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REPORT

Remote video bioassays reveal the potential feeding impact of the rabbitfish *Siganus canaliculatus* (f: Siganidae) on an inner-shelf reef of the Great Barrier Reef

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Abstract Herbivores are widely acknowledged as key elements maintaining the health and resilience of terrestrial and aquatic ecosystems. Understanding and quantifying the impact of herbivores in ecosystems are fundamental to our ability to manage these systems. The traditional method of quantifying the impact of herbivorous fishes on coral reefs has been to use transplanted pieces of seagrass or algae as "bioassays". However, these experiments leave a key question unanswered, namely: Which species are responsible for the impact being quantified? This study revisits the use of bioassays and tested the assumption that the visual abundance of species reflects their role in the removal of assay material. Using remote video cameras to film removal of assay material on an inner-shelf reef of the Great Barrier Reef, the species responsible for assay-based herbivory were identified. The video footage revealed that *Siganus canaliculatus*, a species not previously recorded at the study site, was primarily responsible for removal of macroalgal biomass. The average percentage decrease in thallus length of whole plants of *Sargassum* at the reef crest was 54 ± 8.9% (mean ± SE), and 50.4 ± 9.8% for individually presented *Sargassum* strands (for a 4.5-h deployment). Of the 14,656 bites taken from *Sargassum* plants and strands across all reef zones, nearly half (6,784 bites or 46%) were taken by *S. canaliculatus*, with the majority of the remainder attributable to *Siganus doliatus*. However, multiple regression analysis demonstrated that only the bites of *S. canaliculatus* were removing macroalgal biomass. The results indicate that, even with detailed observations, the species of herbivore that may be responsible for maintaining benthic community structure can go unnoticed. Some of our fundamental ideas of the relative importance of individual species in ecosystem processes may be in need of re-evaluation.

Keywords Herbivory · Macroalgae · Bioassays · *Siganus canaliculatus* · Coral reef · Phase-shift

Introduction

Herbivores are widely acknowledged as a key element in determining the structure and resilience of terrestrial (McNaughton et al.1997; Frank et al. 2002) and aquatic (Steneck et al. 1991; Burkepile and Hay 2006) ecosystems. Understanding and quantifying the impact of herbivores on their ecosystem are therefore fundamental to our ability to devise strategies for protecting these ecosystems (Feeley and Terborgh 2005; Hughes et al. 2005, 2007; Mumby et al. 2006). Within coral reef ecosystems the removal of herbivores through over-fishing, particularly in the Caribbean, and the subsequent degradation of those reefs has highlighted the importance of the role that the group plays in determining benthic community succession and maintaining a healthy balance between corals and macroalgae (Hughes 1994; McClanahan et al. 2003; Bellwood et al. 2004; Mumby et al. 2006). Protection and management of the health of coral reefs into the future will require an understanding of the impact (both realized and potential) of individual species of herbivore on the benthic community.

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Within the field of coral reef ecology, methods of quantifying the impact of herbivores have tended to concentrate around the measurement of the overall impact of the trophic group, rather than its individual functional components (highlighted by Choat 1991). For example, a large number of experiments have been conducted to assess the impact of herbivores on the benthic community using transplanted pieces of seagrass or algal material (see review by Littler and Littler 2007). These bioassays have been used as a metric for the intensity of herbivory across reef gradients (e.g. Lewis and Wainwright 1985; McClanahan et al. 1994; Lapointe et al. 2004) or as a means of demonstrating the role of herbivores in determining zonation patterns of macroalgae and seagrasses (e.g. Randall 1965; Hay 1981; Lewis 1985; McCook 1996). In the majority of these experiments, the identity of those species of herbivore responsible for the removal of assay material was either not considered critical (Reinthal and Macintyre 1994) or assumed to be in proportion to their relative abundance in visual censuses of the study area. The problems with such an approach are twofold. Firstly, it offers no guarantee that what is being measured as herbivory is representative of feeding by the whole guild. For example, Sluka and Miller (2001) used assays of the seagrass *Thalassia* to assess levels of herbivory across reefs in the Indian Ocean and found that consumption rates corresponded only with abundance of parrotfishes (Labridae), rather than overall herbivore abundance (see also Steneck 1983). Second, and more importantly in terms of our understanding of ecosystem processes, the inability to attribute assay removal to particular species overlooks the potential variety of functional roles played by different parts of the herbivore guild. The bioassay experiments therefore leave a key question about herbivory unanswered: which species or species are responsible for the herbivory being quantified?

The aim of this study was to revisit the use of bioassays as a means of quantifying herbivory and test the traditional assumption that the observed numerical abundance of herbivorous species equates to their role in rates of bioassay removal. To do this, a range of algal and seagrass assays commonly used in the literature were tested as a means of recording the intensity of herbivory across a reef gradient. Remote underwater video cameras were used to simultaneously film the removal of assay material in order to identify the species responsible for the herbivory being quantified by the bioassays.

Materials and methods

The study was conducted in December 2005 at Orpheus Island, Great Barrier Reef (GBR) (18°35′ S, 146°20′ E). Pioneer Bay, on the leeward side of the island, displays a well-developed fringing reef, characteristic of the inner-shelf reefs of the GBR. An extensive reef flat stretches approximately 150 m from the shoreline out to the reef crest. From there, the reef gradually slopes down to approximately 20 m. The reef displays five distinct zones running parallel to the shoreline which are defined by changes in benthic composition moving from macroalgal dominance (*Sargassum* and *Padina*) closest to shore to coral dominance and absence of macroalgae at the reef crest and down the reef slope (see Fox and Bellwood 2007 for details of percentage benthic composition across the depth gradient). The five zones are: inner reef flat, mid reef flat, outer reef flat, reef crest and reef slope. Two sites within Pioneer Bay were selected for the study where these zones were clearly delineated.

