Latitudinal variation in macroalgal consumption by fishes on the Great Barrier Reef

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ABSTRACT: On coral reefs, herbivory is a key factor in maintaining coral-dominated systems. Despite this, few studies have investigated the process of herbivory over broad spatial scales. We examined the patterns of herbivory across sites spanning 900 km along the Great Barrier Reef (GBR), Australia. Assays were used to directly quantify the removal rates of the brown macroalgae *Sargassum*, while feeding rates of herbivorous fishes were measured using remote underwater video. Removal rates of *Sargassum* by herbivores exhibited a significant regional decline from north to south, driven primarily by changes in the behaviour of the 4 most dominant species and to a lesser extent by a regional decline in herbivore diversity. Whilst the 4 species (*Naso unicornis*, *Kyphosus vaigiensis*, *Siganus doliatus* and *S. canaliculatus*) consistently dominated feeding, jointly accounting for 85, 99 and 98 % of mass standardised bites within the north, central and southern regions, respectively, they recorded over an order of magnitude fewer bites in the south. Interestingly, the decline in bites and the lower feeding diversity was not a result of lower herbivore biomass or density in the southern region. Rather, the major difference between fish herbivory among regions was the feeding propensity of the 4 dominant feeders toward the transplanted *Sargassum*. Reefs with intact and structurally comparable herbivore communities therefore cannot be assumed to have the same realised functional impact on the reef. Local behaviour may be an important factor.

KEY WORDS: Herbivory · Spatial scale · Phase-shift · Resilience · Coral reef

INTRODUCTION

Uncovering the role of individual species in maintaining and shaping ecological processes is among the great challenges in ecology (Turner 1989, Levin 1992). Part of the reason for the complexity of the relationship between patterns and processes is that different processes prevail as the drivers of ecosystem states at different spatial and temporal scales (Hughes et al. 1999). Small-scale experiments result in a localised understanding of how processes may operate, specific to the spatial and temporal scale of observation, but may be out of context in the broader ecological landscape (Ricklefs 1987, Eberhardt & Thomas 1991, Levin 1992). Only by understanding the dynamic role of processes and the functional groups that interact with them, at a

range of scales, can we obtain a clearer picture of the function, resilience and future trajectory of ecological systems (Chapin et al. 1997, Nyström & Folke 2001, Bellwood et al. 2004, Nyström et al. 2008).

The Great Barrier Reef (GBR), the world's largest single coral reef system, provides an ideal setting to examine the role of functional groups and ecological processes over broad spatial scales. The GBR extends over 2000 km down the east Australian coastline, from 10 to 23° S, and is considered to be one of the few remaining relatively functionally-intact coral reef systems in the world (Pandolfi et al. 2003, Bellwood et al. 2004, Wilkinson 2004). The GBR is characterised by a clear cross-continental shelf gradient in macroalgal abundance, with many inner-shelf reefs being characterised by relatively high erect macroalgal cover

(McCook et al. 1997, Done et al. 2007, Diaz-Pulido et al. 2009) compared to the low macroalgal cover of the mid- and outer shelf (Wismer et al. 2009). The abundance of macroalgae on the inner-shelf reefs has raised questions about the vulnerability of inshore reefs to a phase-shift from coral to macroalgal dominance (Done et al. 2007), mirroring observed changes in other coral reef systems around the world (Hughes 1994, McClanahan et al. 2001, Graham et al. 2006, Ledlie et al. 2007). Herbivory is an ecological interaction which is considered critical in preventing such shifts to macroalgal dominance (Done 1992, McCook 1996, Hughes et al. 2003, Mumby 2006, Hughes et al. 2007). Understanding the nature of herbivory is therefore crucial to understanding the existing functioning and future trajectory of the GBR.

