

Limited Functional Redundancy in a High Diversity System: Single Species Dominates Key Ecological Process on Coral Reefs

Andrew S. Hoey* and David R. Bellwood

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

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 alternate states. On coral reefs, regional reductions in herbivores have underpinned shifts from coral to dominance by leathery macroalgae. These shifts appear difficult to reverse as these macroalgae are unpalatable to the majority of herbivores, and the macroalgae suppress the recruitment and growth of corals. The removal of macroalgae is, therefore, viewed as a key ecological process on coral reefs. On the Great Barrier Reef, *Sargassum* is a dominant macroalgal species following experimentally induced coral–macroalgal phase-shifts. We, therefore, used *Sargassum* assays and remote video cameras to directly quantify the species responsible for removing macroalgae across a range of coral reef habitats on Lizard Island, northern Great Barrier Reef. Despite supporting over 50 herbivorous fish species and six macroalgal

browsing species, the video footage revealed that a single species, *Naso unicornis*, was almost solely responsible for the removal of *Sargassum* biomass across all habitats. 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. This limited redundancy, both within and across local scales, underscores the need to assess the functional roles of individual 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.

Key words: *Naso unicornis*; functional redundancy; phase-shift; macroalgae; *Sargassum*; coral reef; herbivory.

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*Corresponding author; e-mail: andrew.hoey@jcu.edu.au

INTRODUCTION

Herbivory is widely acknowledged as a key process structuring plant communities in both terrestrial and aquatic ecosystems (Scheffer and others 2001). Whilst there are fundamental differences among ecosystems in the nature of herbivory and its importance relative to other processes (Shurin and others 2006; Gruner and others 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 has often led 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 and others 1981; Archer and others 1988; Dublin and others 1990), mesic grasslands (Dobson and Crawley 1994), and salt marshes (Bazely and Jefferies 1986). In marine systems, shifts to macroalgal, or seaweed, dominance have been documented on coral reefs and temperate rocky shores following reductions in herbivore populations (Hughes 1994; Steneck and others 2002). The persistence of these shifts long after herbivore populations have been restored highlight the difficulty of reversing such shifts as the dominant vegetation reaches a size refuge from herbivory. Seedlings of woody plants and macroalgal propagules are easily eliminated by grazing herbivores (Holmgren and others 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. Within these reefs over 90% of the daily algal production is consumed by a diverse assemblage of grazing fishes and invertebrates (Polunin and Klumpp 1992; Bellwood and others 2004). 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 and others 2005), suggesting there is an innate capacity to compensate for the increased algal production. However, regional reductions in herbivorous fishes through overfishing have limited the ability of many reefs to absorb the increased algal production. This disequilibrium between algal production and consumption may release macroalgal propagules from top-down control, and ultimately lead to a shift to dominance by erect brown macroalgae (Hughes 1994; McClanahan and others 2001; Graham and

others 2006). Once established these shifts appear difficult to reverse as these macroalgae are unpalatable to the majority of herbivores (Bellwood and others 2006) and have been shown to suppress the survival, fecundity, and recruitment of corals (Jompa and McCook 2002; Hughes and others 2007; Mumby and others 2007). Given the potential importance of macroalgae in coral reef phase-shifts, our ability to successfully manage coral reefs into the future requires 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 and others 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 (that is, macroalgal browsers) appears to represent a separate but critical process in the reversal of phase-shifts (Bellwood and others 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 and others 2006; Mantyka and Bellwood 2007; Fox and Bellwood 2008; 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 and others 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 and others 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 50% of the substratum (Bellwood and others 2006; Wismer and others 2009). In contrast, erect brown macroalgae are present in low densities on mid- and outer-shelf reefs (McCook and others 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 identities 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 among habitats. The identification of these species is an essential step to understand the resilience of these habitats, and the reef as a whole.

MATERIALS AND METHODS

Study Location

The study was conducted during a 3 week period in November 2007 on Lizard Island (14°40'S, 145°28'E) in the northern GBR (Figure 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 (Figure 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 (Figure 1C).