Fish species included in the study were herbivorous and “nominally” herbivorous (*sensu* Choat et al. 2002) members of the families Labridae (parrotfishes), Acanthuridae, Siganidae and Kyphosidae. Measures of herbivore abundance were obtained using underwater visual censuses (data taken from Fox and Bellwood 2007). Six censuses were conducted in each of the five zones at the two sites ($n = 60$). To minimize disturbance, censuses were based on 5-min timed swims along a 5-m-wide transect. Fishes were recorded by size class (5–7.5 cm, 7.5–10 cm, then in 5-cm intervals to 30 cm and >30 cm. Individuals less than 5 cm were not recorded). Abundances were standardized to a 250-m^2 area by measuring swum distances, and abundances converted to biomass using published length–weight relationships (Kulbicki et al. 2005).

The assays used in this study, arrangement on the reef and methods of attachment to the reef were all deliberately selected to mirror methods used in previous assay experiments. Blades of seagrass, *Thalassia hemprichii*, approximately 7 cm in length were collected from the reef, measured, photographed and placed within labelled clothes pegs (following Hay 1981). Strands of the phaeophyte *Sargassum* were similarly measured and photographed. Whole plants of the phaeophytes *Sargassum* and *Padina* attached to small pieces of dead coral and loose rock were also collected from the reef, photographed and the longest thallus measured as a proxy for overall plant size. Three blades of *T. hemprichii* and two individual strands of *Saragssum* were attached by means of the clothes pegs to a 70-cm length of fishing line laid across the reef substratum using the pegs. Three blades of *T. hemprichii* and two strands of *Sargassum* were also attached to a 70-cm length of fishing line oriented vertically in the water column using a small float, in order to determine if height from the substratum would affect feeding by different species of herbivore. One *Sargassum* plant and one *Padina* plant each still attached to reef substrata were placed adjacent to the fishing lines in order to determine whether a natural presentation of macroalgae would elicit a different feeding response to the artificial presentation on a fishing line. Assays were set out in identical arrangements across the five reef zones.

Assays were deployed for 4.5-h periods, from 06:30 to 11:00 h and from 13:30 to 18:00 h. These times were selected to represent equal periods over the "morning" and "afternoon" that encompassed most of the herbivore feeding day. All assays were filmed simultaneously in all zones using remotely deployed video cameras (Sony DCR-TRV950E in Amphibico 950 housings on weighted tripods). After each 4.5-h period, the seagrass and algal material were collected, re-measured and re-photographed. Grazing intensity was calculated in terms of the percentage decrease in blade or strand length (following Lewis 1986; Hay 1981; Hay et al. 1983; Lewis and Wainwright 1985; Reinthal and Macintyre 1994). The procedure was repeated in all five reef zones over 6 days (3 days at each site). Each deployment was at a different location within the site, giving a total of three independent replicates at each time of day in each zone at each site ($n = 60$), and a total of 270 h of video footage.

From the footage, the number of bites taken from each type of assay and the species identity and size class of the herbivores taking those bites were noted (classes as above). In most cases, fishes made successive bites off the algal material without discernable intervals; therefore, bites taken were conservatively recorded in terms of the number of forays, with a single foray taken as one bite (following Bellwood and Choat 1990; McClanahan et al. 1999).

Data analysis

Percentage decreases in length of *T. hemprichii* blades and *Sargassum* strands were analysed using a four-way ANOVA, with site, zone, time of day (morning or afternoon) and orientation (horizontal or vertical) treated as fixed factors. In all cases data were $\log(x + 1)$ transformed to meet ANOVA assumptions of normality and homoscedasticity. Percentage decreases in thallus length of the whole plant assays of *Sargassum* and *Padina* were analysed using a three-way ANOVA with site, zone and time of day treated as fixed factors. Again, data were $\log(x + 1)$ transformed to meet ANOVA assumptions. Where no interaction between factors was observed, data were pooled at the zone level for presentation. Post hoc multiple comparisons of means were performed using the Student–Newman–Keuls test.

The pattern of feeding and relative contributions to removal of algal material of the two predominant species observed feeding on the *Sargassum* assays were assessed using a one-way ANOVA and simultaneous multiple regression analysis, respectively. For whole *Sargassum* plants and strands, in turn, the number of bites taken by each species of siganid was adjusted for variation in body size (x 1 for large, x 0.3 for medium, x 0.02 for small individuals; relative bite sizes were taken from Fox and Bellwood 2007). All bites taken by *S. canaliculatus* were by large (>20 cm) individuals and therefore did not require adjustment. The number of (size adjusted) bites taken by each species between reef zones was analysed via a one-way ANOVA. Data were $\log(x + 1)$ transformed to meet assumptions of normality and homoscedasticity. Post hoc comparisons of means were performed using the Student–Newman–Keuls test. The number of (size adjusted) bites taken by the two species was then regressed against the proportional decrease in length of the *Sargassum* plant or the proportional decrease in length of the detached *Sargassum* strands.

Feeding behaviour of the two species in terms of the total number of bites taken from the assays and the number taken directly from the benthic substratum within the 1-m^2 experimental area were compared using a two-way ANOVA, with zone and bite location (assay versus substratum) as fixed factors. Data were $\log(x + 1)$ transformed in order to meet ANOVA assumptions of normality and homoscedasticity.

Results

The seagrass *T. hemprichii* showed very low rates of removal by herbivores across all reef zones, ranging from just 1.2 ± 0.4% (mean ± SE) decrease in blade length over 4.5 h on the mid flat to 6.0 ± 1.9% at the reef crest. There was no clear pattern of statistical difference in removal rates among zones (Fig. 1a), although the crest had higher removal rates than the mid flat. The brown alga *Padina* proved to be a slightly better indicator of levels of herbivory across the reef gradient, with reductions in thallus length during the 4.5-h deployment period ranging from 2.5 ± 2.4% at the mid reef flat to 33.0 ± 11.0% at the reef crest (Fig. 1b). However, there was still broad overlap among zones with only the crest and inner flat exhibiting statistically significant differences in removal rates. Rates of removal of *Sargassum* showed the clearest differentiation in levels of herbivory across the reef gradient. In the case of both whole plants and strands, highest removal rates were again observed at the reef crest, with the whole plants showing an average 54 ± 8.9% decrease in thallus length and the strands an average 50.4 ± 9.8% decrease over 4.5 h (Fig. 1c, d). No significant difference was observed between removal rates of *Sargassum* presented as whole plants or strands. With the exception of