Coral reef herbivory itself can be divided into one of 2 types, based on the functional grouping of the algal material consumed. The current study is focused on species which consume fleshy macroalgae (e.g. leathery or foliose algae sensu Steneck 1988) and are defined here as browsers. The second type of herbivory is by grazers, i.e. species which consume the epilithic algal matrix (EAM, sensu Wilson & Bellwood 1997). Whilst the 2 groups are not mutually exclusive, the distinction has arisen following observations that many dominant grazers, such as members of the families Labridae (parrotfishes) and Acanthuridae (surgeonfishes), have a relatively low functional impact in the removal of larger fleshy macroalgae (e.g. *Sargassum* spp.) from the reef (Bellwood et al. 2006, Fox & Bellwood 2008, Hoey & Bellwood 2009). This functional dichotomy within coral reef herbivory may have important ecological implications in macroalgae-rich systems such as the inshore reefs of the GBR.

Currently, the vast majority of herbivory studies on the GBR have been carried out at a local (single reef) scale, within just a few reefs (however, see McCook 1996 and Hoey & Bellwood 2010 for exceptions). Furthermore, studies of browsers on inshore reefs have revealed high variability in the role of species within and between studies at a local scale (Fox & Bellwood 2008, Cvitanovic & Bellwood 2009). Given such local scale variability in the relative importance of browsing species, it is currently unclear how the realised importance of browsing herbivores may change over regional scales, particularly on the southern margins of the GBR, close to the tropical–temperate convergence, where the composition of herbivore communities begins to shift (Choat 1991). By observing patterns of macroalgal removal along the length of the GBR, we can begin to uncover the drivers of herbivory at different spatial scales and thus the relative levels of resilience across the different regions to withstand or regenerate following potential shifts to macroalgal dominance.

Our goal, therefore, was to examine herbivory on fleshy macroalgae and quantify rates of removal across regional scales. To do this, we took advantage of the unique latitudinal spread of the GBR system by examining 18 sites from reefs within 3 separate regions of the inner-shelf of the GBR, spanning 900 km from 16 to 23° S. Using remote underwater video (RUV) cameras, we directly quantified the removal rates of macroalgal (*Sargassum* sp.) bioassays and the feeding rates and relative importance of individual species of herbivorous fishes within 3 inshore regions of the GBR. Furthermore, the use of RUV also provided the opportunity to examine the mechanisms driving patterns of removal such as the feeding propensity of herbivores, i.e. the proportion of fishes in the vicinity of the bioassays that feed when given the opportunity. These data provide a direct evaluation of the agents driving patterns of algal removal across regional scales and a detailed comparison of the process of macroalgal removal between different regions of the GBR.

MATERIALS AND METHODS

Study sites. The study was conducted in 3 distinct inshore regions along the GBR, Queensland, Australia. The Low Island group (16° 20′ S, 145° 33′ E), Whitsunday Island group (20° 05′ S, 148° 52′ E) and Keppel Island group (23° 10′ S, 155° 55′ E) were selected to represent north, central and southern regions, respectively. Sampling was staggered between October and December 2008, working from north to south, to coincide with the warming waters in order to minimise latitudinal gradients in temperature. Within each region, 3 fringing reefs (locations) were chosen which displayed moderate to high coral cover (>30%) and had naturally low abundances of *Sargassum* spp. on the reef crest, in order to maximise the equality of assay availability (or novelty) to herbivores among reefs. All locations were between 3 and 3.5 m depth at high tide and relatively protected from wave action by either their leeward projection or short fetch to larger neighbouring land masses (e.g. Hayman Island, see Table S1 in the supplement at www.int-res.com/articles/suppl/m426p241_supp.pdf). At each location, 2 sites were haphazardly selected on the reef crest, approximately 100 m apart.

