within damselfish territories with only the foliose brown alga *Padina* being recorded outside territories. No *Sargassum* was recorded outside damselfish territories during the benthic surveys or extensive searches of the four sites. *Padina* (5.1 %) and the leathery brown alga *Sargassum* (2.6 %) were the most abundant algal genera recorded within damselfish territories across the four sites. The cover of *Padina* and *Sargassum* were generally greater at the three sites on the northwest aspect of the island (6.6 % and 3.5 %, respectively) than the Lagoon site (0.3 % and 0 %, respectively). Details of the variation in the benthic community structure among the four sites are given in Appendix D.

Damselfish territories covered 24.2 ± 1.9 % of the substratum across the four sites, with *D. prosopotaenia* accounting for over half of the territories recorded; covering 13.6 % of the substratum. *D. prosopotaenia* was more abundant and their territories occupied a greater proportion of the substratum in the three sites on the northwest aspect of the island (Mermaid Cove: 11.1 %; Watsons Bay 18.4 %; Osprey Islet: 21.7 %), than in the Lagoon (3.3 %; Fig. 5.3). Collectively, the territories of *D. perspicillatus*, *D. pseudochrysopoecilus*, *H. plagiometopon*, *P. lacymatus* and *S. nigricans* accounted for 6.4 % of the substratum across the four sites (Mermaid Cove: 4.0 %; Watsons Bay: 3.5 %; Osprey Islet: 6.8 %; Lagoon 11.4 %; Fig. 5.3a). The Lagoon site supported a greater number of species than the other three sites, with space occupation and abundance spread more evenly amongst species (Fig. 5.3). *S. nigricans* (6.3 %), *Pomacentrus* spp. (4.8 %), *Stegastes apicalis* (3.5 %), *D. prosopotaenia* (3.3 %), *P. lacymatus* (2.8 %), and *Dischistodus melannotus* (1.8%) accounted for the majority of the space occupied by damselfish territories at the Lagoon site (Fig. 5.3a).

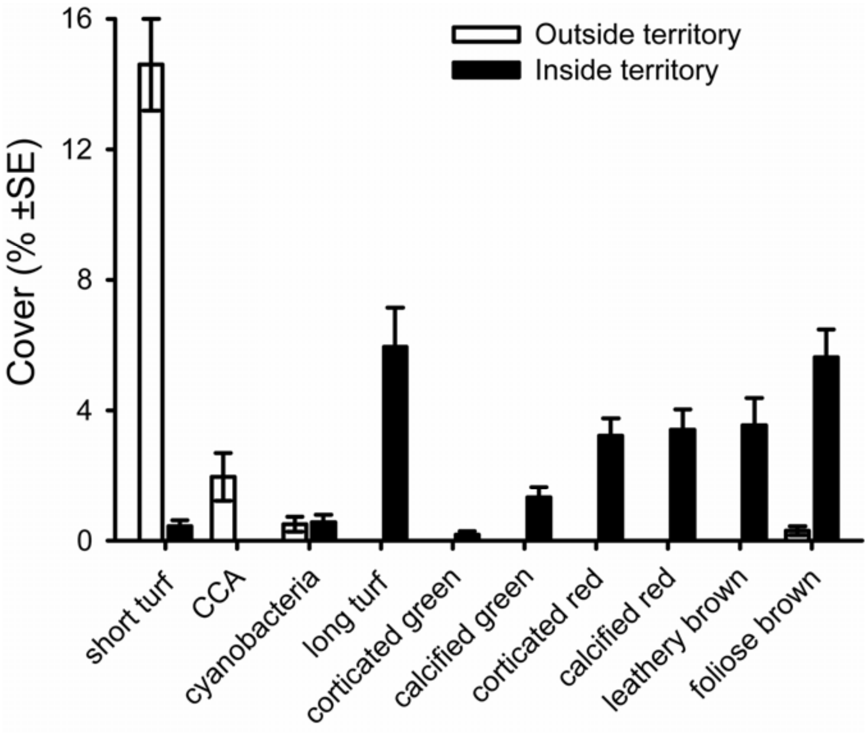


Fig. 5.2: Composition of benthic algal communities inside and outside territories of damselfishes on Lizard Island. The mean cover is based twelve point intercept transects within each of four sites (total n = 48). CCA: crustose coralline algae. Corticated green and red algae, calcified green and red algae, and foliose and leathery brown algae are all macroalgal groups.

The composition of damselfish territories varied significantly amongst species and sites (MANOVA: $F_{238,1652} = 10.30$, $p < 0.001$). The CDA detected four distinct groupings of damselfish territories based on their benthic composition, with the first two canonical variates explaining 75.1 % and 13.5 % of the total variation, respectively (Fig. 5.4). Five of the six species examined displayed similarities in territory composition among sites. The exception to this pattern was *D. prosopotaenia*, with territories of this species belonging to three of the four groups identified (Fig. 5.4). *D. perspillatus* territories were separated from all other species along the first canonical variate and were characterized by a high cover of tall cyanobacteria mats over sand. The remaining three groups were separated along the second canonical variate. Group 1 (*D. pseudochrysopoecilus*, *P. lacrymatus*, *S. nigricans*, and Lagoon and Coconut Beach *D.*

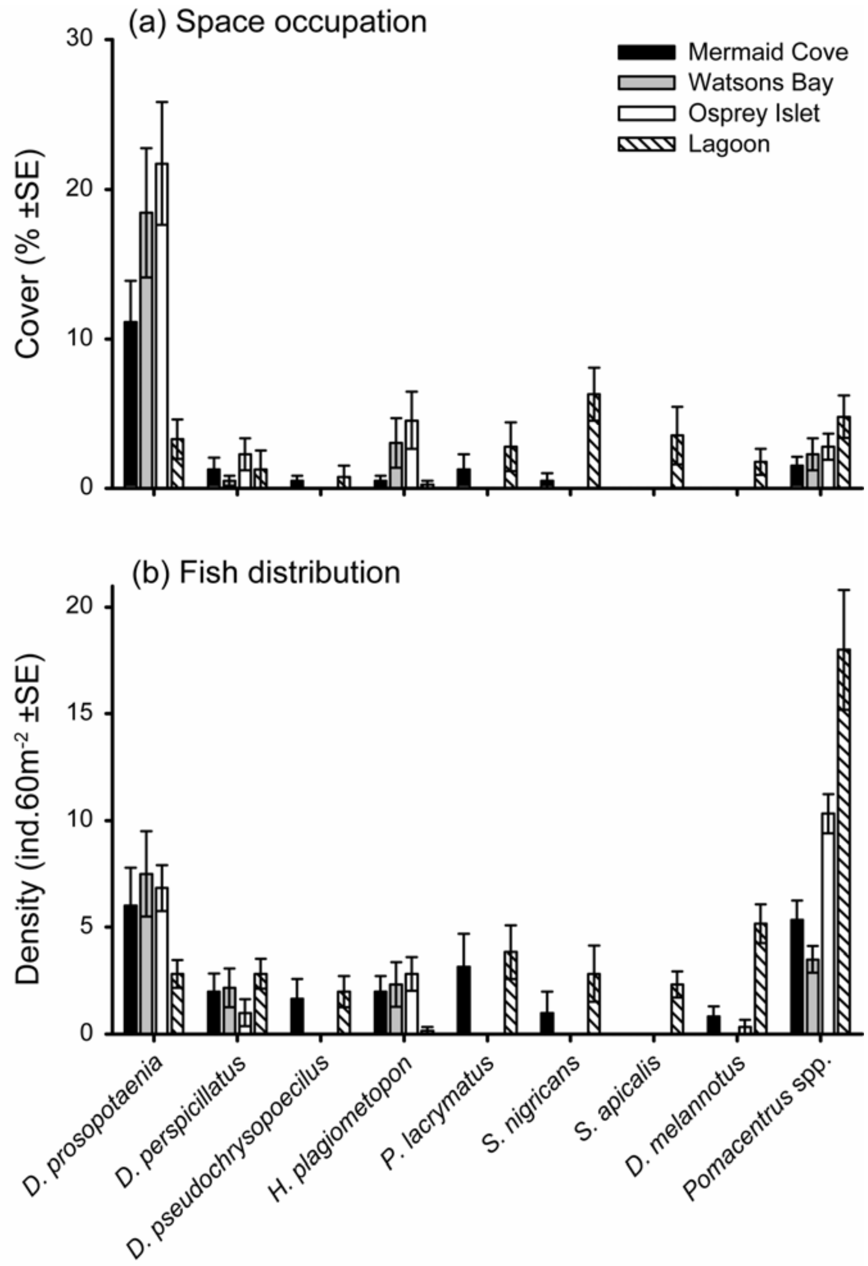


Fig. 5.3: Spatial variation in (a) the percent of substratum occupied by damselfish territories, and (b) the density of territorial damselfishes across four sheltered sites on Lizard Island. The mean substratum cover is based on twelve 10 m point intercept transects within each site. The densities of territorial damselfishes are based on six 30 × 2 m transects within each site. *D*.: *Dischistodus*; *H*.: *Hemiglyphidodon*; *P*.: *Plectroglyphidodon*; *S*.: *Stegastes*. *Pomacentrus* spp. includes *Pomacentrus adelis*, *Pomacentrus bankanensis*, *Pomacentrus brachialis*, *Pomacentrus chrysurus*, *Pomacentrus grammorhynchus*, and *Pomacentrus wardi*.

prosopotaenia) was characterized by a high cover of long turf algae and live coral. Group 2 (*H. plagiometopon* and Mermaid Cove *D. prosopotaenia*) and Group 3 (Watsons Bay and Osprey Islet *D. prosopotaenia*) were characterized by a high cover of foliose and leathery brown algae, and calcified and corticated red algae (Fig. 5.4).

D. prosopotaenia territories from Watsons Bay and Osprey Islet contained high cover of *Sargassum* (mean = 20.0 %), *Padina* (8.0 %), *Galaxaura* (6.5 %) and *Acanthophora* (5.4 %), while those from Mermaid Cove had a lower cover of *Sargassum* (12.6 %), *Padina* (3.3 %), and *Galaxaura* (0.6 %). *Sargassum* was absent from all *D. prosopotaenia* territories within the Lagoon and Coconut Beach sites, with these territories having a high cover of calcified green (*Halimeda*: 11.0 %) and corticated red algae (9.4 %); and low cover of calcified red (1.1 %), foliose brown (*Padina*: 1.1%; *Dictyota*: 0.8 %) and leathery brown algae (*Turbinaria*: 0.1 %). *H. plagiometopon* territories had a high cover of *Padina* (18.4 %), but low cover of *Sargassum* (0.6 %) across all sites. Details of the variation in algal composition among species and sites are given in Appendix D.

The transplant experiment showed that the removal rates of *Sargassum* were influenced by a significant interaction between damselfish species and position relative to the territory ($F_{5,233} = 234.07$, $p < 0.001$; Fig. 5.5). No significant variation was detected in relation to the third order interaction between damselfish species, site and position relative to the territory ($F_{4,233} = 1.34$, $p = 0.25$), or the second order interaction between site and position relative to the territory ($F_{1,233} = 1.09$, $p = 0.30$). There was a marked difference in the removal rates of *Sargassum* transplanted within the territories of *D. prosopotaenia* (1.1 $\%.d^{-1}$) and that of *Sargassum* transplanted adjacent to the same territories (83.8 $\%.d^{-1}$; Fig. 5.5). The removal rates of *Sargassum* were relatively high, both within and adjacent to the territories of the five remaining damselfish species (76.2

– 92.5 %.d^{-1}). On numerous occasions the *Sargassum* assays collected from both inside and adjacent to territories of these five species were almost completely removed, with only the holdfast and the primary axes held within the rubber band remaining. No significant effect of territory was detected for any of these species. Details of the Tukeys HSD test are given in Appendix D.

On several occasions *Naso unicornis* (20 – 30 cm TL), *Naso lituratus* (20 - 25 cm TL), and *Kyphosus vaigiensis* (20 - 30 cm TL) were observed feeding on *Sargassum* transplanted within the territories of *D. pseudochrysopoecilus*, *H. plagiometopon*, and *S. nigricans* at Mermaid Cove. All observations were made within the first 10-minutes of the deployment, with none of these damselfish showing signs of aggression towards the intruders. On one occasion, *D. prosopotaenia* was observed displaying aggressive behaviour (i.e., rushing) toward two *N. unicornis* (20 - 23 cm TL) feeding on a *Sargassum* assay 1.5 m outside its territory. The six damselfish species displayed little interest in the presence of transplanted *Sargassum* within their territories, with no attempts to 'weed' or move the *Sargassum* outside the territory. Furthermore, all lead weights and remaining *Sargassum* biomass were located within the territories after the 24-h experimental period.

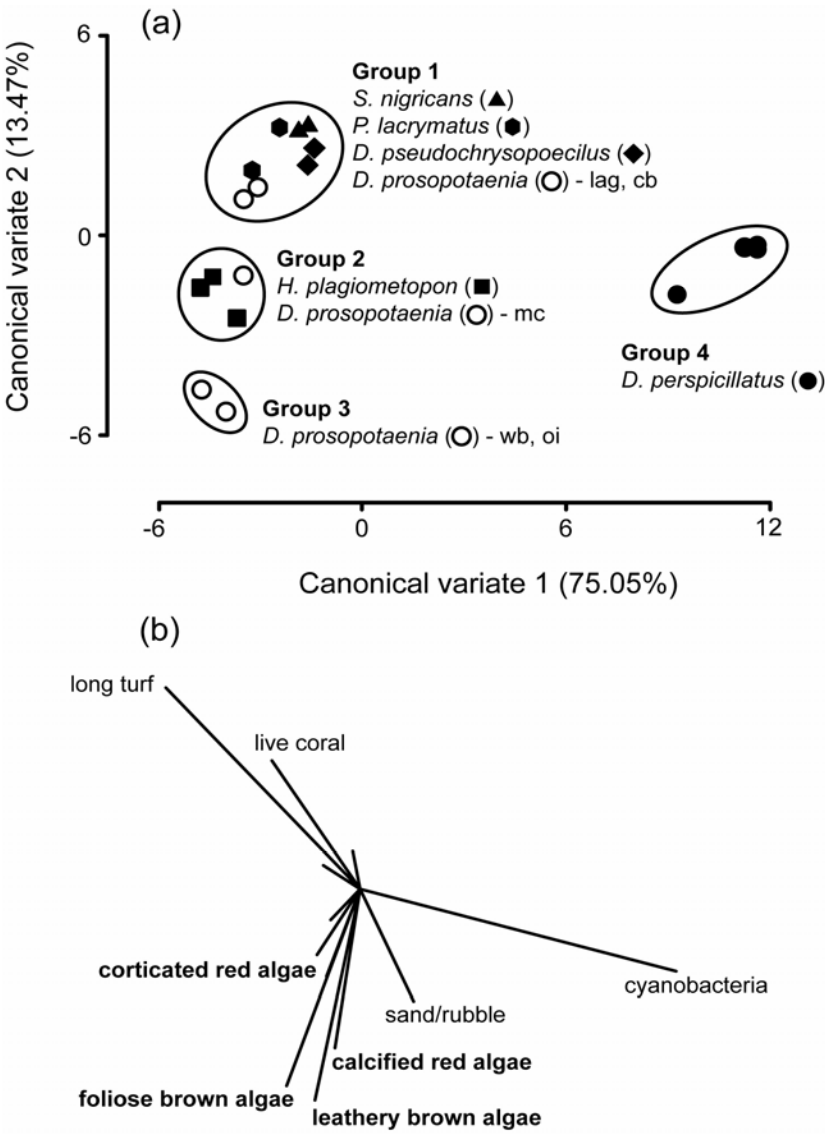


Fig. 5.4: Canonical discriminant analysis showing the relationship among the benthic assemblages of damselfish territories on Lizard Island. a). Ordination plot showing relationship between the territory composition of six damselfish species across two to five sites. Centroids for each species at each site are plotted. Ellipses represent significant groupings identified from overlapping 95% confidence intervals. *Dischistodus perspicillatus*: filled circles; *Dischistodus prosopotaenia*: open circles; *Dischistodus pseudochrysopoecilus*: filled diamonds; *Hemiglyphidodon plagiometopon*: filled squares; *Plectroglyphidodon lacrymatus* filled hexagons; *Stegastes nigricans* filled triangles. Sites are indicated for *D. prosopotaenia* territories: cb: Coconut Beach; lag: Lagoon; mc: Mermaid Cove; oi: Osprey Islet; wb: Watsons Bay. b). Factor structure showing the relative contributions of each of the substrata categories to the observed differences in territory composition. Macroalgal groups are shown in bold. Leathery brown algae: *Sargassum*, *Turbinaria*, *Hormophysa*; foliose brown algae: *Padina*, *Dictyota*; calcified red algae: *Amphiroa*, *Galaxaura*; corticated red algae: *Acanthophora*, *Gelidiella*, *Gracilaria*, *Hypnea*, *Laurencia*.

