NOTE

Size matters: macroalgal height influences the feeding response of coral reef herbivores

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ABSTRACT: Algal size has often been related to shifts in the susceptibility of algae to herbivores. Within coral reef systems, macroalgal assays have been widely used to quantify herbivory; however, the effect of macroalgal size has been largely overlooked. I used *Sargassum polycystum* assays that spanned the range of available heights (10 to 80 cm) and underwater video cameras to examine the effect of macroalgal height on the rates and agents of herbivory on an inner-shelf reef of the Great Barrier Reef. Rates of herbivory were high and displayed limited variation among heights, ranging from 86.4 to 95.2% $5h^{-1}$. There was, however, significant variation in the species recorded feeding from *S. polycystum* of different heights. *Naso unicornis* dominated feeding on the shortest (10 cm) assays, while *Kyphosus vaigiensis* dominated feeding on the larger (20 to 80 cm) assays. This variation appears to be related to interspecific differences in foraging behaviour, and suggests that the roles of these fishes may change at different stages of benthic community succession.

KEY WORDS: Herbivory · *Sargassum* spp. · Algal succession · Resilience

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INTRODUCTION

Herbivory is widely acknowledged as a key process determining the structure and resilience of coastal marine ecosystems (Hughes 1994, Steneck et al. 2002). Variation in grazing intensity has been related to differences in the distribution, standing biomass, productivity and succession of temperate and tropical algal communities (Lubchenco & Gaines 1981, Lewis 1986). In areas of high grazing intensity, the algal communities are maintained in a cropped state dominated by algal turfs and crustose coralline algae (Steneck & Dethier 1994). However, at reduced levels of grazing, algal production may exceed consumption and ultimately lead to a transition from algal turfs to larger canopy-forming fucalean macroalgae (Steneck et al. 2002, Hughes et al. 2007). Smaller forms, or early developmental stages, of fucalean macroalgae are easily eliminated by grazing herbivores; however, as they grow they become less susceptible to the same suite of herbivores (Lubchenco & Gaines 1981, Bellwood et al.

2006). Such shifts not only highlight the importance of herbivory in determining benthic community succession, but also the potential importance of algal size in determining the susceptibility of algae to herbivores.

Within coral reef systems, macrophyte assays have been used extensively as a metric for the intensity of herbivory among locations (e.g. Lewis 1986), to determine the susceptibility of various algal species to herbivory (e.g. Paul & Hay 1986) or to identify the herbivores responsible for removing algal biomass (e.g. Hoey & Bellwood 2009). While the majority of these studies have controlled for size, using assays of similar sizes, few have examined the effect of algal size (see Mantyka & Bellwood 2007 for an exception). This is surprising given that the majority of fishes, the dominant herbivores on relatively intact reefs, are visual predators (Myrberg & Fuiman 2002), and the assays are often positioned in locations where the algae are naturally rare. The ability of fishes to detect the assays is likely to be directly related to size, or apparency, of the algae (Lubchenco & Gaines 1981). The aim of the present study, therefore, was to ex-

amine the effect of macroalgal height on rates of herbivory and to identify the species responsible for removing erect brown macroalgae, *Sargassum polycystum*, of different heights. The genus *Sargassum* was selected for the assays as it is the largest coral reef alga, attaining heights of 3 m (Bellwood et al. 2006), has been used extensively in previous studies (e.g. Steinberg et al. 1991) and was the dominant taxa following an experimentally induced phase-shift to macroalgal dominance at this site (Hughes et al. 2007).

MATERIALS AND METHODS

The study was conducted during April 2008 in Pioneer Bay on Orpheus Island (18° 37′ S, 146° 30′ E), an inshore island in the central region of the Great Barrier Reef (GBR). Pioneer Bay is located on the leeward side of the island and has a well-developed fringing reef with a clearly defined reef crest at a depth of 2 to 3 m, marking the transition between the extensive reef flat and steeply inclined reef slope.