Benthic Surveys

To quantify the variation in the algal community and benthic community structure 12 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 1 m either side was recorded at 1 m 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, or algal turf (EAM; sensu Wilson and others 2003, ≤ 10 mm in height), crustose coralline algae (CCA), live scleractinian coral, damselfish territory (marked by long algal turf defended by a damselfish), soft coral, sand, sand and rubble, and "other." To detect less abundant macroalgal taxa each transect area (that is, 10 × 2 m) was systematically searched and the presence of all macroalgal species recorded. Finally,

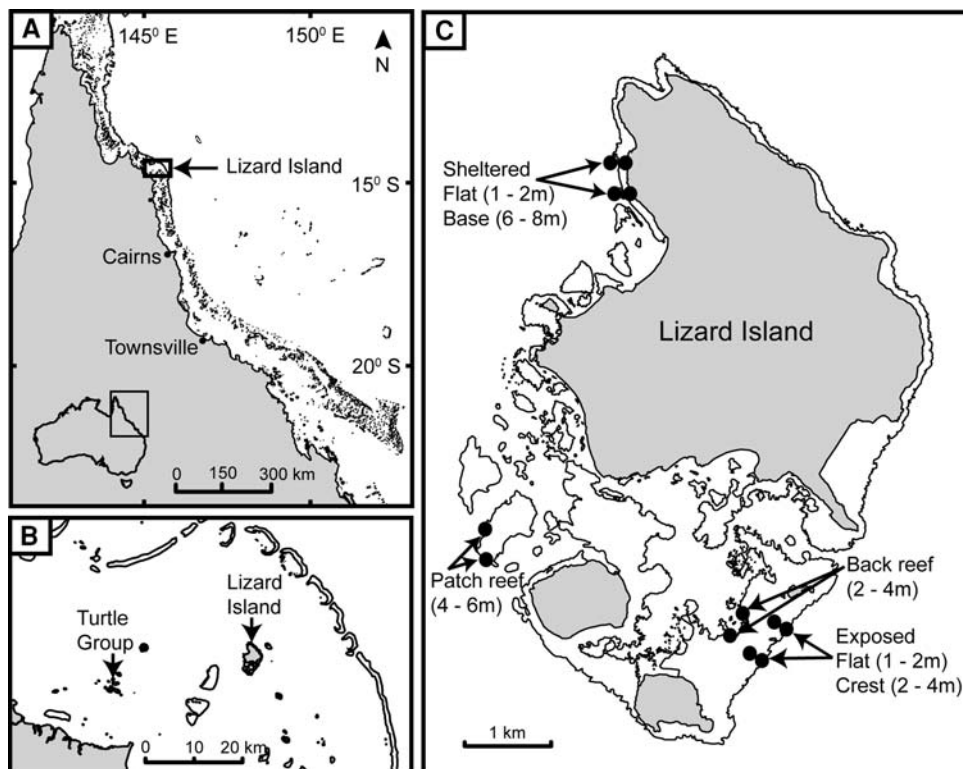


Figure 1. Map of the Great Barrier Reef (GBR) showing the location of the study sites. **A** Geographic location of Lizard Island. **B** Position of Lizard Island across the continental shelf in the northern GBR. The location of the Turtle Group, the site of collection of *Sargassum*, on the inner-shelf 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.

a thorough search of the 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 among 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 (Figure 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 in a salad spinner for 30 s to remove excess water, and the wet weight and maximum height of the thallus were recorded. 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 8 h. 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 $1000 \times 600 \times 600$ mm; 50 mm square polyethylene mesh) to control 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 8 h, 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 3 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 8 h experimental period, with only a brief (2–4 min) interval after 4 h to allow for an obligatory battery change. This procedure was replicated three times within each site resulting in 48 h 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 and others 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. *Sargassum 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 and others 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 minimizing 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 behavior, 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*, and *Turbinaria*) based on diet (Robertson and Gaines 1986; Choat and others 2002) and direct video observations (Bellwood and others 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 8 h 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 versus 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. We therefore calculated a grazing preference index (GPI) for each habitat:

$$\text{GPI} = \sum p_i \cdot c_i,$$

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 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 browsing 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.