Benthic surveys. At each reef, benthic cover was quantified along 8×20 m transects along the reef crest using a diver-operated underwater video (Sony DCR-HC1000E camera, with an Amphibico housing). For each transect, the camera lens was maintained approximately 1 m above the substratum, at a height necessary to produce a 50×70 cm field of view. Each transect ran alongside a tape measure to provide a scale of

reference during video analysis. For video analysis, the transect duration was divided equally to provide 20 still frames captured from the video. The substratum directly under 3 points within the captured frame was then recorded. The benthic surface under each point was classified into 1 of 7 functional categories: hard coral, soft coral, turf algae, macroalgae, crustose coralline algae, sand and sponge. Hard corals were further categorised according to 6 growth form categories: branching, digitate, encrusting, foliose, massive and plate. Where possible, coral and algae were classified to the generic level, with the exception of turf algae, which were categorised as EAM (sensu Wilson & Bellwood 1997).

Macroalgal transplants. Throughout the study, a small-leaf *Sargassum* (cf. *S. myriocystum*) was used for transplant experiments as it was readily available in all 3 regions. *Sargassum* is the most abundant macroalgal genus on inshore GBR reefs (McCook et al. 1997, Wismer et al. 2009) and comprised the dominant successional algae in a herbivore-exclusion experiment conducted on an inner-shelf GBR reef (Hughes et al. 2007). Quantities of *Sargassum* were removed from the reef flat, returned to the laboratory and spun for 10 s in a salad spinner to remove excess water. Between 1 and 3 individual plants were combined to form standardised assays of approximately 200 to 300 g (mean 233.6 ± 3.2 g) using a rubber band, and the fresh weight of each assay (to the nearest 0.1 g) was recorded. At each site, 6 *Sargassum* assays were haphazardly deployed onto the reef crest and secured to dead coral substrata using PVC-coated gardening wire. Of the 6 assays, one was caged to exclude herbivores and to control for loss of algae due to handling. Control cages were $50 \times 50 \times 50$ cm PVC frames, covered with PVC-coated wire mesh (1.44 cm^2 mesh size). Whilst the control cages did not prevent mesograzers (e.g. crustaceans, gastropods or small fish) from feeding on the *Sargassum*, neither the presence of these herbivores nor their feeding scars were observed; therefore, their impact was assumed to be limited (most observed losses were due to handling). Assays were deployed for a 4.5 h sampling period between 08:00 and 16:00 h daily. The length of the sampling period was chosen based on observed *Sargassum* removal rates at Orpheus Island in the central inshore GBR (Cvitanovic & Bellwood 2009, Lefèvre & Bellwood 2010). After 4.5 h, assays were collected and reweighed. Sampling was repeated for 3 d within each site using fresh algal assays each day, yielding 90 treatment assays per region. The mean proportional reductions in mass (g) from the caged controls (n = 6), used over the 3 sampling days on each reef, were used to estimate handling (non-herbivore) loss from assays. The percentage of handling loss recorded from caged assays ranged

from 7.4 ± 2.0 to 11.3 ± 1.8 and 11.9 ± 3.1 % (mean ± SE) on northern, central and southern reefs, respectively. The tissue losses due to herbivory were estimated using the equation:

$$T_{loss} = 1 - A_a / (A_i \times [1 - H_{loss}]) \tag{1}$$

where T_{loss} is the proportion of tissue loss, or algae removed, A_a is the algal mass (g) after 4.5 h, A_i is the initial algal mass and H_{loss} is the mean percentage of handling loss.

Feeding observations. Of the 5 treatment assays deployed at each site, one was filmed using a stationary RUV camera (Sony DCR-HC1000E, in an Amphibico housing). Cameras were mounted on concrete blocks, 2 to 3 m from the algae, enabling the assay and the behaviour of fish in the vicinity of the algae to be recorded in frame. In the initial seconds of recording, a scale bar was held next to the assay to allow calibration of fish sizes when viewing the footage. Cameras were left to record continuously for 4.5 h, except for an obligatory tape and battery change (of less than 5 min) carried out at 1.5 and 3 h into recording. This procedure was repeated for 3 d within each site, yielding 81 h of footage per region.