To examine the effect of macroalgal height on browsing intensity, a series of assays were conducted. *Sargassum polycystum* of varying heights were collected from the reef flat by cutting the holdfast at the point of attachment. Four thallus heights were selected that spanned the range of available sizes at the time of the study: 10, 20, 40 and 80 cm. All *S. polycystum* thalli were placed in raceways with flow-through seawater within 15 min of collection, and were transplanted to the reef within 24 h.

Individual thalli were spun in a salad spinner for 30 s to remove excess water, and weighed. The mean (±SE) mass of each thallus was 12.5 ± 0.6, 38.2 ± 1.1, 73.6 ± 2.7 and 135.5 ± 7.3 g for the 10, 20, 40 and 80 cm assays, respectively. Four thalli of each height were haphazardly selected and transplanted to each of 2 sites on the reef crest. These sites had similar benthic structure and were separated by approximately 200 m of contiguous reef. Each thallus was attached to a numbered lead weight using a rubber band and a cable tie, enabling the 16 assays to be deployed simultaneously with minimum disturbance. All assays were deployed between 07:00 and 08:00 h and collected between 12:00 and 13:00 h to coincide with the period of greatest water depth at the time of the study. Within each site, one thallus of each height was placed inside an exclusion cage ($900 \times 500 \times 500$ mm; 20 mm mesh) to control for the effects of handling and translocation. The 12 remaining thalli (i.e. 3 thalli of each height) were exposed to herbivores. All thalli were haphazardly placed within each site with adjacent transplanted thalli separated by a minimum of 3 m. After 5 h, all assays were collected, spun and measured as described above. This procedure was repeated 3 times within each site.

To quantify feeding on the assays, stationary underwater digital video cameras (Sony DCR-SR100 HDD cameras in Ikelite housings mounted on concrete blocks) were used. Four cameras were deployed at each site, with one camera positioned 1.5 to 2 m from a haphazardly selected assay of each of the 4 heights. Filming commenced immediately after the assays were deployed and continued without disturbance for the 5 h experimental period. All video footage was viewed and the number of bites taken from the assays 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 fish body mass and number of bites taken by each fish (following Hoey & Bellwood 2009).

To determine if the rate of removal of *Sargassum polycystum* varied among thallus heights, sites, or days, a 3-factor ANOVA was used. The analysis was based on the proportion of the initial biomass removed during 5 h on the reef. Variation in feeding by herbivorous fishes among thallus heights and sites was analysed using a 2-factor multivariate ANOVA (MANOVA). Temporal variation was not included in the model as feeding by the dominant herbivores displayed no shift among thallus heights during the 5 h experimental period (see Tables S1 & S2, Fig. S1 in the supplementary material for details, www.int-res.com/articles/suppl/m411p299_supp.pdf). Therefore, the analysis was based on the proportion of mass-standardized bites taken from each assay by the 3 dominant herbivore species. These species accounted for over 99% of all bites recorded. The proportion of *S. polycystum* biomass removed and the proportion of mass standardized bites were arcsine-square root transformed to improve normality and homoscedasticity.

RESULTS

There was almost complete removal of all *Sargassum polycystum* assays (Fig. 1a), with removal rates varying from 86.4 to 95.2% $5 \, h^{-1}$ for the 10 and 80 cm thalli, respectively. Overall small but significant differences in removal rates were influenced by an interaction between thallus height, site and day ($F_{6,48} = 3.14$, p = 0.01; see Table S3 in the supplementary material for further details). Variation among thallus heights was largely attributed to differences in the proportion of each assay that was contained within the rubber band and unavailable to herbivores. Assays held within exclusion cages experienced limited reductions across all thallus heights (4.2 to 6.6% $5 \, h^{-1}$).