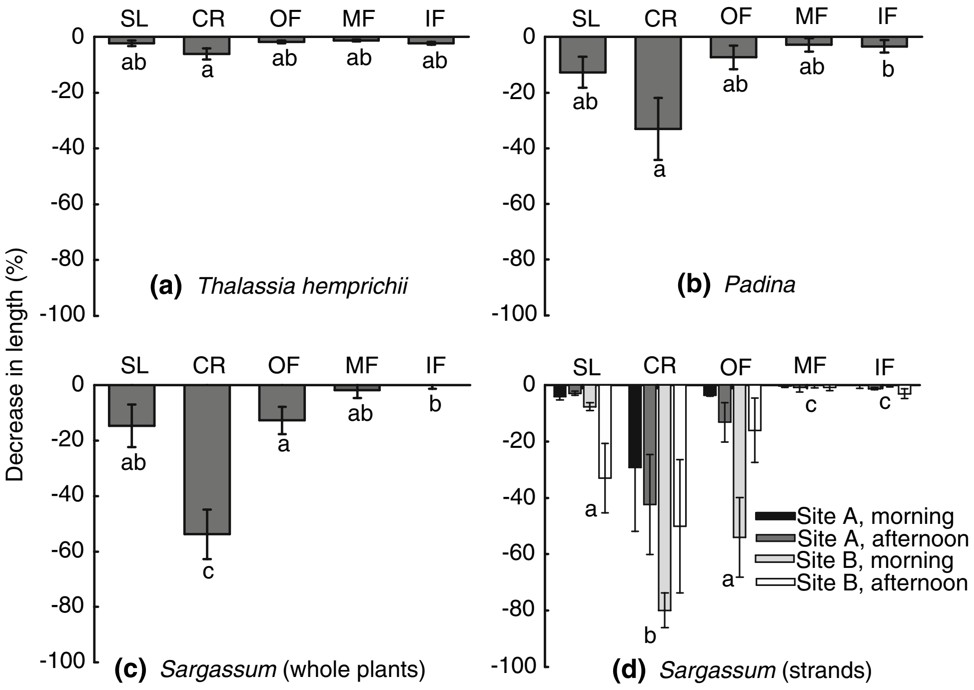

Fig. 1 Consumption of bioassays by roving herbivores in Pioneer Bay (**a**) *Thalassia hemprichii* blades (**b**) *Padina* (**c**) *Sargassum* whole plant and (**d**) *Sargassum* suspended strands. Consumption shown as mean percentage decrease in blade/thallus length over 4.5-h deployment period (±SE) in each of five reef zones: Slope (SL), Crest (CR), Outer reef flat (OF), Mid reef flat (MF) and Inner reef flat (IF). Homogeneous subsets (SNK) are indicated with letters

Sargassum strands (where there was a significant site, zone and time of day interaction), all ANOVAs revealed no significant site, time of day or orientation effects, nor any significant interaction terms but all zone comparisons were significant (see Electronic supplementary material, Tables SM1–4). For the whole *Sargassum* plants, the removal rates at the crest were significantly higher than in any other zone. The rates of removal of *Sargassum* whole plants and strands at the mid and inner reef flat were found to be not significantly different from zero (see Electronic supplementary material, Table SM5), and these zones were therefore not included in subsequent analyses.

The species of herbivores responsible for removal of the *Sargassum* plant material at the reef crest, slope and outer flat as revealed by the video were not predictable from the distribution of species observed during visual censuses (Fig. 2). Across the reef gradient, the biomass of roving herbivores recorded by divers was overwhelmingly dominated by three species, the parrotfishes *Scarus rivulatus* and *Chlorurus microrhinos* and the siganid *Siganus doliatus* (Fig. 2b). At the reef crest, where the rate of bioassay removal was greatest, these three species made up 89 ± 2.8% (mean ± SE) of the total herbivore biomass. However, of the 14,656 bites taken from *Sargassum* plants and strands across all reef zones, nearly half (6,784 bites or 46%) were attributable to *Siganus canaliculatus*, a species not recorded during visual censuses (Fig. 2c). (Species identification follows Randall et al. 1997; possible synonyms include *Siganus fuscecens* and *Siganus margaritiferus* (Kuiter and Debelius 2001).) Just one other species (the visually dominant *S. doliatus*) accounted for the majority of the remaining 54% of bites taken from *Sargassum* plants and strands across all reef zones (Fig. 2c). *S. doliatus* was responsible for 46.6% of the total bites taken from whole *Sargassum* plants and 56.3% of bites taken from *Sargassum* strands; *S. canaliculatus* was responsible for 49.6% of total bites taken from whole *Sargassum* plants and 42.4% of bites taken from *Sargassum* strands.

The pattern of (size-adjusted) bites taken by the two dominant *Sargassum* feeders, *S. doliatus* and *S. canaliculatus* was examined in greater detail to determine patterns of feeding across the reef depth gradient and the relative impact of the two species on actual removal of macroalgal material. Significant variation in the feeding pattern of the two species was observed across the reef gradient (Figs. 3, 4). In the case of the whole *Sargassum* plant assays, no significant difference was observed in the number of (size-adjusted) bites ($\log(x + 1)$ transformed) taken by *S. doliatus* across the three reef zones (Fig. 3). In contrast, the impact of *S. canaliculatus* was concentrated on the reef crest, with a significantly different number of bites ($\log(x + 1)$ transformed) observed across the reef gradient (ANOVA, $F_{(2,33)} = 5.838$, $P < 0.05$), mirroring the observed differences in rates of removal of algal material across that same gradient (Fig. 3).

Significant variation in the feeding pattern of the two species was also observed in terms of bites taken from the *Sargassum* strands (Fig. 4). In this case, a significant difference was observed in the number of (size-adjusted) bites ($\log(x + 1)$ transformed) taken by *S. doliatus* across the three reef zones (ANOVA, $F_{(2,33)} = 8.974$, $P < 0.05$).