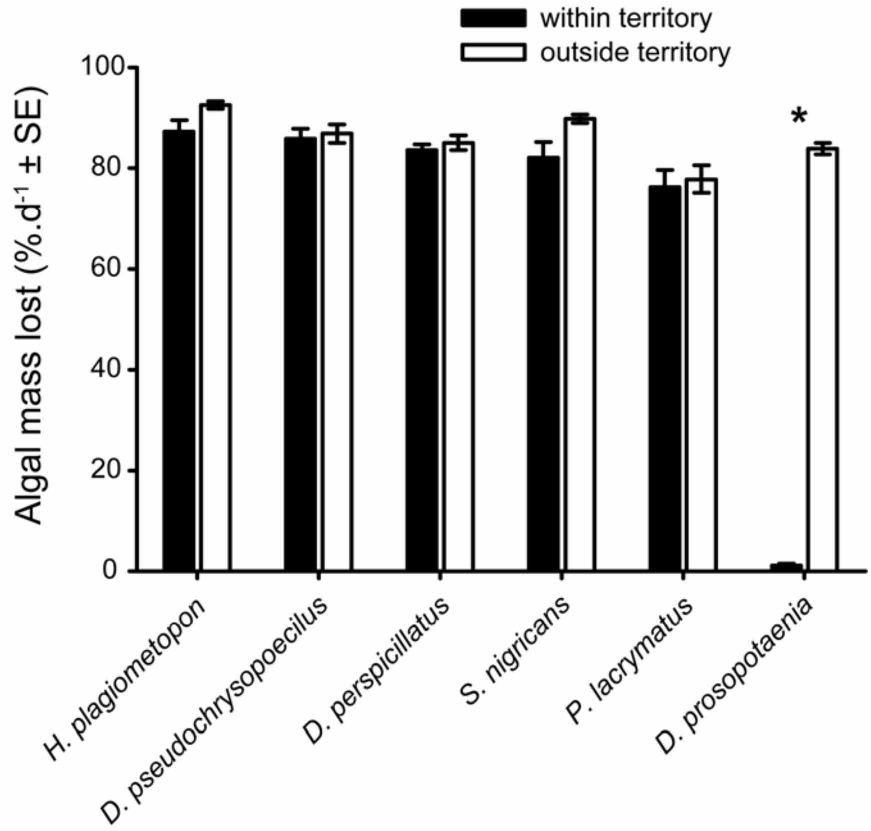


Fig. 5.5: Variation in the removal rates of *Sargassum* transplanted within (filled bars) and adjacent (open bars) to the territories of six damselfish species at Lizard Island. Means are based on a minimum of 16 thalli (mean = 21 thalli) transplanted within and adjacent to territories at each of two sites. Only one site was used for *Hemiglyphidodon plagiometopon* due to a lack of individuals at the second site. * indicates significant ($p < 0.05$) difference identified by Tukeys HSD test. *D.*: *Dischistodus*; *H.*: *Hemiglyphidodon*; *P.*: *Plectroglyphidodon*; *S.*: *Stegastes*.

There was a significant interaction between site and position relative to the territories of *D. prosopotaenia* across the four sites ($F_{3,86} = 7.58$, $p < 0.001$). Overall, the removal rates of *Sargassum* were significantly reduced within the territories of *D. prosopotaenia* across all four sites (Fig. 5.6). A reduction in the magnitude of the differences between *Sargassum* transplanted within and adjacent to territories at Watsons Bay was responsible for the interaction. The reduction in *Sargassum* biomass within territories varied from 1.0 %.d^{-1} at Lagoon to 4.9 %.d^{-1} at Watsons Bay, and adjacent to territories varied from 76.9 %.d^{-1} at Watsons Bay to 84.2 %.d^{-1} at Lagoon (Fig. 5.6).

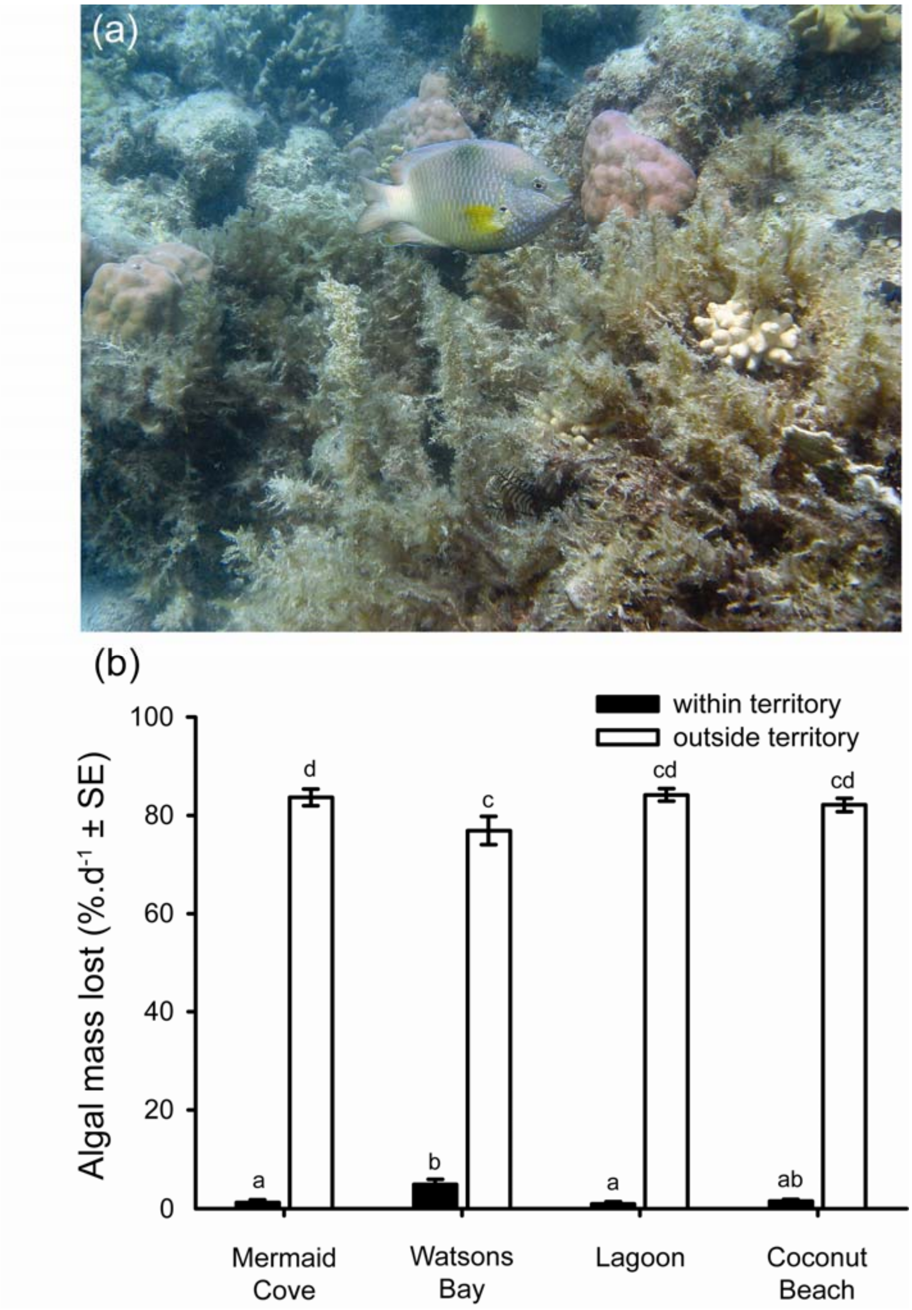


Fig. 5.6: a) Photograph of a typical *Dischistodus prosopotaenia* territory from Watsons Bay, Lizard Island. The territory contains a diversity of macroalgae, dominated by *Sargassum*. b) Variation in the removal rates of *Sargassum* transplanted within (filled bars) and adjacent (open bars) to *Dischistodus prosopotaenia* territories among four sites on Lizard Island. Means are based on a minimum of 20 thalli (mean = 23 thalli). Letters represent homogeneous groups identified by Tukeys HSD test.

5.4. Discussion

Territorial damselfish have long been recognized to have a major influence on the algal communities within their territories (e.g., Brawley and Adey 1977; Ebersole 1977). Although differences have been documented among damselfish species and geographic locations (Ceccarelli et al. 2001), the algal community within defended territories is generally dominated by long algal turfs and finely corticated red algae (reviewed by Ceccarelli 2007). Indeed, the territories of four (*D. perspicillatus*, *D. pseudochrysopoecilus*, *P. lacrymatus*, and *S. nigricans*) of the six damselfish species examined in the present study were characterized by long algal turfs (including cyanobacteria). The territories of the two remaining species (*D. prosopotaenia* and *H. plagiometopon*), were characterized by diverse algal assemblages dominated by foliose and leathery brown macroalgae. However, only one species (*D. prosopotaenia*) supported significant quantities of leathery macroalgae within their territories. The bioassays provided evidence that this *Sargassum* was actively protected. This highlights a significant difference among territorial damselfish that may have important ramifications for coral reef benthic ecology.

The algal composition within damselfish territories is likely to be determined by the relative intensity of territory defense and/or farming activities, and the availability of algal propagules. Herbivore exclusion experiments have demonstrated that the effect of damselfish on algal communities is not simply a result of reduced grazing intensity within their territories (Hata and Kato 2003; Ceccarelli et al. 2005a). Large variations in the territory composition of two species of *Stegastes* have been related to interspecific differences in behaviour (Hata and Kato 2004). *S. nigricans*, through weeding of undesirable algae and prompt exclusion of herbivores (i.e., intensive management), maintained relatively small territories (0.3 m^2) dominated by a red filamentous alga; *Polysiphonia* sp. In contrast *Stegastes obreptus*, through the delayed exclusion of herbivores and an absence of weeding (i.e., extensive management), maintained larger territories (6.3 m^2) containing a diverse assemblage of fleshy macroalgae. While such correlative approaches provide some insight into the underlying mechanisms, they are unable to distinguish between the relative importance of territory defense and farming activities. Ceccarelli et al. (2005a) using an orthogonal combination of damselfish removal and roving herbivore exclusion found that the effects of territorial defense were minimal when compared to farming activities, at least for two relatively small species of damselfish, *P. lacrymatus* and *Pomacentrus adelus*.

The composition of *D. prosopotaenia* and *H. plagiometopon* territories in the present study suggests that they may employ a management strategy similar to that of *S. obreptus*, with limited weeding and delayed exclusion of herbivores (extensive management; sensu Hata and Kato 2004). Nevertheless, *D. prosopotaenia* was the only species to have an effect on the removal of *Sargassum* assays. The low removal rates of *Sargassum* assays within their territories, when compared to the high removal rates of assays positioned approximately 1.5 m outside the territories, suggest that *D. prosopotaenia* may be actively defending this resource from herbivores that are capable of consuming *Sargassum* (i.e., macroalgal browsers). This is supported by an observation of aggressive behaviour displayed toward two *N. unicornis* feeding on a *Sargassum* assay outside a territory. Furthermore, recent studies have demonstrated that transplanted *Sargassum* is rapidly removed by macroalgal browsing fishes (primarily *N. unicornis*) from multiple habitats around Lizard Island, including the Lagoon (Chapter 2, 3).

In marked contrast to *D. prosopotaenia*, there was almost complete removal of *Sargassum* biomass within the territories of the five remaining species. This reduction in *Sargassum* biomass may be attributable to weeding activities of the resident damselfish or feeding by macroalgal browsing fishes. The only other study to have used macroalgal assays to assess the effect of a territorial damselfish reported that *Eupomacentrus lividus* dislodged the macroalgae from their attachment strings, and subsequently carried or pushed the algae outside their territory; while macroalgae positioned outside territories remained largely intact (Lassuy 1980). No weeding behaviour or attempts to move the *Sargassum* outside the territories were observed in the present study, with all lead weights and remaining *Sargassum* biomass being collected from the approximate centre of the territories. In the majority of cases the *Sargassum* was almost completely removed, with only the holdfast and a short length of the primary axis with distinct bite marks remaining. *S. swartzii* has flattened axes, or branches, that are typically 1 – 1.5 mm thick. Whilst the physical toughness of the axes was not quantified, it appears unlikely that the resident damselfish could have sheared through the axis. Whilst the potential for weeding activities to account for the reduction in biomass of transplanted *Sargassum* cannot be discounted, it appears unlikely. That said, the absence of *Sargassum* from the territories of these five species may suggest they are removing *Sargassum* from their territories at an earlier development stage or smaller size.

Direct observations of macroalgal browsing fishes (*N. unicornis*, *N. lituratus* and *K. vaigiensis*) feeding on the *Sargassum* assays within their territories and the absence of aggression toward these intrusions suggests that these damselfish species (*D. perspicillatus*, *D. pseudochrysopoecilus*, *H. plagiometopon*, *P. lacrymatus*, *S. nigricans*) were not defending this alga from macroalgal browsers. Previous studies have observed

S. nigricans to promptly exclude herbivorous fish from its territories (Hata and Kato 2003, 2004). However, these different responses are likely to reflect the identity of the intruding fishes and the algal resource they are targeting. Several studies have documented variation in the response of resident damselfish to intrusions by a range of species (Ebersole 1977; Mahoney 1981; Robertson 1984). Although they have focused on the distinction between herbivorous and non-herbivorous fishes, it is probable that this distinction could equally apply to the variation among herbivorous fish species.

Traditionally, territorial damselfish were assumed to promote the growth of apparently palatable algae that would be used directly as a food source by the resident fish (Brawley and Adey 1977; Polunin 1988). While some species may directly consume the algae (e.g., *Stegastes apicalis*), gut content analyses have shown that many territorial pomacentrids are detritivores, suggesting that they may be selecting algae that maximizes the production and accumulation of detritus rather than algal production per se (Wilson and Bellwood 1997; Ceccarelli 2007). On algal dominated inshore reefs of the GBR, *Pomacentrus tripunctatus* and *Pomacentrus wardi* used the surface of *Sargassum* for the growth of epiphytic algae (Ceccarelli et al. 2005b), although the epiphytes may also trap detritus. While the use of *Sargassum* by *D. prosopotaenia* remains to be determined, the high proportion of detritus in their gut (ca. 40 %: Bay 1999) suggests they may be using *Sargassum* for the production and collection of detrital material, rather than a primary source of nutrition. Detritus is the principle dietary item for *H. plagiometopon* and it has been demonstrated to actively avoid ingesting algae within its territories (Wilson and Bellwood 1997). In the present study, *H. plagiometopon* territories contained a diverse assemblage of macroalgae, yet did not appear to favour *Sargassum*.

The absence of *Sargassum* from all *D. prosopotaenia* territories within the two sites on the south-eastern aspect of the island (i.e., Lagoon and Coconut Beach) is consistent with previous work at Lizard Island. *D. prosopotaenia* territories have been reported to be composed primarily of filamentous and corticated red algae (ca. 40 – 45 %) and thallate green algae (ca. 40 %) in both the lagoon (Bay 1999) and exposed north-eastern aspect of the island (Green 1994). Differences in algal composition among locations have been documented for several damselfish species (e.g., Ceccarelli 2007) and may be related to variation in the physical environment, preferences of the resident damselfish, or the availability of algal propagules. Broadly comparable hydrodynamic forces between the lagoon and sheltered sites (Fulton and Bellwood 2005) suggest that these alone cannot explain the variation among sites. In the present study, *D. prosopotaenia* defended the *Sargassum* bioassays within their territories across all sites, including those where *Sargassum* was not naturally present. Therefore, the absence of *Sargassum* in *D. prosopotaenia* territories within the Lagoon and Coconut Beach sites appears not to be related to a lack of protection, but rather a lack of colonization by *Sargassum* propagules.

Sargassum, like most fucalean algae, has limited dispersal potential when attached to the substratum with over 98 % of all propagules settling within one metre of the parent thalli (Kendrick and Walker 1995; Stiger and Payri 1999). Dispersal and establishment over larger distances, presumably through floating mats of fertile thalli, has been documented in several locations (Deysher and Norton 1982; Martinez et al. 2007). Large mats of floating *Sargassum* are often present in the bays on the northwestern side of Lizard Island following extended periods of westerly or north-westerly winds (A. Hoey pers. obs.). These mats often include fertile thalli and are presumably transported by currents from inshore reefs where *Sargassum* is locally abundant (Wismer et al. 2009). This potential source of propagules may not only explain the among site variation in the composition of *D. prosopotaenia* territories in the present study, but also a potential mechanism by which *Sargassum* could disperse and establish in new locations. Territories of *D. prosopotaenia* appear to represent a spatial refuge from herbivory for *Sargassum*, and if allowed to attain maturity may provide a local source of *Sargassum* propagules.

Within the Great Barrier Reef (GBR), *Sargassum* is often a dominant feature of inshore reefs where it can cover more than fifty percent of the substratum (McCook and Price 1997; Wismer et al. 2009). On mid- and outer-shelf reefs *Sargassum* has been reported to be extremely rare or even absent. The results of the present study indicate that *Sargassum* may be more common on mid-shelf reefs of the GBR than previously thought. *Sargassum* was abundant within *D. prosopotaenia* territories on the leeward side of the island, and covered approximately four percent of the reef substratum within these locations. Whether this represents a relatively recent range expansion or a previously undocumented presence remains unclear. Wismer et al. (2009) recorded no *Sargassum* on mid-shelf reefs in the northern GBR, including Lizard Island. The apparent failure to detect *Sargassum* may be related to the habitats examined or the functional categorization of the substrata. The four habitats (reef slope, crest, flat, back reef) examined by Wismer et al. (2009) were all located on the southeastern aspect of Lizard Island, and coincide with the area in which no *Sargassum* was recorded in the present study. Furthermore the categorization of the substrata as ‘damselfish territory’ rather than identifying taxonomic components may have underestimated the density of macroalgae. Over 98 % of all macroalgae recorded in the present study were contained within damselfish territories, and the composition of these territories, together with variation in the damselfish communities, were major contributors to the variation in benthic community structure among sites. These results not only highlight that *Sargassum* can persist on mid-shelf reefs of the GBR if protected from herbivores, but also the importance of including the taxonomic composition of damselfish territories in assessments of benthic community structure.

Of the six damselfish species examined in the present study, the five species that did not retain *Sargassum* within their territories (i.e., *D. perspicillatus*, *D. pseudochrysopoecilus*, *H. plagiometopon*, *P. lacrymatus*, and *S. nigricans*) may be important in controlling *Sargassum* colonization. Collectively, the territories of these species occupied 6.4 % of the substrata across the four sites, and by removing *Sargassum* at an early developmental stage, or allowing *Sargassum* to be removed, will have a positive effect in preventing the colonization and growth of *Sargassum* within their territories. In this respect they may play a positive role in maintaining coral reef resilience. This role is likely to extend beyond the damselfish species examined in the present study, and may be of greater importance in habitats where these species occupy a significant proportion of the substratum. Only one species, *D. prosopotaenia*, appears to be a potential threat in permitting *Sargassum* to persist. However, given that this species accounted for 56.3 % of the space occupied by all damselfish territories, or 13.6 % of the substrata across the four sites, this role as a refuge for *Sargassum* may be a significant one.