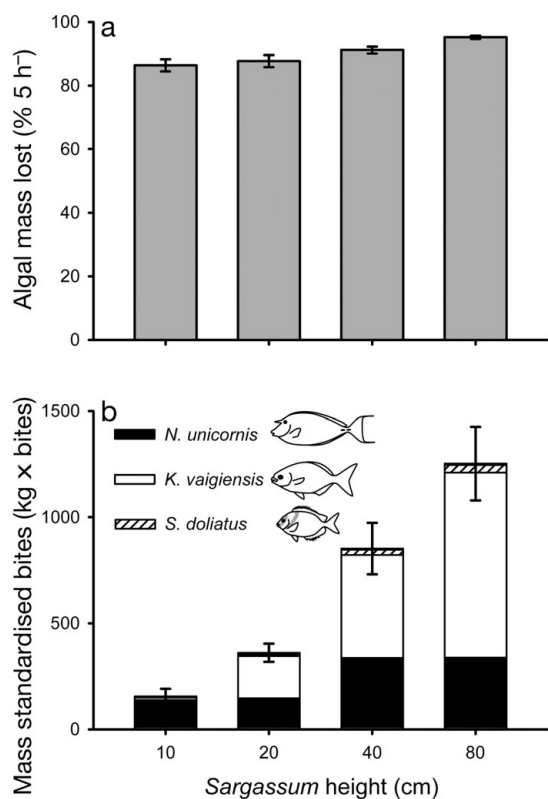Feeding on the assays was dominated by *Naso unicornis* and *Kyphosus vaigeinsis*, which accounted for

Fig. 1. Influence of *Sargassum polycystum* height on feeding by herbivorous fishes. (a) Variation in the removal rates of algal biomass among *S. polycystum thalli* of varying heights. (b) Mean number of mass-standardized bites taken by all species from the assays. Mass-standardized bites are the product of fish body mass and number of bites taken by each individual fish. The relative contributions of the 3 dominant species are shown. Another 15 species included in the figure are not distinguishable as collectively they accounted for <0.9% of all bites. Error bars are ±SE
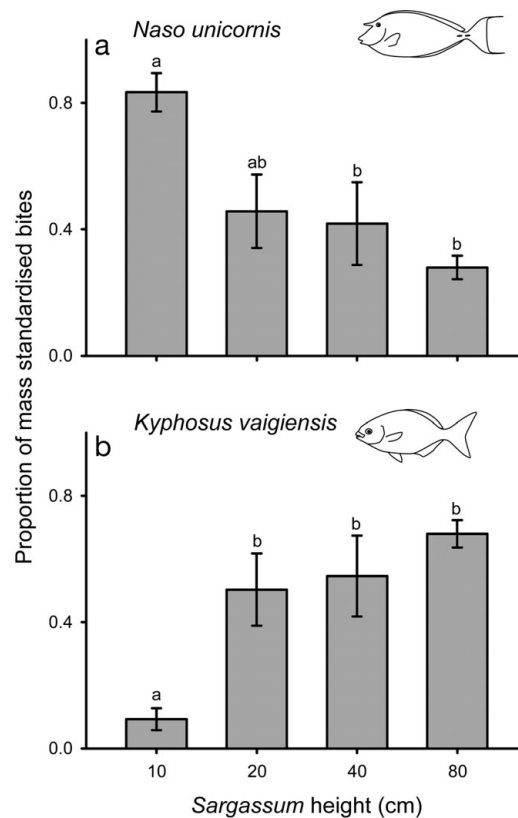

Fig. 2. Proportion of mass-standardized bites taken from *Sargassum polycystum* assays of varying heights by (a) *Naso unicornis* and (b) *Kyphosus vaigiensis.* Means are based on 6 assays of each height. Letters above each bar indicate homogenous groups identified by Tukey's Honestly Significant Difference post hoc analyses. Error bars are ±SE

36.5 and 59.8% of all mass standardized bites, respectively (Fig. 1b). Of the remaining bites, *Siganus doliatus* accounted for 2.7%, while collectively another 15 species accounted for less than 0.9%. *K. vaigiensis*, *N. unicornis* and *S. doliatus* all arrived at the experimental sites within the first 10 min of each deployment and were recorded feeding on assays of all heights; however, their relative contributions differed among thallus heights (MANOVA, $F_{9,34}$ = 2.43, p = 0.028). *N. unicornis* accounted for 83.4% of all mass-standardized bites taken from the 10 cm assays, compared to only 27.9% for the 80 cm assays (Fig. 2a). In contrast, *K. vaigiensis* accounted for a significantly lower proportion of bites from the 10 cm assays (9.3% $5\,h^{-1}$) than the taller assays (50.3 to 68.0% $5\,h^{-1}$; Fig. 2b). Feeding by *S. doliatus* displayed little variation among thallus heights (2.1 to 3.4% $5\,h^{-1}$). These patterns were supported by a resource selection ratio (see Fig. S2 in the supplementary material for details).