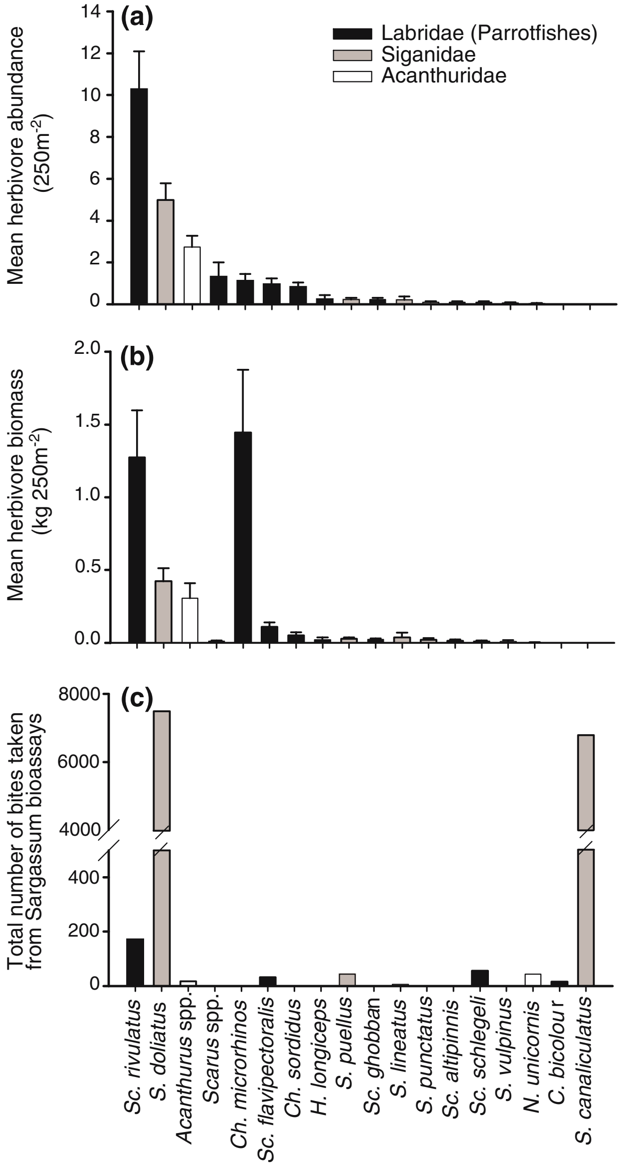

Fig. 2 (**a**) Abundance (mean ± SE) and (**b**) Biomass (mean ± SE) of individual species of roving herbivore within Pioneer Bay shown against (**c**) the total number of bites taken from all *Sargassum* bioassays within the experimental plot (whole plants, horizontal and vertical strands) by each species. To overcome problems of identification, species of acanthurid were grouped at the genus level (*Acanthurus* spp.) and juvenile parrotfish less than 10 cm in length were grouped into the category juvenile *Scarus* spp. *Abbreviations*: *Sc.—Scarus*, *S.—Siganus*, *Ch.—Chlorurus*, *H.—Hipposcarus*, *N.—Naso*, *C.—Cetoscarus*

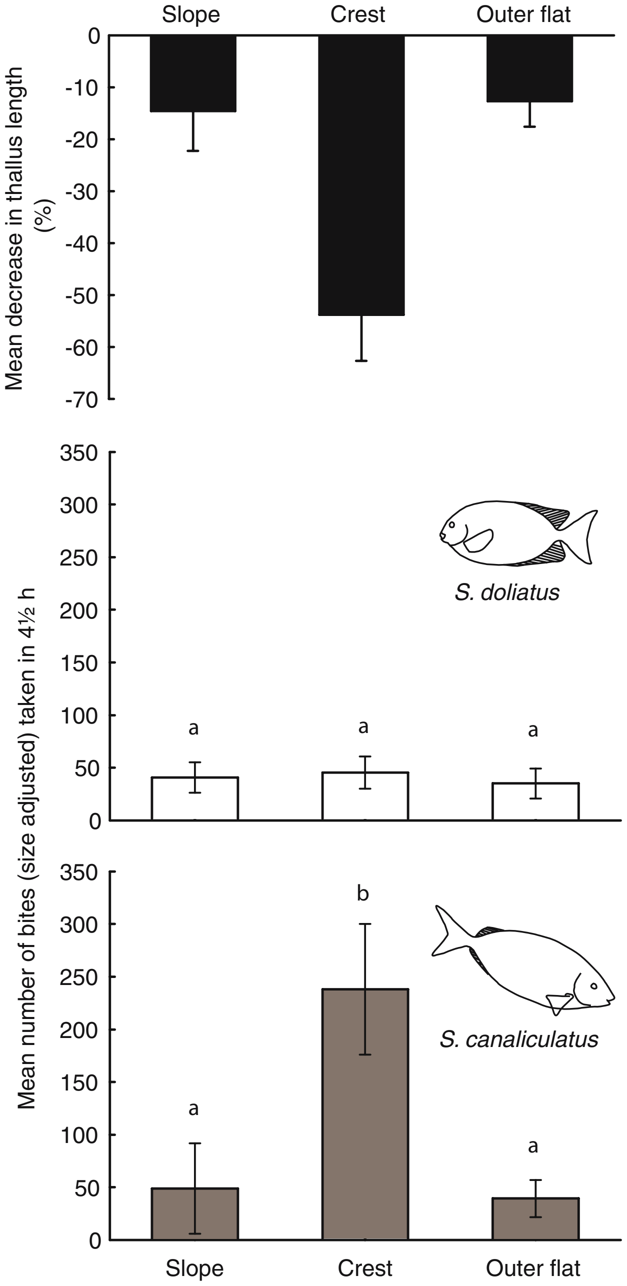

Fig. 3 Pattern of percentage decrease in thallus length of whole plants of *Sargassum* (mean ± SE) across reef zones in relation to the number of (size-adjusted) bites (mean ± SE) taken from the whole *Sargassum* plant in each experimental plot during the 4.5-h deployment period by *Siganus doliatus* and *Siganus canaliculatus*. Homogeneous subsets (SNK) are indicated with letters

However, the zone for which a significantly greater number of bites was observed (SNK) was the reef slope, where levels of removal of *Sargassum* strands were the lowest (Fig. 4). Once again, a significant difference in the number of bites (log($x + 1$) transformed) taken by *S. canaliculatus* across the reef gradient was observed (ANOVA, $F_{(2,33)} = 4.842$, $P < 0.05$), with this species having a high bite rate on the reef crest where observed rates of removal of *Sargassum* strands were the highest (Fig. 4).