Territorial damselfish are a ubiquitous group on coral reefs, yet are often overlooked in ecosystem processes. The diversity in the algal assemblages they promote and the mechanisms through which they are maintained suggest they have the potential to influence patterns of grazing intensity both within and among habitats. Although restricted to a single species of *Sargassum*, the response of damselfish to intrusions by herbivorous taxa appears to be specific to the functional behaviour of the intruder. This variation emphasizes the complexities of the interactions between these damselfish and other herbivorous taxa, and limits generalizations. Nevertheless, damselfishes appear to be capable of influencing the distributions of both epilithic algal turfs (EAM) and erect macroalgae, with at least one species appearing to facilitate the development of fleshy macroalgae within its territory. Damselfish may thus provide a refuge or colonization site for fleshy macroalgae, even on reefs with relatively intact roving herbivore populations. As such they may provide a bridgehead or nucleus for the expansion of fleshy macroalgae on reefs. Although this is unlikely to have any repercussions in intact reef systems, current threats to coral reefs as a result of human activity and climate change are often mediated through changes in algal composition (McCook 1999; Bellwood et al. 2004; Hughes et al. 2007). Territorial damselfishes, and *D. prosopotaenia* in particular, may play a significant role in shaping local transitions in both turf- and fleshy macro-algal cover.

Chapter 6: Suppression of herbivory by macroalgal density: a critical feedback on coral reefs?

Under review in *Ecology Letters*

6.1. 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 and 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 and Schmitt 1988; Hixon and 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 (Fraser and Cerri 1982; Kotler et al. 1991), or their preferred food resources are facilitated by the physical structure itself (Laws 1970; Schmitt and Holbrook 1990). Alternatively, consumers may avoid complex habitats if their ability to detect predators is reduced (Underwood 1982; Riginos and 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 fundamentally changing the physical and ecological structure of many ecosystems.

Within coral reef systems the importance of corals in providing structural complexity, and consequently shaping fish communities has been well established (Friedlander and 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 and Selig 2007) have had significant effects on the structure and function of reef fish communities (Graham et al. 2006; Paddack et al. 2009). Reductions in coral cover are, however, often accompanied by increases in other benthic taxa, in particular algal turfs (filamentous algae and macroalgal propagules), that rapidly colonise the available substrata (Norström et al. 2009). Of these taxa macroalgae, or seaweed, is perhaps the most commonly reported, and in some locations has become the dominant benthic functional group (Hughes 1994; Graham et al. 2006). 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 propougules from top-down control and ultimately resulting in shifts to an alternate 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 alternate states are reinforced or locked in place by positive feedback mechanisms (Scheffer et al. 2001; Mumby and Steneck 2009). 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 and 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 and 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).

This potential for feedbacks, in particular changes in the susceptibility of macroalgae to herbivores, highlights the possibility for fish-coral-macroalgal interactions to not only reinforce alternate macroalgal-dominated states but also to influence the pathway along which the system may return to its original coral-dominated state; leading to hysteresis. Hysteresis is a pattern in which the pathway leading to an alternate state differs from the return pathway to the original state (Scheffer et al. 2001). That is, to reverse a shift from an alternate state the condition or state variable (e.g., herbivore biomass) needs to be restored to a level that greatly exceeds the threshold or tipping point that originally caused the shift. 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., 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 I examine the influence of the physical structure of macroalgal stands on the feeding behaviour of herbivorous coral reef fishes. I 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 I demonstrate the effect of macroalgal-mediated habitat structure on those species that appear to prevent and reverse phase shifts, respectively.

6.2. Materials and Methods

Study site

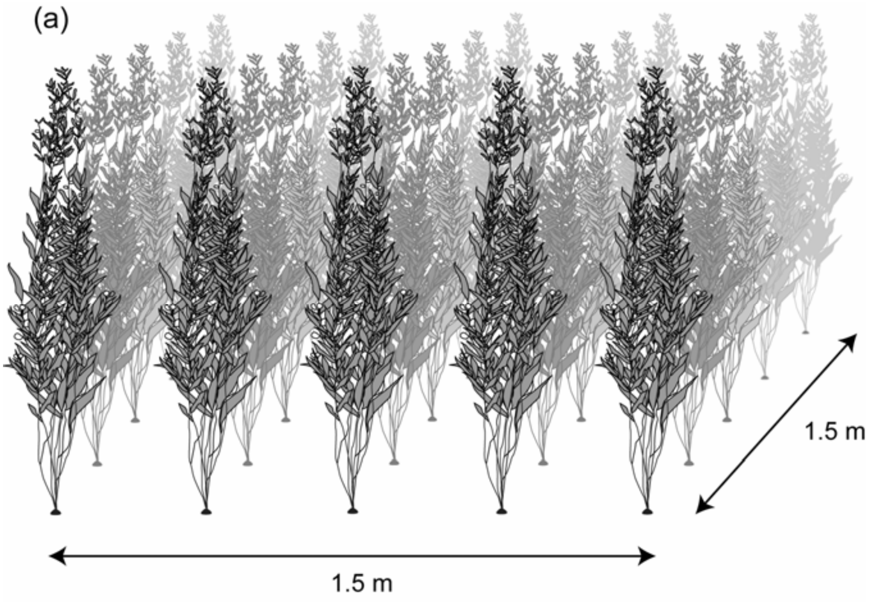
This study was conducted during April 2008 in Pioneer Bay, Orpheus Island (18°37’S, 146°30’E); an inshore island in the central region of the GBR. Pioneer Bay is located on the leeward, or western, side of the island and is approximately 17 km from the mainland. There is a well developed fringing reef within the bay with a clearly defined reef crest at a depth of 2 – 3 m, marking the transition between the reef flat and steeply inclined reef slope. The reef flat stretches approximately 150 m from the shoreline, and is characterized by a high cover of macroalgae (primarily *Sargassum* and *Padina*) interspersed with patches of sand and a low cover of live coral. In contrast, macroalgae are virtually absent from the reef crest with the substratum dominated by an algal turf covered consolidated pavement and interspersed with patches of live coral. Two sites, separated by approximately 250 m, were selected on the reef crest of Pioneer Bay. The reef crest was selected as it is the area of greatest herbivore activity (Hay

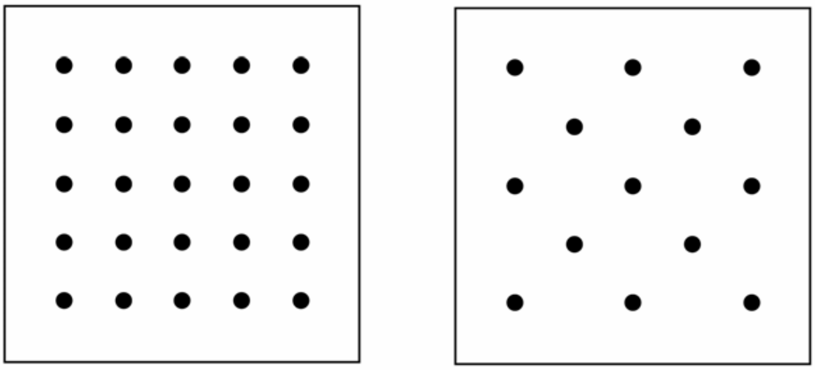
1981; Fox and Bellwood 2008a; Hoey and Bellwood 2008), and it provided relatively large areas free of other structural features (i.e., macroalgae and arborescent corals).

Experimental design

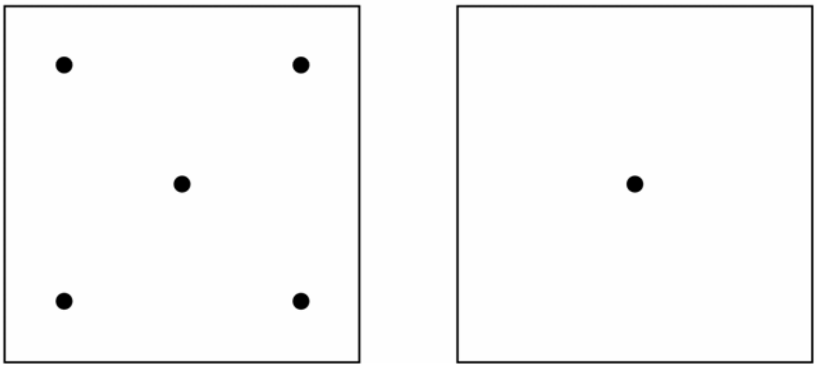
To examine the effect of macroalgal density on herbivory, *Sargassum* was transplanted to the reef at varying densities. *Sargassum* was selected as it is the largest coral reef macroalga, and was the dominant taxon following phase shifts to macroalgal dominance on east African reefs (Graham et al. 2006), and an experimentally-induced phase shift at this location (Hughes et al. 2007). Subsequently, *Sargassum* is often viewed as a sign of reef degradation. *Sargassum* cf. *baccularia* was collected from the reef flat of an adjacent bay, Hazard Bay. *S.* cf. *baccularia* is a relatively tall species (mature thalli >1m height) with smooth cylindrical axes and small ovate blades, or leaves. The *S.* cf. *baccularia* thalli were collected from Hazard Bay as they were considerably larger and appeared to be in better condition than the *Sargassum* within Pioneer Bay. The majority of *Sargassum* within Pioneer Bay at the time of the study were small (height <50 cm), had high loads of epiphytic algae, and were exhibiting signs of senescence with necrotic blades and axes. Individual *Sargassum* thalli of similar height (approximately 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 one hour of collection, and were transplanted to the reef within 24 hours.

Each thallus was spun in a salad spinner for 30 s to remove excess water, and the fresh weight and maximum height recorded. The mean initial mass and height of each thallus was 561.7 ± 6.2 g (SE) and 110.5 ± 0.7 cm, respectively. Each thallus was randomly allocated to one of four density treatments: high (25 thalli), medium (13 thalli), and low density (5 thalli), and a single thallus (Fig. 6.1). These densities were selected so that when distributed throughout a 1.5×1.5 m area they would represent a range of densities with the high density treatment approximating that of natural *Sargassum* stands on the inner-shelf reefs of the Great Barrier Reef (i.e., 5.3–8.1 kg.m^{-2}; Bellwood et al. 2006). Each thallus was attached to an individually numbered lead weight (approximately 450g) using a rubber band and a cable tie (following Chapter 5), enabling the forty-four thalli to be transplanted simultaneously at each site with minimum disturbance. All thalli were transplanted to the reef shortly after dawn (06:30–07:30) and collected after eight hours (14:30-15:30). This period encompassed the majority of the herbivore feeding day with very little activity being recorded at night (see Appendix E), and coincided with the period of greatest water depth at the study sites. The density treatments were haphazardly allocated within each site and were positioned on horizontal surfaces covered with algal turfs and free of live coral. A minimum of 6 m separated adjacent treatments within each site. The thalli within each treatment were positioned in rows (Fig. 6.1) and the location of each thallus noted to ensure they were repositioned in the same configuration on subsequent days. Within each site, an additional thallus was placed inside a free standing exclusion cage (1200×500×500 mm; 20 mm square mesh) to control for the effects of handling and translocation. After eight hours, all thalli were collected, spun and measured as described above, and returned to the raceways where they were held overnight. The *Sargassum* was redeployed in the identical configuration the following morning, and continued until < 25 % of the *Sargassum* biomass remained (i.e., 4-days). The entire




(b) high density

(c) medium density


(d) low density

(e) single thallus

Fig. 6.1: 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.

process was replicated three times within each site, with different 1.5 × 1.5 m plots being used for each deployment.

Video analysis of herbivore feeding

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. A digital video camera (Sony DCR-SR100 HDD camera in an Ikelite housing), mounted on a concrete block, was positioned approximately 2 m from each of the density treatments at each site. This distance enabled the entire height of the *Sargassum* and the substratum within the experimental plot to be viewed simultaneously. The cameras were positioned perpendicular to one side of the experimental plot so that the field of view looked along the rows of *Sargassum* thalli, allowing feeding on the substratum within the plot to be recorded. Filming commenced immediately after the assays were positioned on the reef, with a scale being placed adjacent to each plot for 20 s to allow calibration of fish sizes on the video footage. Video recording was continuous for the 8-h experimental period, with only a brief (2 - 4 min) interval after four hours to allow for an obligatory battery change. Each density treatment was filmed until the majority of the *Sargassum* biomass (>75 % of the initial biomass) had been removed. Therefore, feeding on the single thallus was recorded for two days, the low density treatment for three, and the medium and high density treatments for four days.

To quantify feeding activity by herbivorous fishes within each of the density treatments the video footage for each day was divided into sixteen 30-min segments. Within each of these 30-min segments a randomly selected 5-min interval was viewed, and the number of bites taken from both the *Sargassum* (i.e., browsing) and the algal turf covered substratum (i.e., grazing) by each species was recorded and the size (total length, TL) of each fish estimated. The presence and size of any potential predators within the experimental plots was also recorded. Feeding on the *Sargassum* and substratum were recorded independently on successive runs through the 5-min intervals of video to allow the viewer to concentrate on either browsing or grazing activity and avoid any potential biases. 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 Chapter 3).

Grazing fishes may be broadly classified into three functional groups (i.e., excavators, scrapers, croppers) based on their morphology and feeding behaviour (Bellwood et al. 2004). While all of these groups typically feed on algal turfs, they differ in their functional impact. Therefore, the grazing taxa recorded feeding on the substratum within the experimental plots were classified as either excavators (i.e., *Chlorurus* spp. and *Cetoscarus bicolor*), scrapers (i.e., *Hipposcarus longiceps* and *Scarus* spp.), or croppers (i.e., *Acanthurus* spp., *Pomacanthus* spp., *Siganus* spp., and *Zebrasoma* spp.).

Statistical analyses

To determine if the relative removal rates of *Sargassum* biomass varied among density treatments, sites and days, a three-factor repeated measures ANOVA was used. There was no significant spatial variation in removal rates among thalli within each of the density treatments (see Appendix E). Subsequently, the analysis was based on the proportion of the initial *Sargassum* biomass (pooled across thalli and square-root 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 a three-factor repeated measures multivariate analysis of variance (MANOVA). The analysis was based on the total mass standardized bites (fourth-root transformed to improve multivariate normality and homoscedasticity) taken from the *Sargassum* assays within each experimental plot by the two dominant browsing species. Collectively, these two species accounted for over 97 % of all mass standardized bites taken from the *Sargassum* assays. Variation in the duration of video observations among treatments precluded comparisons across all days. Subsequently, the analysis was restricted to the first two days of each deployment.

To provide an overview of the relative importance of the two dominant browsing species in removing *Sargassum* biomass the proportion of mass standardized bites taken by each species was compared among density treatments and sites using a two-factor MANOVA. This analysis was based on the proportion of mass standardized bites taken by each species (arcsine-square root transformed) from each treatment summed across days.

The influence of macroalgal density on grazing intensity and the biomass of potential predators was examined using linear regressions. The regressions were based on daily estimates of each variable within each of the experimental plots. As *Sargassum* biomass changed throughout the course of a day, it was estimated as the average of the initial and final *Sargassum* biomass for each day. Grazing was estimated as the total mass standardized bites (log transformed) taken from the substratum within each of the experimental plots. Separate analyses were performed for all grazers collectively, and the three grazing functional groups (i.e., excavators, scrapers, and croppers) independently. Bonferroni correction was used to account for the multiple comparisons.

6.3. Results

Removal rates of Sargassum

The total biomass of *Sargassum* removed was relatively constant among days with an average of 10.37 kg.d^{-1} (± 0.76 SE) being removed from the two sites combined. The relative removal rates of *Sargassum* biomass were, however, influenced by an interaction between the density treatment and day within each deployment ($F_{9,48}$ = 2.39, p = 0.025; Appendix E). The single thallus and low density treatments displayed similar trajectories over the four day period with the majority of the *Sargassum* biomass being removed within the first two days of each deployment (75.2 – 86.4 %; Fig. 6.2). In contrast, the medium and high density treatments displayed relatively low but constant reductions in biomass over the 4 day period (Fig. 6.2), with removal rates of 10.0–25.2 %.d^{-1}.

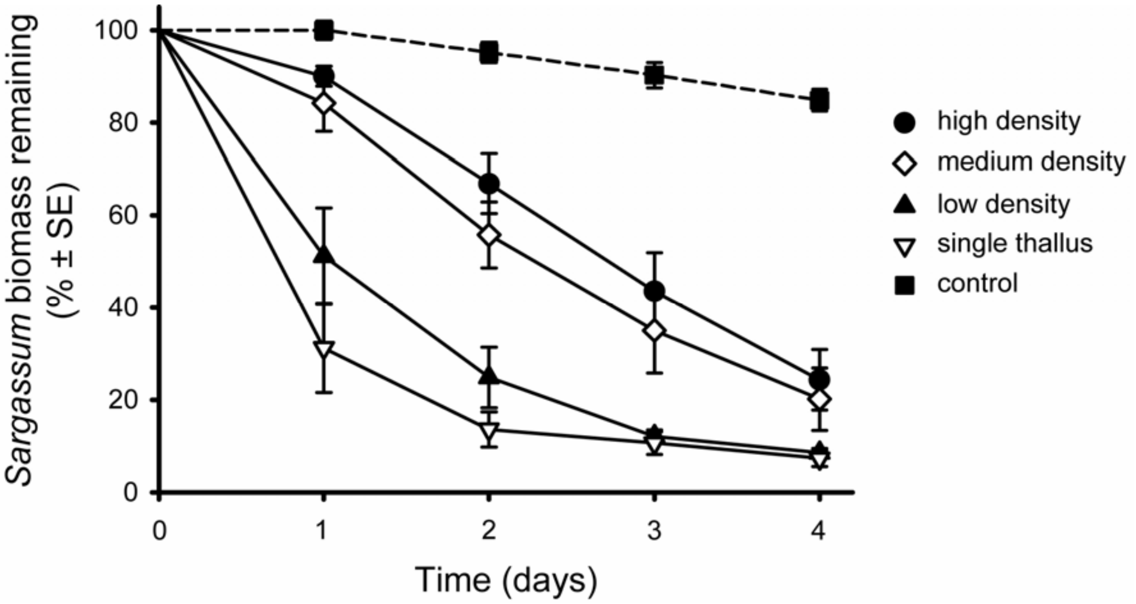


Fig. 6.2: Variation in the removal rates of *Sargassum* cf. *baccularia* among four density treatments on the reef crest of Orpheus Island. The mass remaining was calculated as the proportion of the initial, or transplanted, biomass that remained after each consecutive day (summed across all thalli).