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 to 47.0% (Table 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

Table 1. Summary of the Benthic Community Composition Within the Six Habitats Around Lizard Island

	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						
<i>Halimeda</i> spp.	†	*	0.5 (0.5)	2.5 (0.7)	0	0
<i>Chlorodesmis fastigiata</i>	†	†	*	0.3 (0.3)	0	0.5 (0.3)
Rhodophyta						
<i>Acanthophora spicifera</i>	†	0	†	0.3 (0.3)	0	0
<i>Asparagopsis taxiformis</i>	0	†	†	0	0	0
<i>Amphiroa</i> sp.	1.7 (0.7)	9.3 (2.0)	1.5 (0.6)	3.5 (1.5)	*	0.8 (0.5)
<i>Galaxaura</i> sp.	8.3 (2.1)	33.3 (3.0)	†	†	0	0
Ochrophyta (Phaeophyceae)						
<i>Dictyota</i> spp.	†	†	0	*	0	0
<i>Padina</i> sp.	*	†	1.0 (0.6)	0.3 (0.3)	0	0
<i>Sargassum cristaefolium</i>	0	0	0	0	1.0 (0.6)	*
<i>Sargassum polycystum</i>	*	†	†	0	0	0
<i>Sargassum swartzii</i>	†	0	*	*	0	*
<i>Sargassum</i> sp.	†	0	0	†	0	0
<i>Turbinaria ornata</i>	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 and 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)	—	1.0 (0.4)	0.3 (0.3)	—

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.

on the exposed reef flat (Table 1). Thorough searches of all habitats revealed at least three species of *Sargassum* are 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, whereas *S. polycystum* was restricted to the three sheltered habitats and *S. cristaefolium* was restricted to the exposed reef crest and flat (Table 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% 8 h^{-1}) than the three sheltered habitats (21–31% 8 h^{-1} ;

Figure 2A). The reduction in biomass of *S. swartzii* held within exclusion cages was consistently low (overall mean = 3.9% 8 h^{-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* ($F_{1,2} = 7628.6$, $P = 0.0001$), with diurnal removal rates (94.4 \pm 0.4%) being significantly higher than nocturnal removal rates (3.2 \pm 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} ; Figure 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.*

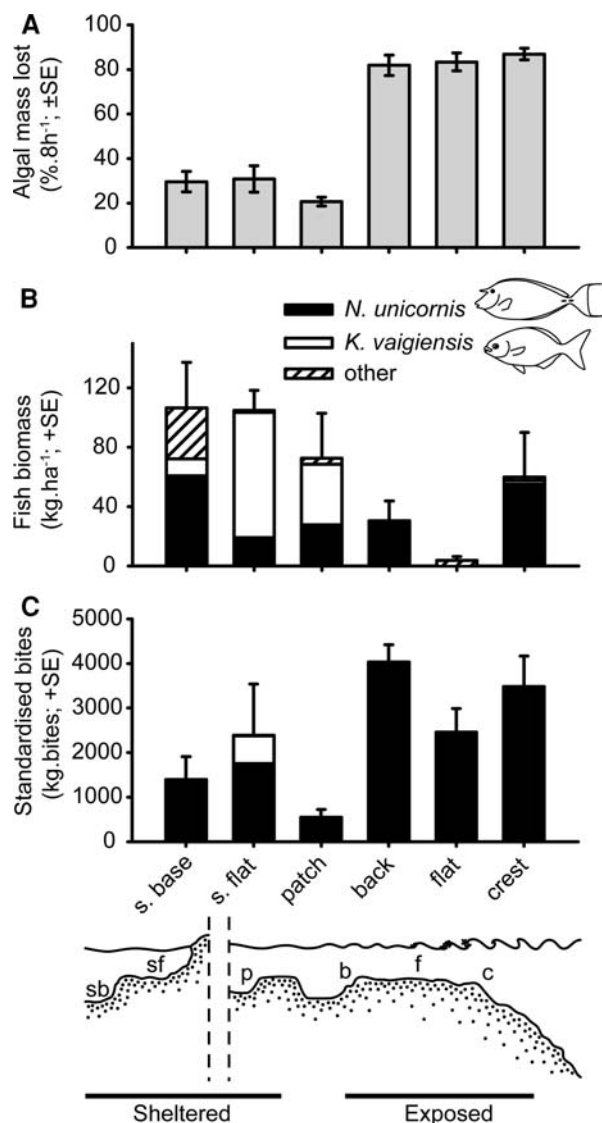


Figure 2. **A** Variation in browsing intensity on *Sargassum swartzii* across six habitats of varying exposure on Lizard Island. The means are based on four thalli transplanted for 8 h into each of two sites within each habitat and replicated over 3 days. **B** Mean biomass of browsers of brown macroalgae 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 \times 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.