The results of simultaneous multiple regression analysis of (size-adjusted) bites taken by *S. doliatus* and *S. canaliculatus* showed that although the overall model was significant in explaining reduction in thallus length of whole *Saragssum* plants (ANOVA, $F_{(2,33)} = 51.029$,

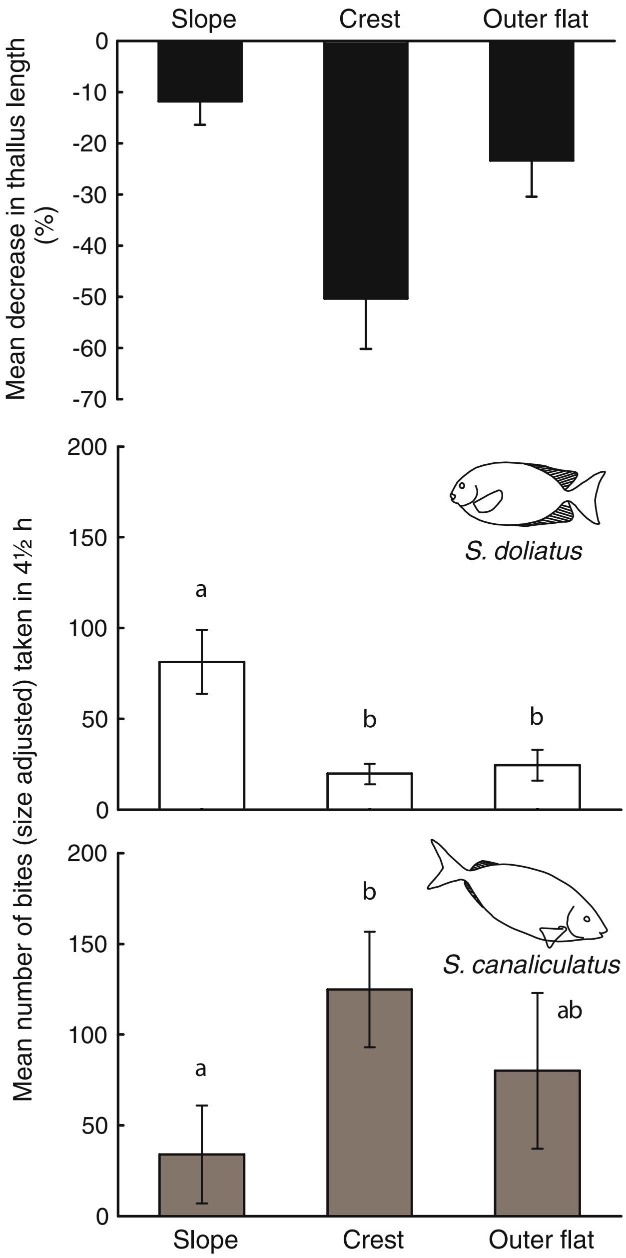

Fig. 4 Pattern of percentage decrease in thallus length of strands of *Sargassum* (mean ± SE) across reef zones in relation to the number of (size-adjusted) bites (mean ± SE) taken from all horizontal and vertical *Sargassum* strands in an experimental plot during the 4.5-h deployment period by *Siganus doliatus* and *Siganus canaliculatus*. Homogeneous subsets (SNK) are indicated with letters

$P < 0.05$, $R^2 = 0.76$), bites taken by *S. doliatus* were not significant in causing reduction in the length of the thallus (Table 1). In fact, there was no relationship between the number of bites taken by *S. doliatus* and the rate of removal of *Sargassum* (Fig. 5a). Bites taken by *S. canaliculatus*, in contrast, had a significant impact in reducing the length of the *Sargassum* thallus (Table 1), and a significant, positive relationship was observed between the number of bites and the percentage decrease in thallus length (ANOVA, $F_{(1,34)} = 101.56$, $P < 0.05$, $R^2 = 0.75$) (Fig. 5b).

Table 1 Results of simultaneous multiple regression analysis of the influence of bites by *Siganus doliatus* and *Siganus canaliculatus* on thallus length of *Sargassum* sp. plants

	B	Standard error of *B*	$t_{(33)}$	*P*
Intercept	**14.737**	3.734	3.947	<0.0001
S. canaliculatus	**0.145**	0.015	9.936	<0.0001
S. doliatus	−0.049	0.052	−0.935	0.357

Coefficients highlighted in bold are significant at the 0.05 level

Similar results were obtained from examination of the impact of the bites of these two species on thallus length of the individual *Sargassum* strands. The overall model was significant in explaining reduction in thallus length (ANOVA, $F_{(2,33)} = 28.99$, $P < 0.05$, $R^2 = 0.64$), but the coefficient term of *S. doliatus* was negative, suggesting that bites by this species were actually causing an increase in algal thallus length (Table 2) and a significant, negative relationship was observed between the number of bites taken by *S. doliatus* and removal of *Sargassum* (ANOVA, $F_{(1,34)} = 5.711$, $P < 0.05$, $R^2 = 0.14$) (Fig. 6a). Bites taken by *S. canaliculatus*, on the other hand, had a significant impact in reducing the length of the *Sargassum* thallus (Table 2), and a significant, positive relationship was observed between the number of bites taken by this species and the percentage decrease in thallus length (ANOVA, $F_{(1,34)} = 45.928$, $P < 0.05$, $R^2 = 0.5746$) (Fig. 6b).