Variation in browsing intensity

Video footage revealed that browsing activity was dominated by two species, *Kyphosus vaigiensis* (Kyphosidae) and *Naso unicornis* (Acanthuridae) (Fig. 6.3). In total, 70,685 bites from 30 fish species were recorded on the transplanted *Sargassum* across all density 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 *Siganus doliatus* (Siganidae), accounting for 1.9 % of the total mass standardized bites. Each of the remaining 27 species accounted for less than 0.4 % of the total mass standardized bites. Interestingly, no bites were recorded by browsing batfish *Platax* spp. despite being regularly observed on the video footage.

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. 6.3). *K. vaigiensis* favored the low macroalgal density patches, while *N. unicornis* favored both the single *Sargassum* thallus and low macroalgal density patches. On subsequent days feeding by these two browsers shifted ($F_{6,30} = 5.16$, $p = 0.001$; Appendix E) as the *Sargassum* biomass was depleted from the single thallus and low density patches (Fig. 6.2). Feeding by *K. vaigiensis* decreased within the single thallus and low density patches, and increased markedly within medium and high macroalgal density patches (Fig. 6.3). Similarly, feeding by *N. unicornis* decreased on the single thallus, and increased within the low and medium macroalgal density patches (Fig. 6.3). This temporal variation in feeding by both species led to significant negative relationships between *Sargassum* biomass and browsing rates within the high and medium density patches (Fig. 6.4)

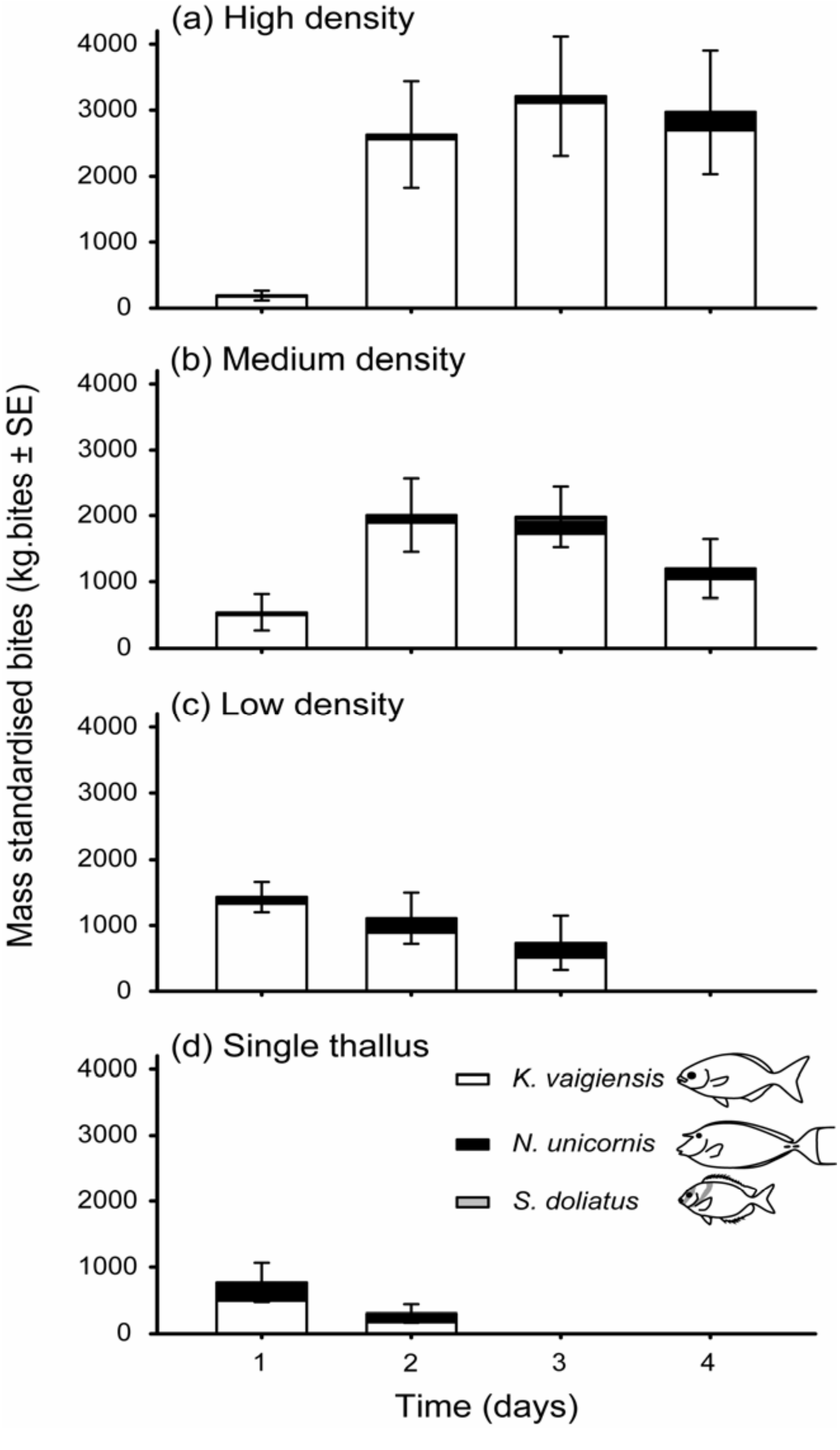


Fig. 6.3: Influence of *Sargassum* density on the browsing intensity by herbivorous fishes. Temporal variation in the number of mass standardized bites taken by all species from *Sargassum* cf. *baccularia* among the four density treatments (a-d). The relative contributions of the three dominant species are shown. The remaining 27 species included in the figure are not distinguishable as collectively they accounted for less than 1.4 % of all bites. The single thallus (d) and low density (c) treatments were only filmed for the first two and three days of each deployment, respectively.

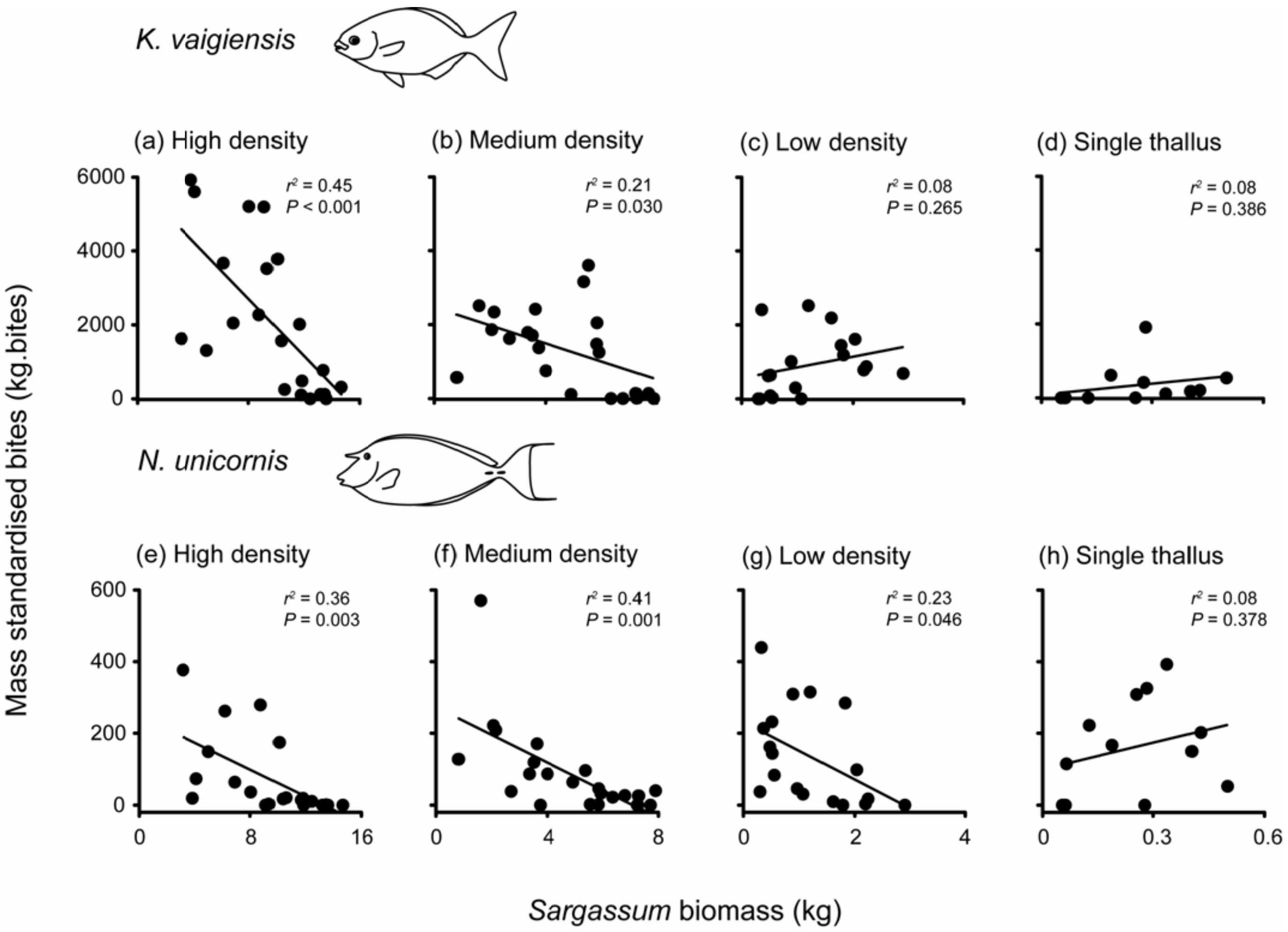


Fig. 6.4: Relationship between *Sargassum* density and browsing intensity by *Kyphosus vaigiensis* (a-d) and *Naso unicornis* (e-h) within each of the density treatments. The best-fit relationships (linear) are given as solid lines, along with r^2 and *P* values.

Overall, there was a small but significant shift in the relative importance of *K. vaigiensis* and *N. unicornis* in removing *Sargassum* biomass from each of the density treatments ($F_{6,30} = 2.44$, $p = 0.048$; Fig. 6.5). *K. vaigiensis* accounted for a significantly greater proportion of the total bites recorded on the high density treatment (94.1 %) than the single thallus (46.3 %). Conversely, *N. unicornis* accounted for a significantly greater proportion of the total bites recorded from the single thallus (42.1 %) than the medium and high density treatments (10.8 and 3.8 % respectively).

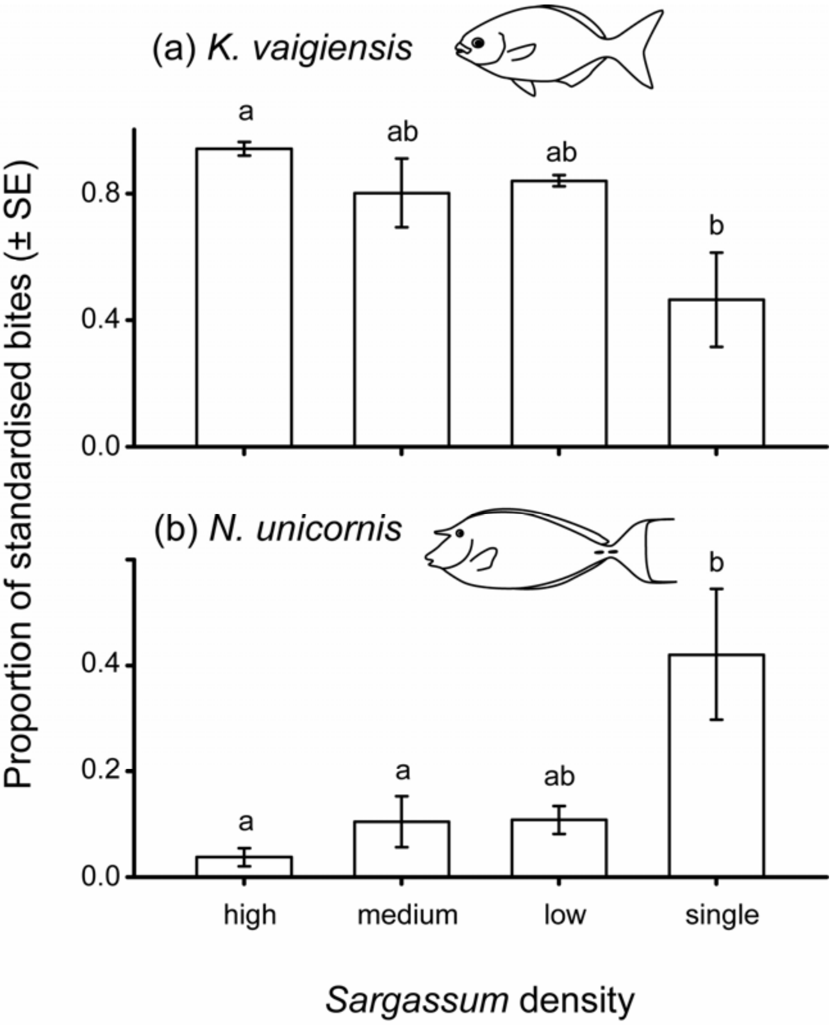


Fig. 6.5: Proportion of total mass standardized bites taken from each of the *Sargassum* density treatments by the two dominant browsing fish species; (a) *Kyphosus vaigiensis* and (b) *Naso unicornis*. The letters above each bar indicate homogenous groups identified by Tukey's HSD post-hoc analyses.

Macroalgal density, grazing intensity and predator biomass

Over 15,000 bites from 28 species were recorded from the substratum within the habitat patches. Scraping and excavating parrotfishes (primarily *Scarus rivulatus* and *Chlorurus microrhinos*, 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 (see Appendix E). 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. 6.6).

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 three days of each deployment (Fig. 6.7). The predator community was dominated by relatively small (< 30 cm total length) generalist carnivores, with few larger piscivorous species being recorded (see Appendix E). Consequently, grazing intensity was negatively related to the biomass of potential predators ($r^2 = 0.202$, $F_{1,72} = 18.26$, $p < 0.001$). 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 ($r^2 = 0.015$, $F_{1,72} = 1.10$, $p = 0.299$).

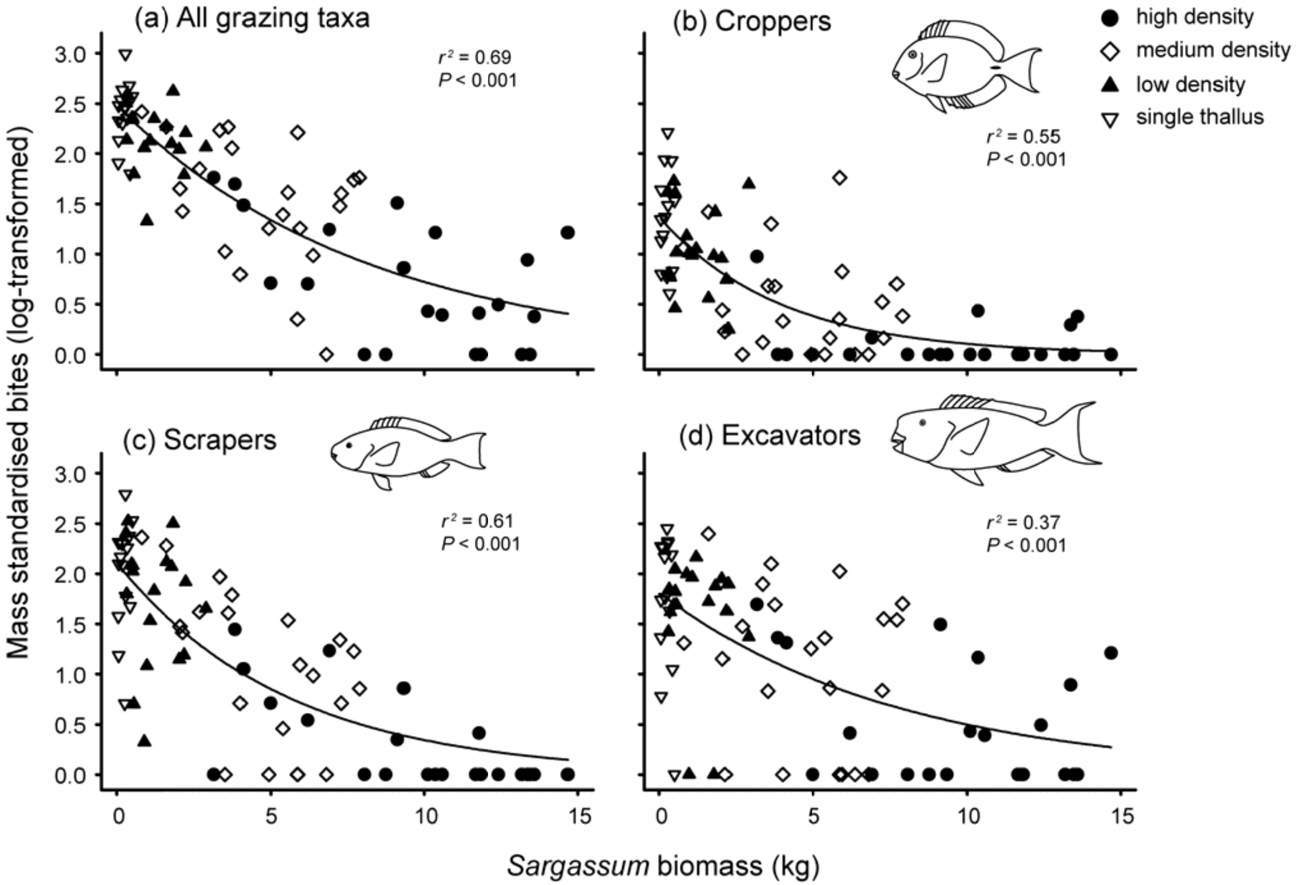


Fig. 6.6: Influence of *Sargassum* density on the grazing intensity of herbivorous fishes. The relationship between the total number of mass standardised bites taken from the substratum and the density of *Sargassum* cf. *baccularia* within each of the experimental plots for (a) all species combined, (b-d) three herbivore functional groups independently (i.e. cropping, scraping and excavating taxa). The best-fit relationships (log-linear) are given as solid lines, along with r^2 and *P* values.