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 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 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 (Figure 2C), with up to 18 individuals observed feeding at any one time (see video files in the supplementary material). 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). 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 (Figure 2C). Each of the remaining 36 species, including the macroalgal browsing *C. carolinus* 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).

DISCUSSION

Despite the reefs around Lizard Island supporting over 50 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 and others 1997; Folke and others 2004; but see Bellwood and others 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

Table 2. Relationship Between Consumption Rates of *Sargassum swartzii* and Herbivorous Fishes

	Bivariate correlation		Partial correlation	
	<i>r</i>	<i>P</i>	ρ	<i>P</i>
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
<i>Calotomus carolinus</i>				
Density	−0.190	0.346	−0.541	0.346
Biomass	−0.525	0.284	−0.898	0.039
<i>Kyphosus vaigiensis</i>				
Density	−0.618	0.191	−0.712	0.178
Biomass	−0.705	0.118	−0.822	0.088
<i>Naso lituratus</i>				
Density	−0.662	0.152	−0.837	0.077
Biomass	−0.595	0.213	−0.745	0.149
<i>Naso unicornis</i>				
Density	0.256	0.625	0.189	0.761
Biomass	−0.158	0.766	−0.338	0.579
<i>Platax pinnatus</i>				
Density	−0.414	0.415	−0.507	0.383
Biomass	−0.414	0.415	−0.507	0.383
<i>Siganus canaliculatus</i>				
Density	0.259	0.620	0.387	0.520
Biomass	0.291	0.576	0.398	0.507

Correlations are based on the mean proportion of *Sargassum swartzii* biomass removed over an 8 h 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 $\alpha = 0.006$. Partial correlations were calculated controlling for the availability and relatively palatability of resident macroalgae within each habitat.

Table 3. Relationship Between Herbivore Feeding Rates and Consumption of *Sargassum swartzii*

	Bites	Mass std bites (kg bites)	β	SE of β	t_{22}	<i>P</i>
Macroalgal browsers						
<i>Calotomus carolinus</i>	101	61.3	0.101	0.083	1.221	0.235
<i>Kyphosus vaigiensis</i>	2077	4026.0	0.028	0.159	0.179	0.860
<i>Naso unicornis</i>	37,992	81,214.4	0.898	0.105	8.581	<0.001
<i>Siganus canaliculatus</i>	17	3.0	0.088	0.078	1.139	0.267
Other herbivores						
<i>Acanthurus</i> spp.	474	156.2	0.165	0.090	1.821	0.082
<i>Naso</i> 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
<i>Kyphosus cinerescens</i>	5	5.5	−0.146	0.182	−0.801	0.431
<i>Pomacanthus</i> spp.	23	6.2	−0.018	0.076	−0.244	0.810
<i>Siganus doliatus</i>	1210	202.6	0.133	0.094	1.424	0.169
<i>Siganus</i> spp.	160	18.5	0.143	0.150	0.953	0.351
Scarine 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

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. nigrofasciatus*, *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. punctatus*; Scarine parrotfishes: *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 jansentii*, *Sufflamen chrysopterus*.

habitats separated by several kilometers. 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. *Naso 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 and others 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% 8 h^{-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% 8 h^{-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 and others 2006; Mantyka and Bellwood 2007; Fox and Bellwood 2008); 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 (that is, 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. We will consider each of these issues 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 2008). 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 and others (2006) reported a batfish, *P. pinnatus*, was responsible for removing most of the *Sargassum* biomass from large (25 m²) 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, whereas 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). Inter-specific 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 and others (1991) found no relationship between the grazing 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 in 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 and others 2007; Wismer and others 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 2008). 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 (C. Lefèvre pers. comm.). 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 2008; 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 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 2008) 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 and others 2006; Fox and Bellwood 2008; 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 *Sargassum* 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 and others 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 and others 2009), erect brown macroalgae accounted for approximately two-thirds of the stomach content volume (Choat and others 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 and others 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 (compare Ledlie and others 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, often forming a large proportion of the total catch (Dalzell and others 1996; Rhodes and others 2008; see Appendix 1 in the supplementary material). The limited available evidence suggests that this fishing pressure has already reduced the abundance and size structure of several of these populations (Wantiez and others 1997; Rhodes and others 2008). Although 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.

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