The feeding behaviour of the two species also differed in terms of the proportion of bites taken from the algal bioassays (*Sargassum* and *Padina*) versus bites taken off the reef substratum within the 1-m^2 experimental area. *S. doliatus* was observed taking similar numbers of bites from the algae and the natural reef substratum around the assays (Fig. 7a). Within-zone comparisons of the number of bites of each type taken were all non-significant at the 0.05 level (Mann–Whitney U tests). *S. canaliculatus*, on the other hand, was observed taking bites almost exclusively from the macroalgal assays (*Sargassum* and *Padina*), and differences in the observed number of bites taken from assays and natural substratum were statistically significant at the crest (Mann–Whitney U, $Z = -2.995$, $P < 0.05$) and outer reef flat (Mann–Whitney U, $Z = -3.384$, $P < 0.05$) (Fig. 7b).

Discussion

The recorded removal rates of *Sargassum* bioassays suggested a strong gradient in herbivory across the reef, with a

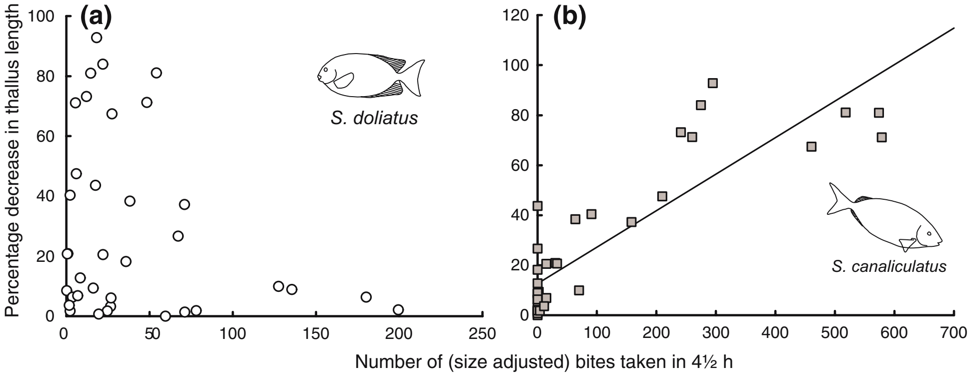

Fig. 5 Relationship between the total number of bites taken by (**a**) *Siganus doliatus* (not significant) and (**b**) *Siganus canaliculatus* (ANOVA $F_{(1,34)} = 101.56$, $P < 0.05$, $R^2 = 0.75$) and the percentage decrease in thallus length of the whole *Sargassum* plant within each experimental plot during the 4.5-h deployment period

Table 2 Results of simultaneous multiple regression analysis of the influence of bites by *Siganus doliatus* and *Siganus canaliculatus* on thallus length of *Sargassum* sp. strands

	B	Standard error of *B*	$t_{(33)}$	*P*
Intercept	**23.429**	5.714	4.099	<0.0001
S. canaliculatus	**0.168**	0.027	6.199	<0.0001
S. doliatus	**−0.083**	0.035	−2.388	0.023

Coefficients highlighted in bold are significant at the 0.05 level

significantly higher rate of herbivory, as proxied by the assays, recorded on the crest and insignificant levels on the mid and inner reef flat. Traditionally, the assumption would be that consumption of the transplanted algae was by the dominant species of herbivores observed during visual censuses of these areas, i.e. that presence equated to function (Nelson and Tsutsui 1981; Reinthal and Macintyre 1994; cf. Bellwood et al. 2006). However, the remote video recordings showed that the species responsible for consumption of the macroalgal assays was one that had not been observed in any of the 60 visual censuses of the study site. Indeed, *S. canaliculatus* has not previously been recorded in visual censuses from this location, despite several decades of research activity. Over the slope, crest and outer reef flat, an average density of 6.1 individuals $m^{-2}\ h^{-1}$ was recorded during the current study. The implications of these results are clear; it cannot be assumed that the herbivores we see are the ones that are responsible for the removal of macroalgae, and the observed numerical abundance of herbivorous species does not necessarily equate to their role in rates of bioassay removal.

Almost as significant as the identity of the species responsible for the macroalgal removal at the reef slope, crest and outer reef flat, is the question of why the same macroalgae resources that were consumed at the reef crest were left virtually untouched on the inner and mid reef flat. The videos revealed that the *Sargassum* plants and strands at the shoreward zones were subject only to bites by juvenile (0–5 cm) scarids, siganids and acanthurids and by pomacentrids. The insignificant decreases in thallus length recorded as a result of these bites make it likely that these fishes were primarily targeting epiphytes attached to the macroalgae. Whether the bites by these juvenile herbivores are able to control the standing crop of macroalgae in the shoreward zones remains to be determined. Indeed it is possible that their feeding activity, in removing epiphytes, may enhance macroalgal growth and longevity.

The low levels of herbivory in terms of decrease in macroalgal thallus length recorded at the two shoreward zones were characteristic of rates observed at the inner and mid reef flat via remote video under natural conditions (no assays present) at the same study site (Fox and Bellwood in press). What the bioassays demonstrated was that the macroalgae itself is a potentially attractive food resource for *S. canaliculatus*, meaning that the low rates of removal

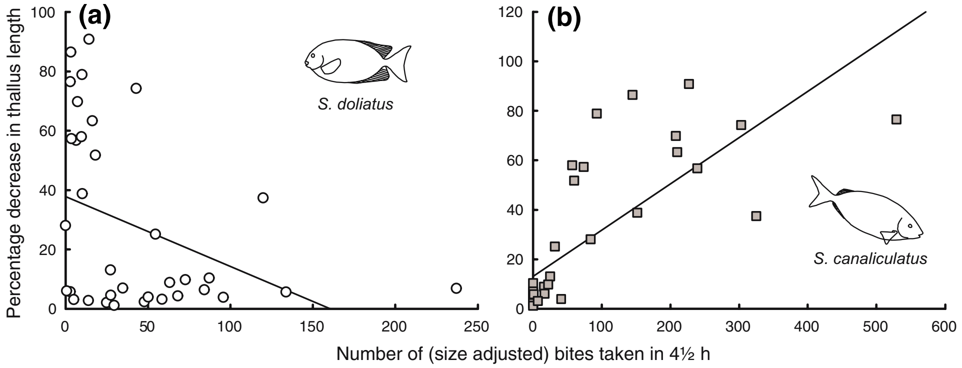

Fig. 6 Relationship between the total number of bites taken by (**a**) *Siganus doliatus* (ANOVA, $F_{(1,34)} = 5.711$, $P = < 0.05$, $R^2 = 0.14$) and (**b**) *Siganus canaliculatus* (ANOVA, $F_{(1,34)} = 45.928$, $P < 0.05$, $R^2 = 0.58$) from all *Sargassum* strands within an experimental plot and the mean percentage decrease in thallus length of all *Sargassum* strands within each 4.5-h deployment period