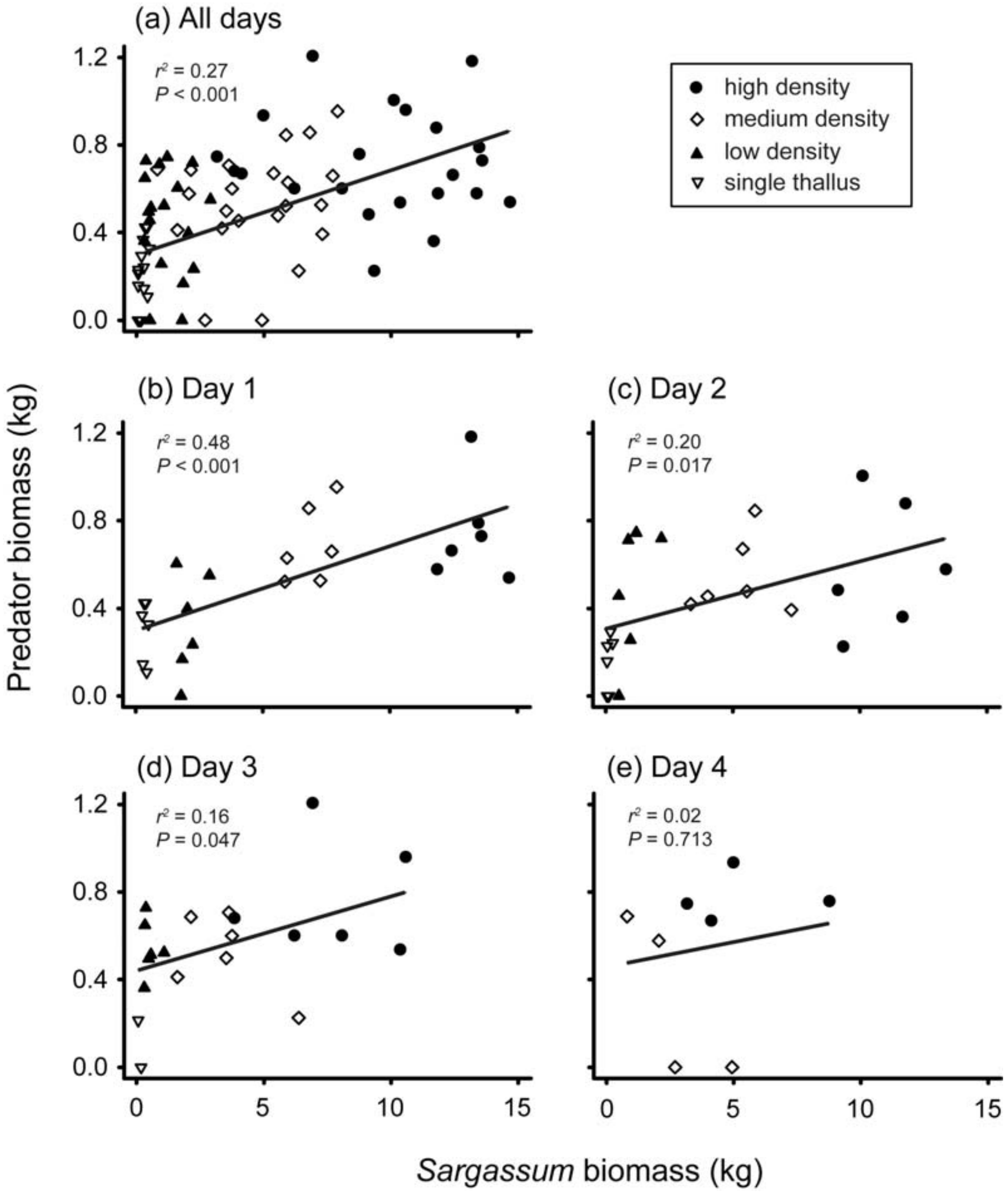


Fig. 6.7: Influence of *Sargassum* density on predator biomass. The relationship between the biomass of potential predators (log-transformed) and the biomass of *Sargassum* within the each of habitat patches for all days combined (a), and days 1 – 4 independently (b – e). The best-fit (linear) relationships are given as a solid line, along with r^2 and *P* values.

6.4. Discussion

Habitat choice is a key determinant of an organism’s fitness, with individuals selecting habitats that maximise their energy intake while minimising their risk of predation (Houston et al. 1993; Brown and 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 and 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. The results of the present study stand in marked contrast, with a strong negative relationship between herbivore activity and the structure provided by macroalgal stands. Herbivorous coral-reef fishes at my 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 habitat preferences may have positive feedbacks on the growth and stability of macroalgal stands. If these observations on Orpheus Island are replicated at larger scales, this type of feedback may be important in reinforcing phase shifts to fleshy macroalgal dominance on coral reefs around the world.

Effects of macroalgal density on herbivorous fish

Habitat associations are often related to differences in the quantity or quality of food resources among habitat patches (McNaughton 1988; Bakker et al. 2005), such bottom-up forcing appears not to be operating within the Pioneer Bay system. The experimental framework in the present study ensured food availability to grazers was broadly comparable among habitat patches. 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 habitat patches; only switching to the higher density patches after the *Sargassum* biomass within the lower density patches had been depleted. Taylor and Shiel (2010) reported similar reductions in fish browsing under the canopy of kelps in New Zealand.

Alternatively, herbivore habitat preferences may have been determined by top-down effects if the availability of refuges or the ability to detect 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 and 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 and Grace 2006). 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 the present 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 is the functional characteristics of structural features that appear to be most important in shaping fish behaviour.

The preference for open habitat patches in the present 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).

Although all browsers and grazers favoured habitat patches with reduced cover of macroalgae, the strength of the response varied among taxa within the two groups of herbivores. This variation may be related to the influence of body size and/or foraging behaviour on predation risk. Body size is an important attribute determining inter- and intra-specific variability in susceptibility to predators, with smaller species and individuals being more susceptible to predation (Werner et al. 1983; Sinclair et al. 2003). If habitat preferences are determined by top-down processes, we would expect smaller-bodied species to exhibit a greater response than those of larger species. Our results support this hypothesis, at least among grazing species. The largest bodied grazers, excavators (ca. 39cm TL), were less deterred by higher macroalgal cover than the smaller scraping or cropping grazers (ca. 30cm and 22cm, respectively). This relationship did not hold for browsing taxa, with the smaller *K. vaigiensis* (ca. 33cm) more willing to feed on the higher density macroalgal patches than the larger *N. unicornis* (ca. 37cm). However, *K. vaigiensis* were generally recorded foraging in large groups with up to 40 individuals being recorded feeding on the *Sargassum* at any one time. This schooling behaviour may have reduced their predation risk, relative to the more solitary foraging of *N. unicornis,* through dilution and increased group vigilance (Turner and Pitcher 1986; Lima 1995), allowing them to exploit food resources in more hazardous habitat patches.

Effects of herbivores on coral reef algal communities

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 and 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 and 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 alternate benthic state..

Previous studies at this location have suggested that macroalgal density has a marked influenced on browsing taxa. *Siganus canaliculatus* and *K. vaigiensis* have been reported to dominate feeding on bioassays of individual *Sargassum* thalli (Fox and

Bellwood 2008a; Cvitanovic and Bellwood 2009) but were rarely observed feeding on dense stands of *Sargassum* (5.3 – 8.1 kg.m^{-2}) from previously caged 25 m^2 areas (Bellwood et al. 2006). Instead the batfish, *Platax pinnatus,* was largely responsible for removing *Sargassum* biomass from these areas. I found no evidence for such a marked transition. Although the results of the present study indicate there was a shift in the relative importance of *K. vaigiensis* and *N. unicornis* among the four macroalgal densities, both species were recorded feeding within each of the density treatments. Surprisingly, batfish were not observed to feed on the *Sargassum* in the present study despite being regularly observed in the immediate vicinity of the habitat patches. This apparent lack of feeding is difficult to explain but may be related to differences in the size of the habitat patches, height of the macroalgal canopy, or condition of the *Sargassum* among studies..

Overall the consistency of the daily removal rates of *Sargassum* (pooled across habitat patches 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.d^{-1} (the mean rate in the present study) and a seasonally adjusted daily growth rate of 1.7 % for *S. baccularia* (Schaffelke and Klumpp 1998a), there is a threshold of approximately 610 ± 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* (ca. 5.3–8.1 kg.m^{-2}; Bellwood et al. 2006) with a spatial extent of just 75–115 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.

The present 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 twenty 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.

Conclusion

Within coral reef systems, habitat complexity, particularly that provided by corals, has been widely regarded as a feature that promotes herbivore activity (Randall 1965). This study has shown, however, that 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 physical structure of the macroalgae. The difference in the response of herbivorous fishes to coral and macroalga appears to be related to be nature of the structures they create, with the flexible macroalgae providing little protection for herbivores from concealed predators. 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.

Chapter 7: Concluding Discussion

Quantifying the ecosystem role of individual species and functional groups, and identifying the locations in which they exert their functional impact is central to our understanding of the processes that structure ecological systems. Examining the role of macroalgal browsing fishes, this thesis reaffirms the pioneering work of McCook (1996, 1997) that described the importance of herbivores in shaping the distribution of *Sargassum* on the Great Barrier Reef (GBR). In these early studies, McCook demonstrated that transplanted *Sargassum* could persist for several weeks on a mid-shelf reef flat, but only if protected from herbivores. Expanding on these findings, this thesis demonstrates the response of herbivores is rapid and widespread. Transplanted *Sargassum* was almost completely removed from all mid- and outer-shelf reefs and habitats examined in a just a few hours (Chapter 2, 3, 4). Overall, these consumption rates provide strong evidence for the potential of browsing fishes to limit the distribution and abundance of adult *Sargassum* on mid- and outer-shelf reefs of the GBR. Browsing intensity was, however, moderated by the presence of *D. prosopotaenia* (Chapter 5), and the density of the *Sargassum* presented (Chapter 6). These negative interactors are important and provide the mechanistic bases through which *Sargassum* may colonize new locations, and expand and persist once established.

Building on a growing body of literature aimed at identifying the species capable of removing leathery macroalgae (sensu Steneck 1988), this thesis consolidates the view that this role is restricted to a limited suite of species. Numerous studies conducted on the leeward reefs of Orpheus Island have reported that only a few species are capable of consuming adult *Sargassum* (Bellwood et al. 2006; Mantyka and Bellwood 2007; Fox and Bellwood 2008b; Cvitanovic and Bellwood 2009). The limited spatial extent of these studies, however, raises questions as to the generality of their results. Examining this process across broader, ecologically relevant spatial scales, this thesis extends the findings of these previous studies, and demonstrates that the vast majority of herbivorous reef fishes (i.e., grazers) have a limited capacity to remove adult *Sargassum*. The removal of adult leathery macroalgae appears to represent a separate process, and is restricted to a limited subset of species; the macroalgal browsers.

Despite some evidence of latitudinal variation on inshore reefs, the dependence on a single species removing *Sargassum* across a wide range of mid- and outer-shelf habitats in the northern GBR was striking. Collectively, *N. unicornis* accounted for 89 % of all mass standardized bites recorded from over 750 h of video observations spanning multiple habitats, reefs, and years (Chapter 3, 4). While previous studies on Orpheus Island have reported the removal of *Sargassum* to be dominated by a single species, there has been marked variation in the identity of the species among adjacent bays, and among studies conducted at the same location. In contrast, the lack of variability in the dominant browser of *Sargassum* among habitats, reefs, shelf position, and years in the northern GBR is remarkable (Chapter 3, 4), and highlights the apparent lack of functional equivalents performing this key ecological process on mid- and outer-shelf reefs of the northern GBR.

Over the past two decades the effect of biodiversity on ecosystem functioning has become a major focus of ecological studies (e.g., Loreau et al. 2001; Hooper et al. 2005), driven largely by the global loss of biodiversity and the prospect of ecosystem collapse (Scheffer et al. 2001; Folke et al. 2004). While these studies have demonstrated that some species exert stronger control over ecological processes than others, the general consensus is that species richness is positively related to a variety of ecosystem functions (Cardinale et al. 2006). The vast majority of these studies, however, have been conducted within relatively simple systems with a limited subset of species (e.g., Naeem et al. 1994; Tilman et al. 2001). The results of this thesis question this view. The reliance on *N. unicornis*, both within and across local (0.1 – 40 km) scales, highlights the potential for single-species functional groups even within high diversity systems and emphasizes the importance of looking beyond biological diversity as a source of ecological stability.

Collectively, the results of this thesis suggest that the browsers of adult leathery macroalgae perform an analogous role to that of browsing ungulates on terrestrial savannas. It is well established that these two ecosystems display congruent responses to marked reductions in grazing intensity, shifting from highly productive, herbaceous vegetation to larger, less productive plants or macroalgae (Dublin et al. 1990; Hughes et al. 2007). However, the capacity of these systems to reverse such shifts appears to be constrained by the limited number of browsing taxa and the avoidance of areas of dense vegetation by all herbivores. Both coral reef and savanna herbivore communities are characterised by an abundant and diverse assemblage of grazers, with relative few browsing species. Additionally, grazing and browsing taxa in both systems display a preference for relatively open habitats, avoiding areas of high tree or high macroalgal density (e.g., Riginos and Grace 2008; Chapter 6). Despite fundamental differences in the size of herbivores (Choat and Clements 1998), the nature and relative importance of bottom-up forces (e.g., water availability) and disturbance regimes (e.g., fire vs. coral bleaching) between savanna and coral reef ecosystems, the similarities in the functional composition and habitat use of herbivores are striking. These markedly different systems appear to operating under a similar set of ecological processes. Comparisons among different ecological systems may provide further insight into the function, resilience and future trajectory of these systems.

Understanding the ecosystem role of individual species and functional groups is a fundamental step to understanding the functioning of ecosystems. Overall, this thesis has provided direct evidence for the potential importance of macroalgal browsing fishes on coral reefs. While distribution patterns of macroalgae may also be influenced by a suite of physical and biological factors (McCook 1999), this thesis found evidence of strong top-down control by macroalgal browsing fishes. Although this function appears to be restricted to a small suite of species, the reliance on a single species performing this role across a range of spatial scales was surprising and highlights a disparity between biological diversity and ecological function. The loss of a single species may severely erode this ecological function and subsequently the capacity of reefs to deal with change. Given the deteriorating health of coral reefs, the capacity to remove macroalgae is increasingly recognized as a key process. Ultimately, the removal of leathery macroalgae is dependent on a limited suite of species, a critical functional group on coral reefs.

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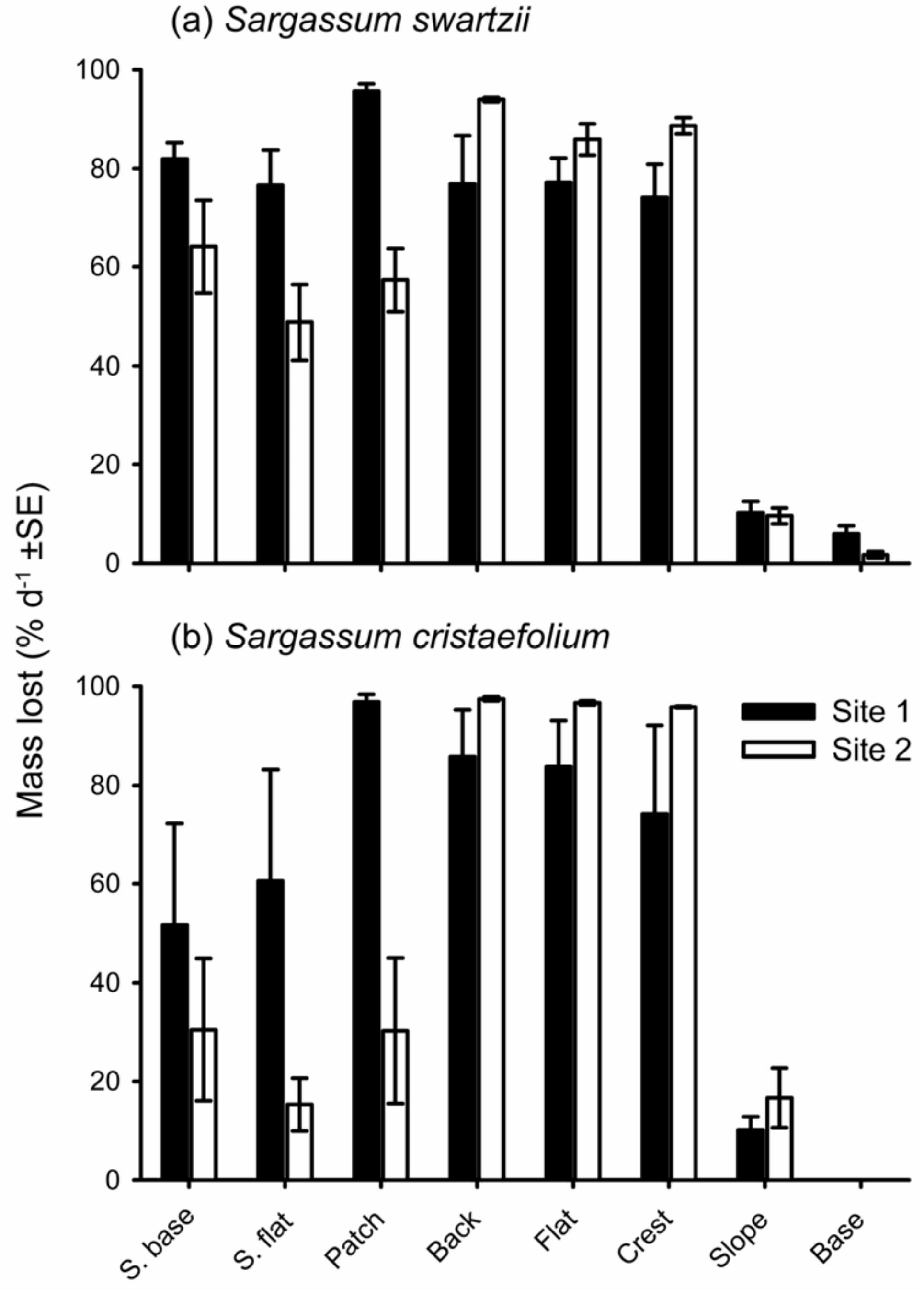

Fig. A1: Variation among habitats and sites in the relative removal rates of (a) *Sargassum swartzii* and (b) *Sargassum cristaefolium* on Lizard Island. The means are based on ten thalli for *S. swartzii* and six thalli for *S. cristaefolium*.