DISCUSSION

The recorded removal rates of *Sargassum polycystum* suggested algal height had a negligible influence on browsing intensity, at least across the range and scales examined. There was, however, marked variation in the species responsible for removing *S. polycystum* biomass from assays of varying heights. This variation was primarily driven by a transition from the shortest (10 cm) to the taller (20 to 80 cm) assays, with *Naso unicornis* being almost solely responsible for removing algal biomass from the shortest assays. In contrast, *Kyphosus vaigiensis* appeared to avoid the shortest assays, yet accounted for over half of all bites recorded on the taller assays. This transition may be related to variation in the defenses of the alga. Interspecific and ontogenetic variation in the chemical and morphological defenses of macroalgae has frequently been related to their susceptibility to herbivores (Paul & Hay 1986, Van Alstyne et al. 2001). While this cannot be discounted as a potential mechanism, Steinberg et al. (1991) demonstrated that grazing on 11 species

of *Sargassum* on the GBR was not related to their physical or chemical composition. Alternatively, the recorded variation may be related to differences in the foraging behaviour of the 2 herbivore species. *N. unicornis* is a benthic forager, whereas kyphosids tend to forage higher in the water column, where they often feed on floating *Sargassum* (Paddack et al. 2006). Marked increases in the removal of fucalean macroalgae when suspended above the substratum have been attributed to kyphosids on both tropical (Littler et al. 1983) and temperate reefs (Vanderklift et al. 2009). Therefore, the foraging behaviour of kyphosids is likely to reduce their ability to detect, and subsequently consume, small benthic algae.

Naso unicornis has been reported to be the dominant browser of *Sargassum* on mid-shelf reefs of the GBR (Hoey & Bellwood 2009); however, the present study is the first to report significant feeding by *N. unicornis* on inner-shelf reefs of the GBR. Previous studies at Orpheus Island have reported *Siganus canaliculatus* and *Kyphosus vaigiensis* to be the dominant browsers of moderate to large *Sargassum* thalli (ca. 50 to 300 g; Mantyka & Bellwood 2007, Cvitanovic & Bellwood 2009). The lack of feeding by *N. unicornis* in these studies may be related to the size, or apparency, of the assays. Furthermore, the presentation of large stands of *Sargassum* (5.3 to 8.1 kg m^{-2}) on the same reef yielded yet another response, with *Platax pinnatus* removing most of the algal mass (Bellwood et al. 2006) and suggesting the physical structure of the 3 m high canopy of *Sargassum* may have influenced herbivore foraging decisions. While it is difficult to isolate the effect of algal size from other factors such as temporal variation among studies, or the relative palatability of the algae (see Hoey & Bellwood 2009 for discussion of these factors), the height, or developmental stage, of the *Sargassum* appears to influence the response of the herbivore community on this reef.

Size has often been related to the susceptibility of plants to herbivores, with increasing size related to a transition in susceptibility from grazing to browsing taxa. While a diversity of grazing herbivores appear capable of removing macroalgal propagules, the removal of larger macroalgae appears to be restricted to a small suite of browsing species (Bellwood et al. 2006, Hoey & Bellwood 2009). Even within this group there appears to be a shift in the relative importance of each species with algal size and density. This transition not only highlights the potential role of these species at varying stages of algal succession and reef degradation, but also the importance of species richness in maintaining ecological function on these reefs. Understanding the impact of individual herbivorous taxa, and how they vary among stages of algal succession, are therefore critical to understanding the resilience and future trajectories of coral reefs.

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