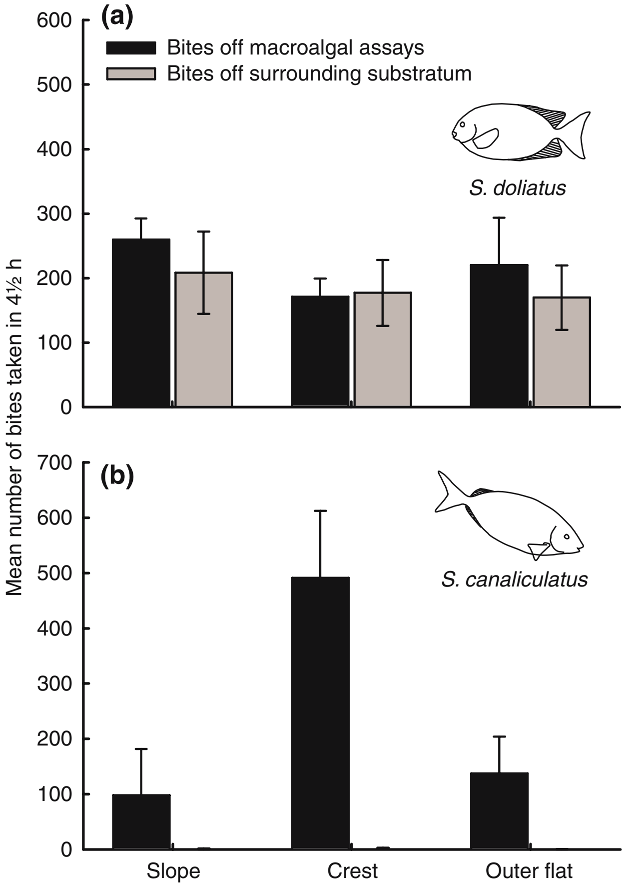

Fig. 7 Number of bites (mean ± SE) taken by (**a**) *Siganus doliatus* and (**b**) *Siganus canaliculatus* from all macroalgal assays (*Sargassum* and *Padina*) within each 4.5-h deployment period compared with the number of bites (mean ± SE) taken during the same period from the reef substratum surrounding the assays

at the mid and inner reef flat are being driven by factors relating to the habitats themselves. This suggests that low rates of herbivory in the shoreward zones are driven by a mixture of biological (e.g. risk of predation) and physical (e.g. tidal inundation) factors (see Fox and Bellwood 2007 for a full discussion of such factors in relation to the study site). Moving the macroalgae out to the reef crest had the effect of making a potential food target more attractive by situating it in a less risky or more accessible habitat. Alternatively, the macroalgae positioned at the reef crest may simply have been made more attractive by virtue of it being a novel food item within that particular habitat. However, the fact that other species of roving herbivore within Pioneer Bay were observed taking so few (or zero) bites from the macroalgal assays (although they can exhibit strong preferences for other macroalgal species; Mantyka and Bellwood 2007a, b) makes the latter explanation unlikely.

Schools of up to 15 *S. canaliculatus* were recorded feeding on macroalgal bioassays on the reef slope, crest and outer reef flat, while assays deployed just 25 m away at the mid and inner reef flat were left untouched. This raises questions about the feeding behaviour and habitat of *S. canaliculatus*. Although the demographic characteristics of *S. canaliculatus* have been documented (Grandcourt et al. 2007), relatively little information exists on the trophic ecology of the species. Previous stomach content analyses suggested that it feeds on *Enteromorpha* (von Westernhagen 1973), while its gut enzymes have been shown to be capable of breaking down laminarin, one of the storage polysaccharides in brown algae (Sabapathy and Teo 1995). *S. canaliculatus* tissues also possess unusually high levels of $n-6$ polyunsaturated fatty acids, which occur in high amounts in macroalgae (Saito et al. 1999). Field observations record it feeding on a range of green and brown algae, although *Sargassum* may predominate (von Westernhagen 1973; Mantyka and Bellwood 2007a, b). In the current study, *S. canaliculatus* took bites almost exclusively from the algal assays rather than from the reef substrate around the assay, suggesting that fishes were actually targeting the macroalgae. *S. canaliculatus* therefore appears to be a macroalgal feeder. This selectivity was significant in comparison with the observed feeding behaviour of *S. doliatus* which took approximately equal numbers of bites from the macroalgal assays and reef substratum. Whilst differences in dietary preferences between siganids have been recognized previously in the literature (e.g. Tsuda and Bryan 1973; Bryan 1975; Lundberg and Lipkin 1979; Pillans et al. 2004), the significance of these differences for reef systems has not been fully explored.

The bioassays used in this study effectively allowed the simulation of grazing conditions on a reef facing increased macroalgal abundance (as seen in reefs experiencing a phase shift; Bellwood et al. 2004; Mumby et al. 2006; Hughes et al. 2007). In the process they revealed, albeit in an artificial bioassay setting, that siganids may play a crucial functional role in restoring the balance between corals and algae. The failure of reefs to recover following coral bleaching, while exhibiting a shift to macroalgal dominance (Ledlie et al. 2007), may therefore reflect the regional overharvesting of such critical functional groups (cf. Laroche and Ramananarivo 1995; Wantiez et al. 1997). Areas of the Indian and the Pacific Ocean where siganids form a high proportion of commercial and artisanal fishing catches may be eroding reef resilience and limiting future options in terms of agents of regeneration should the system undergo a shift to macroalgal dominance. The fact that the family is not present on Caribbean reefs (Choat 1991) may constitute yet another example of the absence of important functional groups from this particular region (Bellwood et al. 2004).