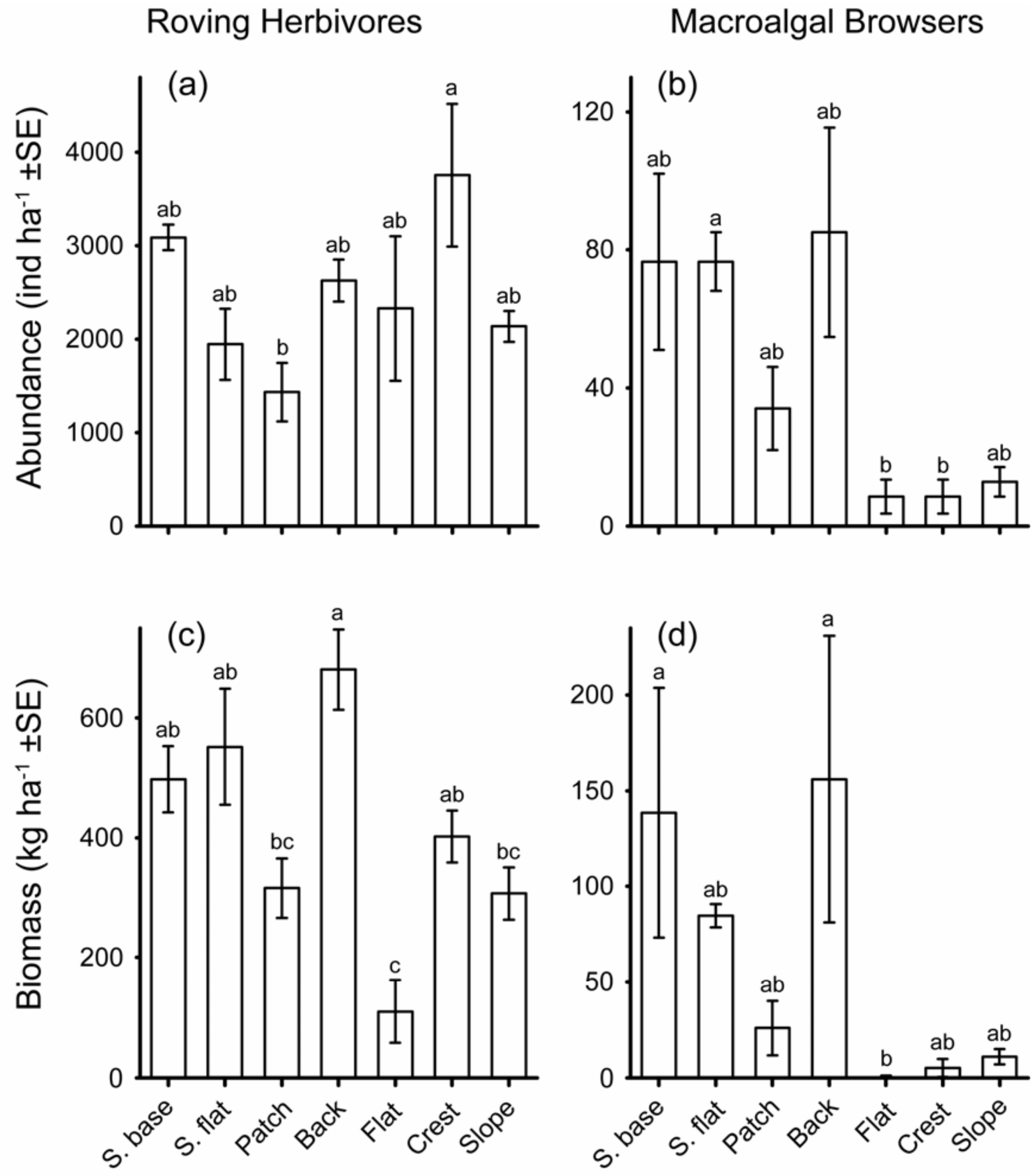

Fig. A2: Variation in the density and biomass of all roving herbivorous fishes and macroalgal browsers across seven habitats of varying water depth and wave exposure on Lizard Island. Means are based on four 10-min timed swims within each habitat. The letter/s above each bar indicate homogenous groups identified by Tukey's HSD post-hoc analyses.

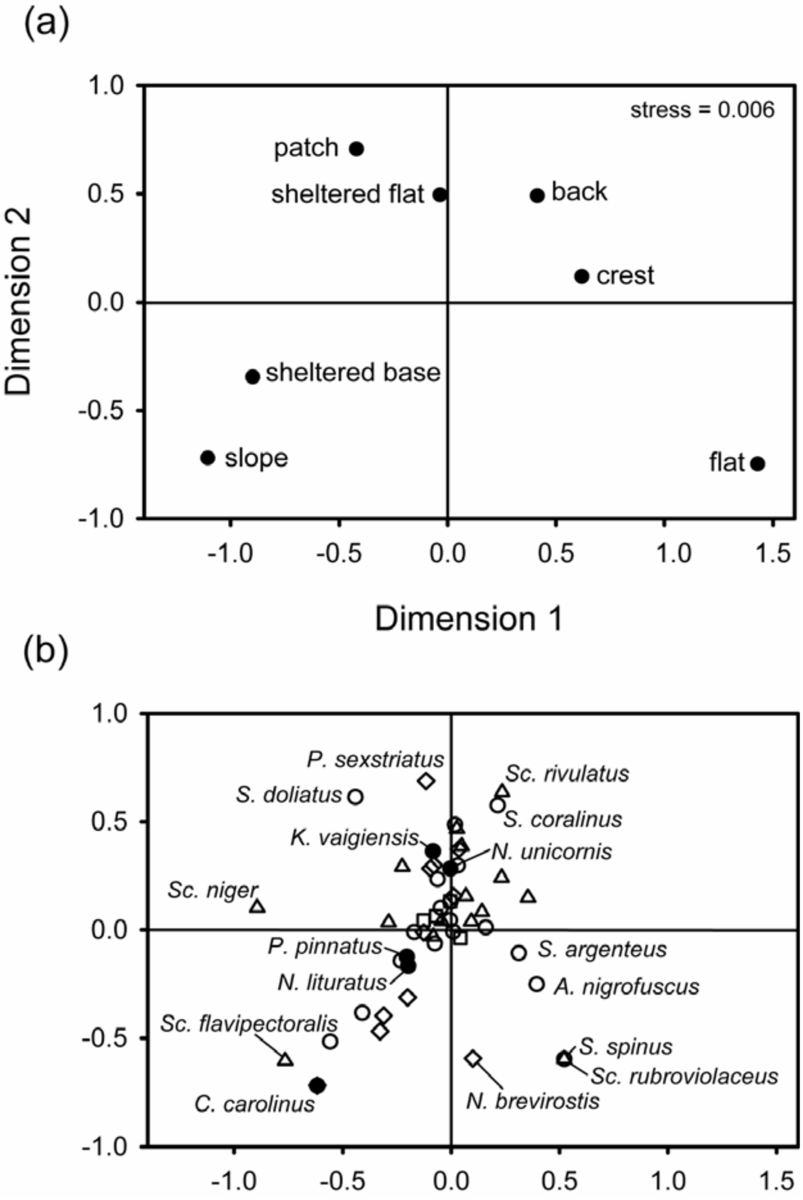

Fig. A3: Multidimensional scaling analysis showing the relationships among roving herbivorous fish assemblages across seven habitats on Lizard Island. a) Two dimensional solution from non-metric multidimensional scaling based on Bray-Curtis similarities of $\log_{10}$ transformed abundance data showing relationship between seven habitats. Each habitat is based on four 10-minute transects. b) Vectors represent the partial regression coefficients of the original variables (species) with the two dimensions. Lengths of the vectors are proportional to the squared multiple correlation coefficient. Symbols represent functional groupings: *open squares*, excavators; *open triangles*, scrapers; *open circles*, turf algal grazers; *closed circles*, macroalgal browsers; *open diamonds*, 'other'. Species names: *Acanthurus nigrofuscus*, *Calotomus carolinus*, *Kyphosus vaigiensis*, *Naso brevirotris*, *Naso lituratus*, *Naso unicornis*, *Platax pinnatus*, *Pomacanthus sexstriatus*, *Scarus flavipectoralis*, *Scarus niger*, *Scarus rivulatus*, *Scarus rubroviolaceus*, *Siganus argenteus*, *Siganus coralinus*, *Siganus doliatus*.

The multidimensional scaling analysis showed marked variation in herbivorous fish community structure among the seven habitats on Lizard Island. There was a clear separation of the three shallow exposed habitats (i.e., exposed reef crest, flat and back reef) from the deeper exposed reef slope and the three sheltered habitats (i.e., patch reef and sheltered reef base and flat) along the first dimension of the MDS (Fig. A3a). There was further separation of the reef slope and sheltered reef base from the two shallow sheltered habitats along the second dimension. The sheltered reef base and exposed reef slope were characterized by *Calotomus carolinus* and *Scarus flavipectoralis*, and the patch reef and sheltered reef flat were characterized by *Pomacanthus sexstriatus*, *Siganus doliatus* and *Kyphosus vaigiensis* (Fig. A3b). The exposed reef flat was characterized by *Siganus spinus* and *Scarus rubroviolaceus*, while the exposed reef crest and back reef habitats were characterized by *Siganus coralinus* and *Scarus rivulatus*.

Partial correlations

As the rates of removal of *Sargassum* may have been influenced by the availability and relative palatability of the macroalgal community within each habitat an index incorporating these two factors (i.e., grazing preference index) was calculated for each habitat. This index was then included in the correlation model and the partial correlation coefficients calculated for the rate of removal of the two species of S*argassum* and the density and biomass of the herbivorous fishes.

The grazing preference index was calculated as follows:

Grazing preference index (GPI) = $\Sigma\, p_i .\, c_i$

where p_i is the proportion of biomass removed from the *i*th macroalgal species in a 3 hour period (from Mantyka and Bellwood 2007); c_i is the proportional cover of the *i*th macroalgal species within each habitat (based on the mean of twelve 10m point intercept transects)

For those macroalgal species that were recorded during a thorough search of each transect area (i.e., 20m^{-2}) but not recorded using the point intercept method, their proportional cover was estimated as 0.001 (0.1 %) if it was identified within 2 or more transects (indicated by ++ in Table 2.1), and 0.0005 (0.05 %) if it was identified within a single transect (indicated by + in Table 2.1). The grazing preference index would therefore approach 1.0 if there was complete cover of a macroalga that was highly susceptible to grazing. Conversely the index would approach zero if there was a low cover of macroalgae or high cover of a largely unpalatable macroalgae.

Incorporating the grazing preference index into the model had little effect on the relationships between the density or biomass of the herbivorous fishes and the removal rates of the two species of *Sargassum* (Table A1). The only significant relationships detected were negative correlations between the removal rate of *S. cristaefolium* and the density and biomass of *Calotomus carolinus*, suggesting that as the density or biomass of *C. carolinus* increased, grazing on the *Sargassum* decreased. All other relationships were weak and non-significant.

Table A1: Partial correlations between the rate of removal of the two species of *Sargassum* and the density and biomass herbivorous fishes across seven habitats around Lizard Island. An index of the relative availability and palatability of macroalgal species in each habitat are controlled for. Analyses are based on the mean proportion of biomass removed in a 24h period within each habitat (*S. swartzii*: n = 20, *S. cristaefolium*: n =12). Density and biomass estimates are based on the mean of four 10-min timed swims within each habitat. [Grazing preference index = Σ $p_i.c_i$, where p_i is the proportion of biomass removed from the *i*th macroalgal species in 3 hours (from Mantyka and Bellwood 2007), and c_i is the proportional cover of the *i*th macroalgal species in each habitat]. Significant correlations are given in bold.

		Sargassum swartzii		*Sargassum cristaefolium*	
		ρ	**p**	**ρ**	**p**
Roving herbivores	density	0.302	0.561	0.276	0.597
	biomass	0.189	0.720	0.128	0.809
Macroalgal browsers	density	0.312	0.548	0.102	0.848
	biomass	0.294	0.572	0.125	0.814
Calotomus carolinus	density	-0.675	0.141	**-0.849**	**0.032**
	biomass	-0.675	0.141	**-0.849**	**0.032**
Kyphosus vaigiensis	density	-0.100	0.850	-0.244	0.642
	biomass	-0.080	0.808	-0.353	0.492
Naso lituratus	density	0.099	0.853	-0.294	0.572
	biomass	0.099	0.853	-0.294	0.572
Naso unicornis	density	0.345	0.503	0.426	0.399
	biomass	0.314	0.544	0.278	0.594
Platax pinnatus	density	0.087	0.870	-0.308	0.553
	biomass	0.088	0.869	-0.307	0.554

Appendix B: Supplemental information for Chapter 3

Table B1: Summary of the fishing pressure for *Naso unicornis* across the Indo-Pacific. The fishing gears most commonly used in each locality are given and the relative importance of *N. unicornis* in the total catch indicated. Locations are listed from west to east.

Location	**Fishing gears**			**Catch ($t.yr^{-1}$)**	**Importance in catch**	**Source**
	trap	**net**	**spear**			
Red Sea					Targeted	Roberts and Polunin 1992
Kenya	✓	✓			Targeted	Musyoka 2006
Tanzania	✓	✓			Targeted	Darwall 1996
Mozambique	✓	✓			Captured	Gell and Whittington 2002
Madagascar		✓			Targeted	Lewis *et al*. 2004
Mauritius		✓			Top 5 commercially targeted species	Rathacharen et al. 1999
Rodrigues	✓	✓			Relative importance of mass landed dropped from 2nd (2002) to 12th (2006); Perceived decrease in abundance and size	Hardman *et al*. 2006 Bunce *et al*. 2008
Southern India					Commercially important	Kumaraguru *et al*. 2000
Malaysia		✓			Targeted	Wood 2001
Indonesia					Present at fish market	Iwatsuki *et al*. 2001
Philippines					Targeted	Abesamis *et al*. 2006
Palau		✓	✓	35.28 (1985) 12.01 (1990)	Perceived to be becoming scarcer; Catches have declined substantially since mid-1980's	Kittalong and Dalzell 1994
Yap, FSM			✓		Targeted	Gillet and Preston 2006
Guam		✓	✓		Top 10 targeted species	Hensley and Sherwood 1993
Papua New Guinea			✓		Top acanthurid species targeted (1986)	Lock 1986 in Dalzell *et al*. 1996

					Targeted	McClanahan and Cinner 2008
Chuuk, FSM		✓	✓		Commonly caught	Lambeth and Santiago 2001
Pohnpei, FSM		✓	✓		Top 5 targeted species	Rhodes *et al*. 2008
Solomon Isl		✓	✓		Targeted	Green *et al*. 2006
New Caledonia					Dominates surgeonfish landings; 11-fold increase in abundance, and 7-fold increase in biomass following establishment of marine reserve	Dalzell *et al*. 1996 Wantiez *et al*. 1997
Fiji			✓		Targeted; Reduction in size	Jennings and Polunin 1995 Rawlinson *et al*. 1995 Kronen *et al*. 2003 Gillet and Moy 2006
Tuvalu			✓		Very important component of catch	Kaly 1997 Gillet & Preston 2006
Tonga			✓	3.53 (1996)	Targeted; Reduction in size	Uchida 1978 Kronen *et al*. 2003 Gillet and Preston 2006
Samoa			✓	8.92 (1998/9)	One of six species targeted by spearfishers;	Skelton *et al*. 2000 Gillet and Preston 2006
Tokelau		✓			Targeted	Van Pel 1958 Ono and Addison 2009
Cook Isl		✓	✓		Targeted	Solomona *et al*. 2009
Hawaii			✓		84% reduction in biomass and 17% reduction in mean size in fished area	Meyer 2003 Williams *et al*. 2006
French Polynesia			✓		17% of spearfishing catch	Gillet and Preston 2006 Malpot *et al*. 2008

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Appendix C: Supplemental information for Chapter 4

Table C1: Summary of four factor ANOVA comparing the cover of macroalgae among shelf positions, habitat, reef, and site. Macroalgal cover was square root transformed. Significant effects are shown in bold (p < 0.05)

Source of variation	SS	df	MS	F	P
Shelf	**6.156**	**2**	**3.078**	**77.470**	**0.002**
Habitat	0.103	1	0.103	3.252	0.169
Reef(Shelf)	0.199	3	0.040	1.249	0.430
Shelf × Habitat	**1.644**	**2**	**0.822**	**25.847**	**0.013**
Reef(Shelf × Habitat)	0.095	3	0.032	1.735	0.213
Site(Reef(Shelf × Habitat)	0.223	12	0.018	1.705	0.074
Residual	1.291	120	0.011		

Table C2: Summary of three factor ANOVA comparing the biomass of (a) all roving herbivorous fishes, and (b) macroalgal browsing fishes among shelf position, habitat, and reef. The biomass of roving herbivores was log (*x* + 1) transformed, and the biomass of macroalgal browsers was square root transformed. Significant effects are shown in bold (p < 0.05).

Source of variation	SS	df	MS	F	P
(a) Roving herbivores					
Shelf	**2.363**	**2**	**1.181**	**18.31**	**0.021**
Habitat	**0.916**	**1**	**0.916**	**18.80**	**< 0.001**
Reef(Shelf)	0.194	3	0.065	1.32	0.280
Shelf × Habitat	**0.415**	**2**	**0.207**	**4.25**	**0.021**
Residual	1.901	39	0.049		
(b) Macroalgal browsers					
Shelf	3778.1	2	1889.1	1.382	0.375
Habitat	**26037.2**	**1**	**26037.2**	**17.793**	**< 0.001**
Reef(Shelf)	4100.5	3	1366.8	0.934	0.433
Shelf × Habitat	8336.9	2	4168.5	2.849	0.070
Residual	57069.2	39	1463.3		

Table C3: Summary of four factor ANOVA comparing the reduction in transplanted *Sargassum swartzii* biomass among shelf position, habitat, reef and site. The analysis was based on the proportion of initial, or transplanted, biomass removed ($\sqrt[4]{}$ transformed) over a 24 h period. Significant effects are shown in bold ($p < 0.05$).

Source of variation	SS	df	MS	F	P
Shelf	**5.402**	**2**	**2.701**	**32.113**	**0.009**
Habitat	0.008	1	0.008	0.183	0.698
Reef(Shelf)	0.252	3	0.084	1.936	0.300
Shelf × Habitat	0.274	2	0.137	3.154	0.183
Reef(Shelf × Habitat)	0.130	3	0.043	1.472	0.272
Site(Reef(Shelf × Habitat)	**0.354**	**12**	**0.030**	**1.862**	**0.041**
Residual	3.043	192	0.016		

Table C4: Summary of four factor ANOVA comparing the reduction in transplanted *Sargassum swartzii* biomass among treatments (cage vs. open), reefs, habitats, and site. The analysis was based on the proportion of initial biomass removed (square root transformed) over a 24 h period. Significant effects are shown in bold ($p < 0.05$).

Source of variation	SS	df	MS	F	P
Treatment	**11.089**	**1**	**11.089**	**1012.348**	**< 0.001**
Reef	0.148	1	0.148	5.538	0.078
Habitat	**0.261**	**1**	**0.261**	**9.773**	**0.035**
Site(Reef × Habitat)	0.107	4	0.026	2.439	0.053
Treatment × Reef	0.026	1	0.026	2.347	0.129
Treatment × Habitat	0.031	1	0.031	2.798	0.098
Reef × Habitat	0.003	1	0.003	0.126	0.740
Treatment ×Reef × Habitat	0.011	1	0.011	0.976	0.326
Residual	0.920	84	0.011		

Table C5: Summary of four factor ANOVA comparing the reduction in transplanted *Sargassum swartzii* biomass among shelf position, habitat, reef and site. The analysis was based on the proportion of initial, or transplanted, biomass removed ($\sqrt[4]{}$ transformed) over a 5-h period. Significant effects are shown in bold ($p < 0.05$).

Source of variation	SS	df	MS	F	P
Shelf	**22.311**	**3**	**7.437**	**59.984**	**<0.001**
Habitat	**1.399**	**1**	**1.399**	**29.850**	**0.005**
Reef(Shelf)	0.496	4	0.124	2.645	0.184
Shelf × Habitat	**1.005**	**3**	**0.335**	**7.144**	**0.044**
Reef(Shelf × Habitat)	0.188	4	0.047	0.353	0.838
Site(Reef(Shelf × Habitat)	**2.126**	**16**	**0.133**	**6.042**	**<0.001**
Residual	7.741	352	0.022		

Table C6: Summary of four factor ANOVA comparing feeding on *Sargassum swartzii* biomass among shelf position, habitat, reef and site. The analysis was based on the total mass standardized bites taken from the transplanted *S. swartzii* (log-transformed) over a 5-h period. Significant effects are shown in bold ($p < 0.05$).

Source of variation	SS	df	MS	F	P
Shelf	**94.964**	**3**	**31.655**	**37.787**	**0.002**
Habitat	0.506	1	0.506	1.176	0.339
Reef(Shelf)	3.351	3	0.838	1.946	0.268
Shelf × Habitat	**9.713**	**2**	**3.238**	**7.519**	**0.040**
Reef(Shelf × Habitat)	1.722	4	0.431	0.599	0.696
Site(Reef(Shelf × Habitat)	**12.322**	**16**	**0.770**	**6.856**	**<0.001**
Residual	7.190	64	0.112		

Table C7: Summary of four factor ANOVA comparing the reduction in *Sargassum swartzii* biomass within exclusion cages among shelf position, habitat, reef and site. The analysis was based on the proportion of initial, or transplanted, biomass removed over a 5 h period. Significant effects are shown in bold ($p < 0.05$).

Source of variation	SS	df	MS	F	P
Shelf	0.008	3	0.003	1.167	0.426
Habitat	0.002	1	0.002	4.535	0.100
Reef(Shelf)	0.009	4	0.002	4.422	0.089
Shelf × Habitat	0.006	3	0.002	4.190	0.100
Reef(Shelf × Habitat)	0.1002	4	0.001	0.868	0.504
Site(Reef(Shelf × Habitat)	0.009	16	0.001	0.538	0.0916
Residual	0.069	64	0.001		

Appendix D: Supplemental information for Chapter 5

Benthic community structure

Variation in benthic community structure among the four sheltered sites was analysed using a one-factor multivariate analysis of variance (MANOVA). Assumptions of the MANOVA were examined by residual analysis. The proportional benthic community data was arcsine-square root transformed to improve multivariate normality. Canonical discriminant analysis (CDA) was then used to examine how sites and species by site combinations differed in benthic community composition. Ninety-five percent confidence ellipses were plotted around the group centroids (Seber 1984).

There was significant variation in the benthic community structure among the four sheltered sites on Lizard Island (MANOVA: $F_{30,103} = 9.06$, $p < 0.001$). The CDA indicated that Watsons Bay and Osprey Islet had similar benthic communities but were clearly separated from Mermaid Cove and Lagoon along the first canonical variate, which explained 61.8 % of the total variation (Fig. D1). This pattern was driven by higher cover of red and brown macroalgae within Watsons Bay (9.3 % and 11.9 %, respectively) and Osprey Islet (9.3 % and 18.4 %, respectively), and lower cover of long algal turf, CCA, live coral and sand and rubble than the remaining two sites. The macroalgae recorded at these two sites were dominated by *Padina* and *Sargassum* (Phaeophyceae), and *Acanthopora* and *Galaxaura* (Rhodophyta). Of all the macroalgae censused across all sites, 98.2 % were recorded within damselfish territories with only *Padina* being recorded outside territories. Interestingly, the benthic community recorded within damselfish territories appeared to have a major influence in separating the sites along the first canonical variate with red and brown macroalgae having positive loadings and long algal turfs and green macroalgae having negative loadings. The second canonical variate, which explained 32.6 % of the total variation, separated Mermaid Cove from Lagoon with Mermaid Cove having a higher cover of live coral and sand and rubble, and lower cover of long algal turf and CCA than Lagoon (Fig. D1).

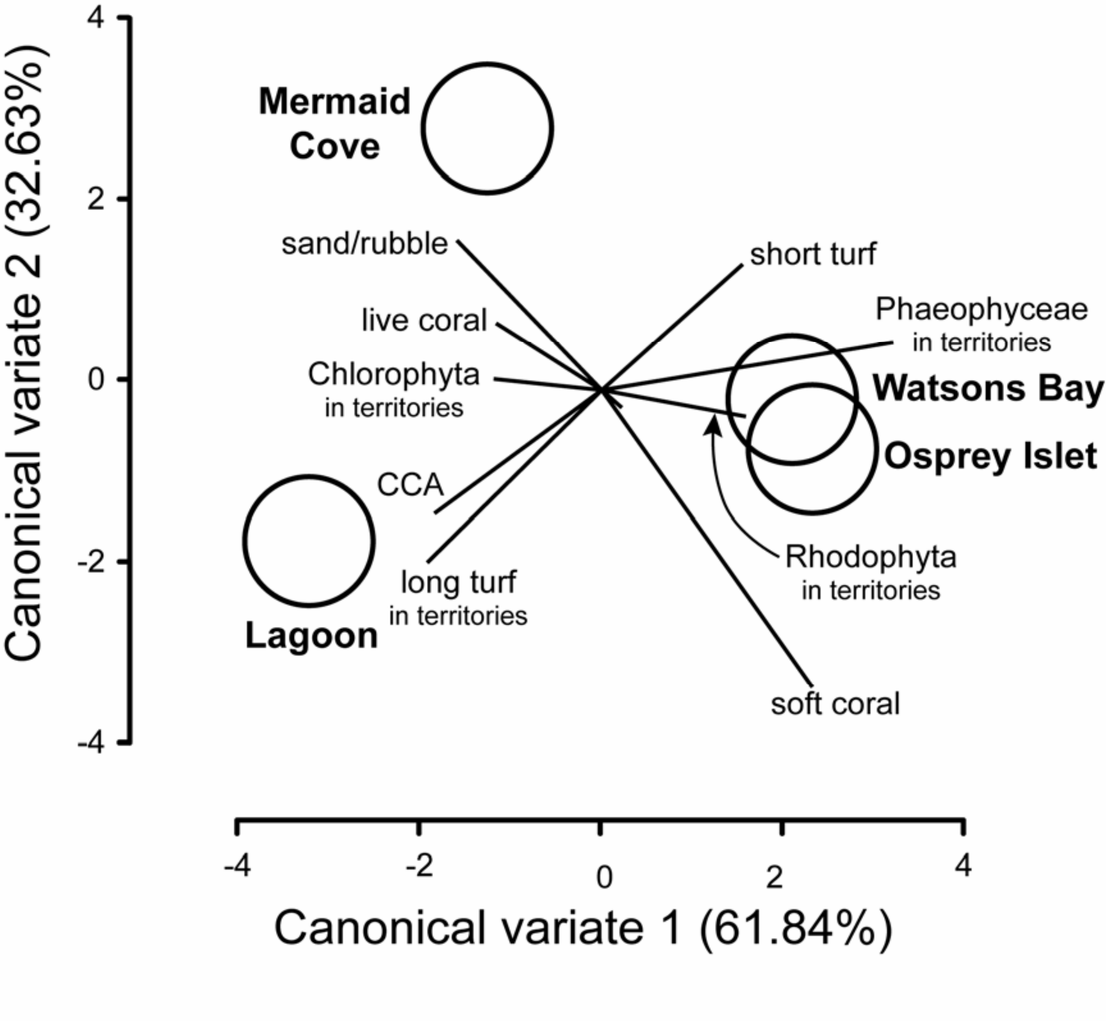

Fig. D1: Canonical discriminant analysis showing the relationship in benthic community structure among four sheltered sites on Lizard Island. Each site is based on twelve 10 m point intercept transects. Ellipses represent 95 % confidence limits around the site centroids. CCA: crustose coralline algae.

Table D1: Variation in the territory composition of six damselfish species across five sites at Lizard Island. Values represent the mean cover (%) of each category based on ten territories within each site. CCA: crustose coralline algae. Macroalgal taxa were identified to genus or species where possible. *Sargassum* that was small and lacked any distinctive features was recorded as *Sargassum* sp. Functional groupings of algae follow Steneck (1988). *D. pros*: *Dischistodus prosopotaenia*; *D. pers*: *Dischistodus perspicillatus*; *D. pseud*: *Dischistodus pseudochrysopoecilus*; *H. plag*: *Hemiglyphidodon plagiometopon*; *P. lac*: *Plectroglyphidodon lacrymatus*; *S. nig*: *Stegastes nigricans*. Sites are as follows: mc: Mermaid Cove; wb: Watsons Bay; oi: Osprey Islet; lag: lagoon; cb: Coconut Beach.

	D. pros					*D. pers*				*H. plag*			*D. pseud*		*P. lac*		*S. nig*	
	mc	wb	oi	lag	cb	mc	wb	oi	lag	mc	wb	oi	mc	lag	mc	lag	mc	lag
hard coral	7.2	4.9	3.0	5.5	8.1	0.3	0.3	0.3	0	11.6	12.4	7.3	21.5	15.6	15.3	21.7	19.4	16.4
soft coral	3.2	2.6	9.4	1.3	2.0	0	0	0.7	0.2	2.9	6.9	13.3	2.9	6.4	2.9	0.2	1.1	0.5
sand/rubble	7.4	17.5	5.1	5.1	2.0	16.0	13.3	16.5	17.1	3.7	5.3	5.3	5.1	1.7	3.2	0.0	1.6	0.9
‘other’ invertebrate	0.3	1.5	0.6	0.4	0.4	0	0	0	0	0.8	3.9	0.6	0.2	0	1.9	0.2	0.3	0.2
long turf	44.9	20.2	26.8	78.4	50.4	0.4	3.4	0	0	55.5	46.7	33.1	61.5	71.6	68.0	70.9	75.7	78.2
CCA	0	0	0	0	0	0	0	0	0	0	0.2	0.2	0.5	0	0.6	0	0.9	1.3
cyanobacteria	0.6	0.6	0	0	0	82.0	74.9	79.9	82.3	0	0	0.3	1.6	1.4	0	0	0.8	0.7
Foliose brown																		
Dictyota	0.3	0.9	2.2	0.7	0.9	0	0.2	0	0	1.5	1.8	0.8	0.3	0	0.6	0	0	0
Padina	3.3	9.8	6.1	0.5	1.7	0	0.5	0	0	15.5	7.9	31.9	1.9	0.5	1.3	0.3	0	0.3
Leathery brown																		
Hormophysa	0	0.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sargassum spp	12.6	23.1	16.9	0	0	0	0	0	0	0	0.2	1.6	0	0	0.1	0	0	0

S. cristaefolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0
S. cf *linearifolium*	8.4	0	8.8	0	0	0	0	0	0	0	0	0.6	0	0	0	0	0	0
S. polycystum	0	7.7	0.8	0	0	0	0	0	0	0	0.1	0.2	0	0	0	0	0	0
S. swartzii	2.7	5.2	2.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S. sp (unident)	1.5	10.2	4.5	0	0	0	0	0	0	0	0.1	0.8	0	0	0	0	0	0
Turbinaria ornata	2.6	1.9	2.1	0.2	0	0	0.2	0	0	0.6	0.9	1.4	0	0	0	0	0	0
Corticated red																		
Acanthophora	4.8	1.3	9.4	1.5	14.0	0	0	0.1	0.1	0	0	0	0	0	0	0	0	0
Gelidiopsis	3.5	4.5	3.1	0	0	0	0	0	0	0	1.7	0	0	0	0	0	0	0
Gracilaria	0	0	0.3	0	0.2	0	0	0	0	0	0	0	0	0	0.2	0	0	0
Hypnea	0	0	0.6	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0
Laurencia	0	0	0	1.4	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0
corticated (unident)	0	0.2	3.6	0	1.1	1.2	0	0.6	0	1.6	0.7	0.3	0	0	2.4	0	0	0
Calcified red																		
Amphiroa	0.9	2.4	1.0	1.1	0.6	0.1	5.3	0	0.3	5.4	4.5	0.9	0.1	0.8	0.7	1.2	0.2	1.0
Galaxaura	0.6	3.9	9.1	0	0	0	1.9	0	0	0	6.2	2.6	0.3	0	0.2	0	0	0
Corticated green																		
Caulerpa	0.1	0	0.3	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0
Chlorodesmis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0	0	0
Calcified green																		
Halimeda	7.5	4	0.4	3.9	18.1	0	0	0	0	0.9	0.6	0.2	4.1	2	2.3	5.5	0	0.5
Seagrass																		
Halophila	0.2	0	0	0	0	0	0	1.9	0	0	0	0	0	0	0	0	0	0

Table D2: Tukeys HSD post hoc test comparing the proportion of *Sargassum* biomass removed from within and outside the territories of six territorial damselfish species at Lizard Island. Values given are the approximate probabilities for the pairwise comparisons. Significant comparisons are given in bold.

		D. perspillatus	*D. perspillatus*	*D. prosopotaenia*	*D. prosopotaenia*	*D. pseudochrysopoecilus*	*D. pseudochrysopoecilus*	*P. lacrymatus*	*P. lacrymatus*	*S. nigricans*	*S. nigricans*	*H. plagiometopon*
		within	outside	within	outside	within	outside	within	outside	within	outside	within
D. perspicillatus	outside	0.999										
D. prosopotaenia	within	**<0.001**	**<0.001**									
D. prosopotaenia	outside	1.000	1.000	**<0.001**								
D. pseudochrysopoecilus	within	0.986	1.000	**<0.001**	0.996							
D. pseudochrysopoecilus	outside	0.781	0.997	**<0.001**	0.906	1.000						
P. lacrymatus	within	0.498	0.068	**<0.001**	0.208	**0.029**	**0.002**					
P. lacrymatus	outside	0.787	0.292	**<0.001**	0.591	0.086	**0.020**	1.000				
S. nigricans	within	1.000	0.999	**<0.001**	1.000	0.980	0.748	0.556	0.831			
S. nigricans	outside	0.105	0.600	**<0.001**	0.197	0.894	0.997	**<0.001**	**<0.001**	0.066		
H. plagiometopon	within	0.906	0.998	**<0.001**	0.945	1.000	1.000	**0.002**	0.064	0.888	1.000	
H. plagiometopon	outside	**0.009**	0.111	**<0.001**	**0.023**	0.269	0.648	**<0.001**	**<0.001**	0.008	0.986	0.772

Appendix E: Supplemental information for Chapter 6

Diurnal versus nocturnal browsing

To quantify variation in the browsing intensity of *Sargassum* between diurnal and nocturnal periods a series of transplants were conducted within the same two reef crest sites. *S*. cf. *baccularia* was collected and processed as previously described prior to transplanting to the reef. The mean mass and height of each thallus was 581.5 ± 16.0 g (SE) and 105.2 ± 2.5 cm, respectively. Three randomly selected thalli were transplanted to the reef for approximately 12 hours with diurnal assays being deployed at dawn (~ 06:00) and collected at dusk (~ 18:00), and nocturnal assays being deployed at dusk and collected at dawn. The diurnal and nocturnal assays were conducted several days after the completion of the density experiment, and replicated three times within each site (total n = 36 thalli). A two-factor ANOVA was used to determine if the rate of removal of *Sargassum* biomass varied between nocturnal and diurnal time periods, or among sites. The proportion of biomass removed was arcsine-square root transformed to improve normality and homoscedasticity.

There was a marked difference in the removal rates of the nocturnal and diurnal assays ($F_{1,32} = 1118.07$, $p < 0.001$; Fig. E1), with 93.8 (± 0.6 SE) % of the *Sargassum* biomass being removed from diurnal assays as opposed to only 7.0 (± 1.4) % from nocturnal assays. There was no significant effect of site on the removal *Sargassum* biomass ($F_{1,32} = 0.71$, $p = 0.40$). On two occasions several *Kyphosus vaigiensis* individuals were observed taking bites from the nocturnal assays immediately prior to their collection at, or shortly after, dawn.