Siganids have been identified as important herbivores on reefs in the tropical western Pacific, where the large numbers of recruits have been linked to extensive removal of macroalgae and seagrasses on reef flats (Tsuda and Bryan 1973; Paul et al. 1990). The present study has highlighted the potential significance of the family, not so much in terms of their impact on the system under healthy conditions, but for the role they can play if the system starts to shift to one characterized by higher macroalgal biomass. Furthermore, the results emphasize the importance of evaluating functional roles at the level of individual species, given the difference in impact between bites from *S. canaliculatus* and the more delicate feeding action of *S. doliatus*, whose bites had no significant impact in reducing macroalgal thallus length. It is possible that the bites of *S. doliatus* may have instead been targeting epiphytes on the leaves of the *Sargassum*.

The limited spatial extent of the current study means that the generality of the impact of *S. canaliculatus* or functional equivalents across other reefs of the GBR cannot be assumed. In addition, the feeding response of *S. canaliculatus* reported here relates to an algal biomass level of approximately 300 g m^{-2}. The results of Bellwood et al. (2006) demonstrate that the presentation of a greater biomass of algae (5–8 kg m^{-2}) in the same location yields a very different system response, with batfishes (f: Ephippidae) removing most algal biomass. The differences are informative and suggest that, instead of a unique tipping point between coral and macroalgal dominance, there may be several intermediate stages in the process of reef degradation and that species of herbivore capable of preventing the shift to macroalgal dominance may change at each of those stages.

The results of this study have also highlighted the fact that the nature of herbivory can vary in different biogeographic regions. The low levels of seagrass removal (<6%) reported here contrast markedly with the results of similar bioassay experiments conducted on Caribbean reefs (Hay 1981, Hay et al. 1983), where rates of 50% per hour or 73–93% in 3 h have been recorded. A comparison of these rates underlines the fact that herbivory in the Caribbean and Indo-Pacific regions may reflect markedly different players and processes. In the Caribbean, *Thalassia* is consumed primarily by parrotfishes in the genus *Sparisoma* (f: Labridae) (Lewis and Wainwright 1985). This genus is not present in the Indo-Pacific (Bellwood 1994) and functional equivalents in terms of seagrass consumption (*Calotomus* and *Leptoscarus*) (Streelman et al. 2002) are relatively rare (Hoey and Bellwood 2007). The full extent of this regional variation is yet to be established.

The questions we are asking in relation to herbivory on coral reefs are changing. We are moving beyond the broad recognition that herbivores play a vital role in terms of shaping reef benthic communities to a new framework in which the absolute, quantitative nature of those interactions at the species level is acknowledged as important. Herbivores are no longer a homogenous group. It is recognized that variation in the composition of the herbivore assemblage will influence the nature and intensity of herbivore disturbance experienced by individual reefs. To understand herbivory, therefore, we have to understand the system impact of individual species of the guild in terms of feeding rates, foraging behaviour, bite size and feeding preferences. Only then can we start to understand how spatial variation in herbivore distribution might be driving variation in algal community composition and processes of benthic community succession.

The practical requirements of such an approach are considerable and time is running out. The effects of fishing are already taking their toll on herbivore biomass in many parts of the world such as Hawaii (Friedlander and DeMartini 2002); the Caribbean (Hawkins and Roberts 2004); Indonesia, Micronesia and French Polynesia (Bellwood et al. 2003). We may have already unwittingly removed the potential agents of reef rehabilitation, or reduced numbers below critical levels at which they can exert their ecological role. As far back as 1997, Hasse et al. documented anecdotal evidence that *S. canaliculatus* in Palau had undergone a precipitous population decline due to intensified fishing practices. Spawning schools that had once covered areas of 100 m^2 were, even then, reduced to areas less than 10 m^2. More recently, data on the demographic parameters of the species have suggested that populations within waters of the Arabian Gulf are being overexploited (Grandcourt et al. 2007). If this species does play a significant role in maintaining a healthy balance between corals and algae, these reductions in numbers could signal a decline in system resilience and may set the scene for the ecological surprises that can characterize phase shifts (cf. Bellwood et al. 2004).

This study has demonstrated that the importance of individual species to particular system processes may not always be apparent from underwater visual assessments by divers quantifying herbivore abundance and feeding patterns. The roles of herbivores in algal bioassay removal were not related to the distribution of species measured in visual censuses, nor were they related to the distribution of those species known to be capable of processing macroalgae such as *Naso unicornis* and *Kyphosus vaigensis* (Choat et al. 2004). The remote video recordings of the bioassays provided a window into the world of herbivory in the absence of divers. What they demonstrated is that we may have to re-examine some of our ideas of herbivory on coral reefs. For example, parrotfishes (f: Labridae) have been widely recognized as a key component of the coral reef herbivore community in terms of their impact on the ecosystem as grazers and bioeroders of the reef substratum (e.g. Bellwood et al. 2003, Mumby et al. 2006). Whilst this is the case under natural grazing conditions (Bellwood et al. 2006, Fox and Bellwood 2007), the bioassays revealed the potential inability of this key group to play a significant role in macroalgal removal.

In sum, whilst bioassays may not be representative of all aspects of herbivory (i.e. background grazing by parrotfishes), they do have the potential to be extremely instructive as to the potential value of species that could go unnoticed in observations of typical grazing patterns but which might be important in maintaining a healthy balance between coral and algae should the system start to undergo a phase or regime shift. The value of bioassay deployments therefore may not be in their traditional use as a method to quantify overall levels of herbivory, but in their ability to answer specific questions about the potential resilience of a system, i.e. its ability to avoid switching to an alternate state or to reverse from a macroalgal dominated state. A methodology used as far back as 1965 (Randall) to demonstrate the overall importance of herbivores in marine ecosystems could yet prove instrumental in furthering our understanding of the balance between corals and algae on reefs and the taxa responsible for maintaining that balance.

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