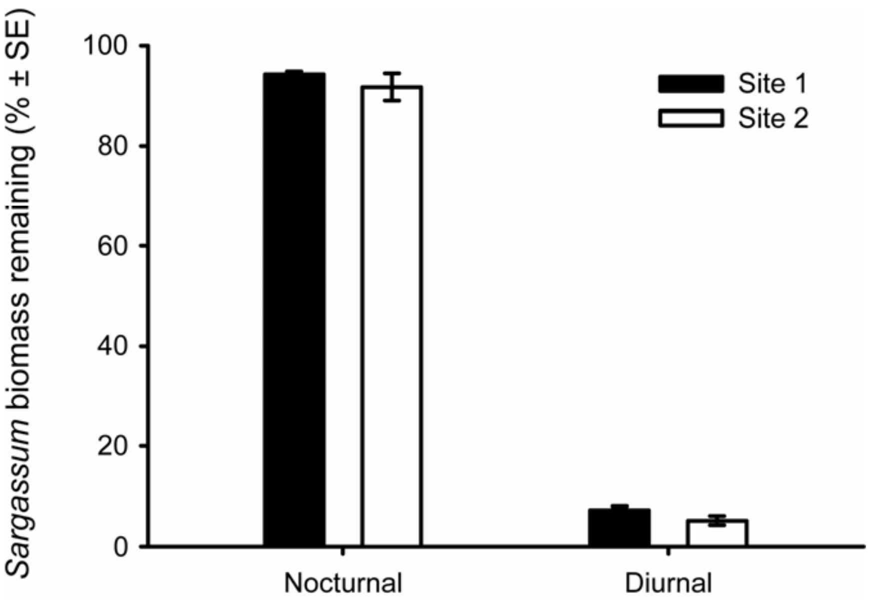

Fig. E1: Variation in the removal rates of *Sargassum* cf. *baccularia* between diurnal and nocturnal periods and among sites on the reef crest of Orpheus Island. The mass remaining was calculated as the proportion of the initial, or transplanted, biomass that remained after 12 hours.

Spatial variation in browsing within macroalgal density treatments

To explore spatial variation in removal rates among thalli within each of the density treatments, each thallus was classified into one of three categories that related to their position within the experimental plots: inner, mid, or outer thalli. The outer thalli were those thalli positioned on the perimeter of the experimental plots, the inner thallus was positioned in the centre of the experimental plot, and the mid thalli were those positioned between the inner and outer thalli. The low density treatment contained only inner and outer thalli. Spatial variation in removal rates within each density treatment was analysed using three repeated measures ANOVA’s. A separate analysis was performed for each density treatment due to the absence of mid thalli from the low density treatment. The analysis was based on the proportion of the initial, or day 0, *Sargassum* biomass that remained after each consecutive day within each of the spatial categories. The proportion of *Sargassum* biomass remaining was $^{4}\sqrt{}$ transformed to improve normality and homoscedasticity.

The position of the *Sargassum* within the experimental plots had no detectable effect on the removal rates for any of the density treatments, either independently, or through second or third order interactions with site or day (Table E1; Fig. E2).

Table E1: Results of repeated measures analysis of variance comparing the spatial variation in removal rates among thalli within each of the density treatments: (a) high density, (b) medium density, and (c) low density. Analyses were based on the proportion of the initial *Sargassum* biomass (fourth-root transformed) that remained after each day on the reef. Significants effects ($p < 0.05$) are shown in bold.

Source of variation	SS	df	MS	F	p
(a) High density					
Site	0.003	1	0.003	0.099	0.758
Position	0.038	2	0.019	0.688	0.521
Site × Position	0.001	2	0.000	0.015	0.985
Residual	0.335	12	0.028		
Day	**0.814**	**3**	**0.271**	**68.363**	**< 0.001**
Day × Site	0.033	3	0.011	2.746	0.057
Day × Position	0.007	6	0.001	0.276	0.945
Day × Site × Position	0.002	6	0.000	0.083	0.998
Residual	0.143	36	0.004		
(b) Medium density					
Site	**0.216**	**1**	**0.216**	**7.671**	**0.017**
Position	0.002	2	0.001	0.039	0.962
Site × Position	0.003	2	0.002	0.059	0.943
Residual	0.338	12	0.028		
Day	**0.997**	**3**	**0.332**	**108.053**	**< 0.001**
Day × Site	**0.031**	**3**	**0.010**	**3.322**	**0.030**
Day × Position	0.001	6	0.000	0.079	0.997
Day × Site × Position	0.003	6	0.000	0.153	0.987
Residual	0.111	36	0.003		
(c) Low density					
Site	0.034	1	0.034	3.901	0.083
Position	0.013	1	0.013	1.440	0.264
Site × Position	0.001	1	0.001	0.150	0.709
Residual	0.070	8	0.009		
Day	**0.610**	**3**	**0.203**	**50.383**	**< 0.001**
Day × Site	**0.041**	**3**	**0.014**	**3.406**	**0.034**
Day × Position	0.000	3	0.000	0.026	0.994
Day × Site × Position	0.000	3	0.000	0.034	0.991
Residual	0.097	24	0.004		

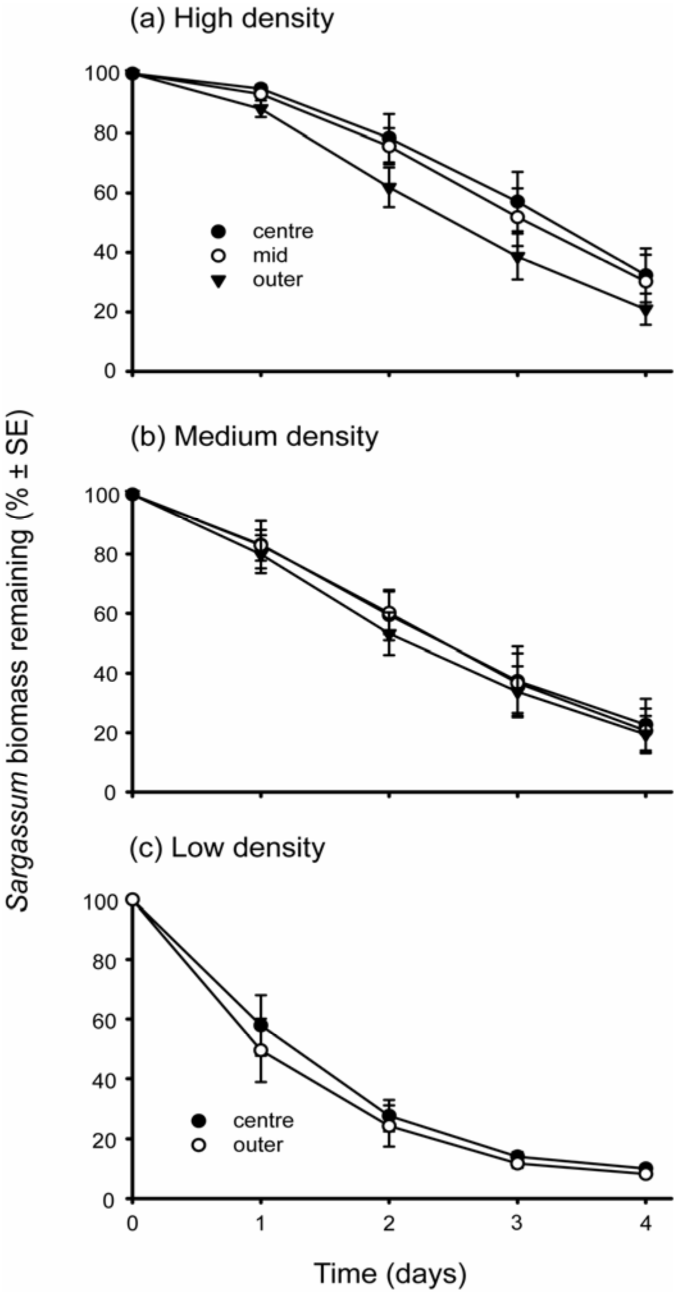

Fig. E2: Spatial and temporal variation in removal rates of *Sargassum* thalli positioned within each of the macroalgal density treatments: (a) high density, (b) medium density, and (c) low density. The mass remaining was calculated as the proportion of the initial, or transplanted, biomass that remained after each consecutive day.

Details of ANOVA and MANOVA results comparing browsing rates among macroalgal density treatments

Table E2: Results of repeated measures analysis of variance comparing relative removal rates of *Sargassum* biomass among density treatments, sites, and days. The analysis was based on the proportion of the initial *Sargassum* biomass that remained after each day on the reef. Significants effects ($p < 0.05$) are shown in bold.

Source of variation	SS	df	MS	F	p
Site	0.052	1	0.052	1.246	0.281
Density	**1.994**	**3**	**0.665**	**15.987**	**< 0.001**
Site × Density	0.178	3	0.059	1.430	0.271
Residual	0.665	16	0.042		
Day	**2.197**	**3**	**0.732**	**96.101**	**< 0.001**
Day × Site	0.022	3	0.007	0.972	0.414
Day × Density	**0.164**	**9**	**0.018**	**2.386**	**0.025**
Day × Site × Density	0.115	9	0.013	1.676	0.121
Residual	0.366	48	0.008		

Table E3: Results of repeated measures multivariate analysis of variance comparing the feeding intensity of the two dominant browsing species among density treatments, sites, and days. The analysis was based on the mass standardized bites taken by each species ($\sqrt[4]{}$ transformed). Significants effects ($p < 0.05$) are shown in bold.

Source of variation	Wilks' λ	F	df_{effect}	df_{error}	p
Site	0.835	1.483	2	15	0.258
Density	**0.309**	**3.995**	**6**	**30**	**0.005**
Site × Density	0.637	1.267	6	30	0.302
Day	0.729	2.791	2	15	0.093
Day × Site	0.892	0.909	2	15	0.424
Day × Density	**0.242**	**5.161**	**6**	**30**	**0.001**
Day × Site × Density	0.701	0.972	6	30	0.461

Table E4: Results of multivariate analysis of variance comparing the relative contribution of the two dominant browsing species among density treatments and sites. The analysis was based on the proportion of mass standardized bites taken by each species (arcsine-square root transformed) from each of the density treatments summed across days. Significants effects ($p < 0.05$) are shown in bold.

Source of variation	Value	F	df_{effect}	df_{error}	p
Site	0.893	0.896	2	15	0.429
Density	**0.452**	**2.436**	**6**	**30**	**0.048**
Site × Density	0.916	0.223	6	30	0.966

Details of predator assemblage and relationship with macroalgal density

Table E5: Summary of predatory fishes recorded within the habitat patches. The total biomass and mean size (total length, TL) of each species is given.

Species	Mean TL (cm)	Number of individuals	Total Biomass (kg)
Carangidae			
Caranx sp.	35	1	3.23
Haemulidae			
Plectorhinchus sp.	38.9	27	29.02
Labridae			
Choerodon anchorago	30.8	46	32.05
Choerodon cyanodus	31.5	2	1.45
Choerodon schoenleinii	35.7	41	44.50
Lethrinidae			
Lethrinus nebulosus	39	1	1.09
Lethrinus olivaceus	37.3	3	2.69
Lutjanidae			
Lutjanus carponotatus	27.1	138	66.84
Lutjanus sebae	33.5	2	1.58
Luyjanus sp.	40.0	1	1.19
Symphorus nematophorus	34.0	17	11.55
Serranidae			
Cephalopholis cyanostigma	23.0	1	0.20
Plectropomus laevis	39.0	1	0.87
Plectropomus leopardus	39.0	31	28.63
Plectropomus maculatus	21.0	2	0.26

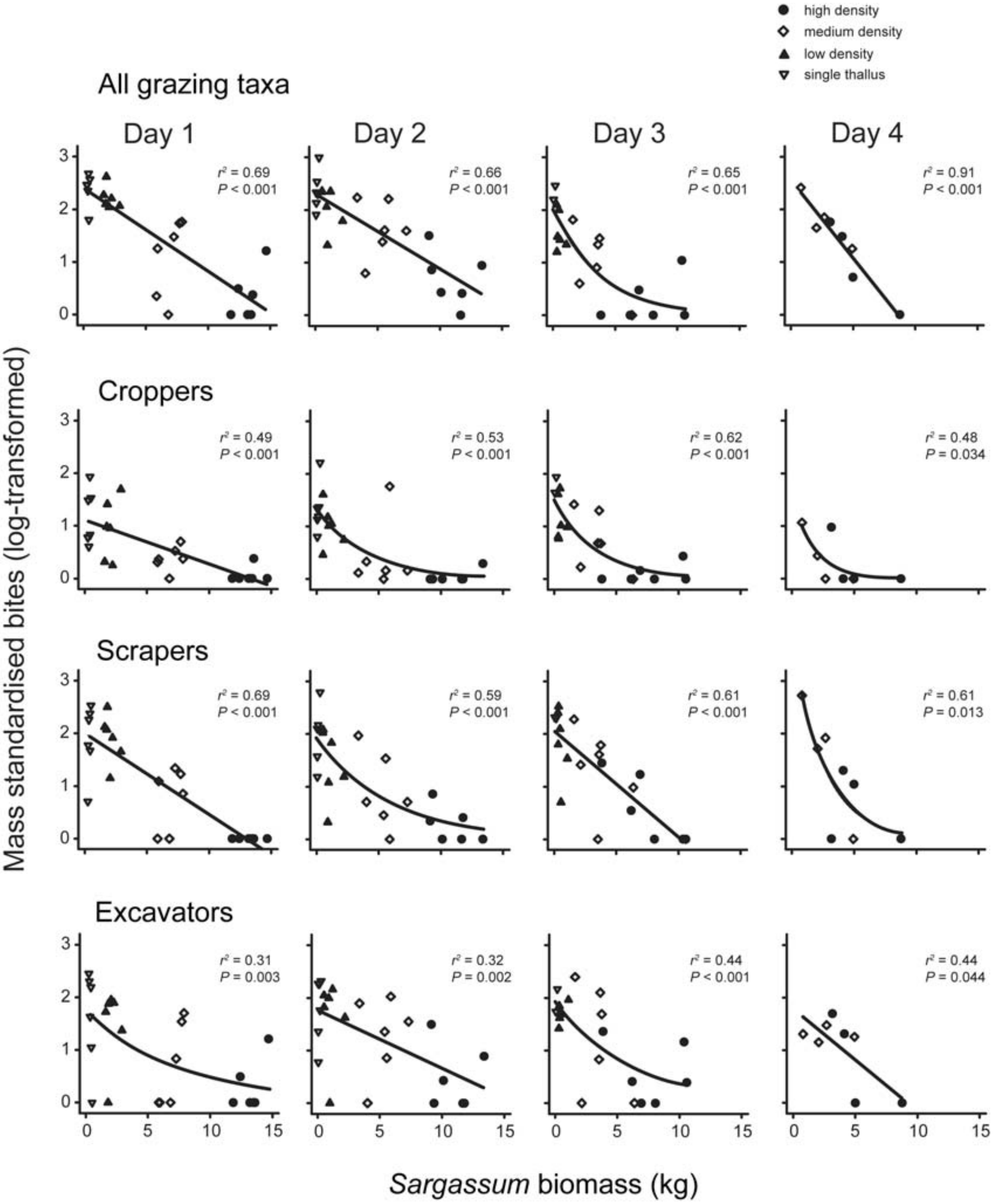

Fig. E3: Influence of *Sargassum* biomass on the grazing intensity of herbivorous fishes for each day of the deployments. The relationship between the total number of mass standardised bites taken from the substratum and the biomass of *Sargassum* within each of the experimental plots on each day of the deployments for all species combined, and the three herbivore functional groups independently. The best-fit relationships (linear and log-linear) are given as solid lines, along with r^2 and *P* values.

Appendix F: Publications arising from thesis

Publications derived from each of the thesis chapters

Hoey AS, Bellwood DR (2009) Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. Ecosystems 12:1316-1328

Hoey AS, Bellwood DR (2010) Among-habitat variation in herbivory on *Sargassum* spp. on a mid-shelf reef in the northern Great Barrier Reef. Mar Biol 157:189-200

Hoey AS, Bellwood DR (2010) Damselfish territories as a refuge for macroalgae on coral reefs. Coral Reefs 29:107-118

Hoey AS, Bellwood DR (2010) Cross-shelf variation in browsing intensity on the Great Barrier Reef. Coral Reefs 29:499-508

Additional publications arising during PhD candidature

Barnett A, Bellwood DR, **Hoey AS** (2006) Trophic ecomorphology of cardinalfish (Apogonidae). Mar Ecol Prog Ser 322:249-257

Bellwood DR, Wainwright PC, Fulton CJ, **Hoey AS** (2006) Functional versatility supports coral reef biodiversity. Proc R Soc London B 273:101-107

Bellwood DR, **Hoey AS**, Ackerman JL, Depczynski M (2006) Reef fish community phase shifts and the resilience of coral reefs. Glob Change Biol 12:1587-1594

Bellwood DR, Hughes TP, **Hoey AS** (2006) Sleeping functional groups drive coral reef recovery. Curr Biol 16:2434-2439

Hoey J, **Hoey AS**, McCormick MI (2007) Influence of a depth gradient on sex-specific growth dynamics of a tropical reef fish. Coral Reefs 26:603-613

Wismer S, **Hoey AS**, Bellwood DR (2009) Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. Mar Ecol Prog Ser 376:45-54

Fox RJ, Sunderland TL, **Hoey AS**, Bellwood DR (2009) Estimating functional roles in coral reef ecosystems: behaviour drives contrasting roles in herbivorous fishes (F: Siganidae) Mar Ecol Prog Ser 385:261-269

Wilson SK, Adjeroud M, Bellwood DR, Berumen ML, Booth D, Bozec Y-M, Chabanet P, Cheal A, Cinner J, Depczynski M, Feary DA, Gagliano M, Graham NAJ, Halford AR, Halpern BS, Harborne AR, **Hoey AS**, Holbrook S, Jones GP, Kulbiki M, Letourneur Y, Lison de Lome T, McClanahan T, McCormick MI, Meekan MG, Mumby PJ, Munday PL, Ohman MC, Pratchett MS, Riegl B, Sano M, Schmitt RJ, Syms C (2010) Critical knowledge gaps in current understanding of climate change impacts on coral reef fishes. J Exp Biol 213:894-900

Cvitanovic C, **Hoey AS** (2010) Benthic composition influences within-habitat variation in macroalgal browsing on the Great Barrier Reef. Mar Freshw Res 61:999-1005

Hoey AS (2010) Size matters: macroalgal height influences the feeding response of coral reef herbivores. Mar Ecol Prog Ser 411:299-301