To quantify the relative removal of *Sargassum* by herbivorous fishes among the different regions, the fish size (total length, TL) and number of bites ind.$^{-1}$ were recorded from video footage for each 4.5 h sampling period. To account for body size-related variation in the bite size, the midpoint of each 5 cm size class was used to calculate mass standardised estimates of bite 'impact' for each fish species (total number of bites × body mass in kg) based on established length–weight relationships from the literature (following Bellwood et al. 2006). A foray, wherein rapid consecutive bites by an individual fish took place without a discernable pause, was conservatively classed as a single bite (Bellwood & Choat 1990).

Feeding behaviour. For the 4 dominant herbivore species, *Kyphosus vaigiensis*, *Naso unicornis, Siganus canaliculatus* and *S. doliatus*, the feeding propensity, i.e. the proportion of total entries (feeding + non-feeding) into the camera frame, was quantified over 3×1 h periods within each site in all locations and regions. Because of the difficulty in tracking individuals moving in and out of the camera frame, a school or pair of fishes was tallied as a single entry based on the movement behaviour of the species. *K. vaigiensis* and *S. canaliculatus* were tallied in schools; *S. doliatus* were recorded in pairs, and *N. unicornis* as individuals.

Herbivore censuses. Abundances of roving herbivorous fishes belonging to the families Labridae (parrotfishes), Acanthuridae, Siganidae, Pomacanthidae and Kyphosidae were quantified using 10 min timed swims along the reef crest by divers on SCUBA (Bellwood &

Wainwright 2001). Twelve replicate censuses were conducted over 3 d within each of the 3 reefs within the 3 regions, recording roving herbivores within 4 m wide transects (all censuses conducted by S.B.). Roving herbivores >10 cm TL were recorded into 5 cm size classes. Due to difficulties in identification, individuals belonging to the species *Acanthurus auranticavus, A. grammoptilus* and *A. blochii* were grouped as *Acanthurus* spp. The transect width was chosen to maximise the area surveyed, whilst allowing for the often limited visibility on inshore reefs. The length of each transect was subsequently measured using tapes (116 ± 8.7 m, mean ± SE). Species abundance was converted to biomass per unit area by using the length–weight relationship for each species.

Statistical analyses. Differences among latitudinal regions in *Sargassum* tissue loss, roving herbivore biomass, fish density and fish feeding propensity were analysed by examining the best fit of theoretical range shapes to the observed distributions across the 3 regions (following Enquist et al. 1995, Sagarin & Gaines 2002). For *Sargassum* tissue loss, we compared tissue loss versus latitude to 2 model distributions where tissue loss (realised herbivory) linearly increases or declines with increasing latitude (Fig. 1). This approach, unlike a conventional regression, does not assume that all northern sites will have high rates of herbivory, thereby acknowledging the patchy nature of herbivory over small spatial and temporal scales (i.e. between sites and days), but examines the bounds on herbivory across the broad latitudinal range (Sagarin & Gaines 2002).

To carry out the analysis, the latitude of each site was converted to a range index (RI), which standardises each site's position over the latitudinal range of the study:

$$RI = 2(L - S) / R \qquad (2)$$

where *L* is the latitude of the site, *S* is the latitudinal midpoint (20°S) of the study, and *R* is the latitudinal extent of the study (8°). RI therefore ranges from –1 to 1, with –1 representing the northern most reefs and 1 the southernmost reefs in the study. Since no reference values were available to predict the rate of herbivory throughout the latitudinal range observed in the study, we arbitrarily prescribed a linear increase (0–100%) or decrease (100–0%) in tissue loss across the observed latitudinal range, to represent the upper limits of the constraint space for the theoretical latitudinal gradients. For each site, a constraint value D_{max} was established from the equation for a straight line:

$$D_{max} = ax + b \qquad (3)$$

where *a* is the slope, *x* is the position in the range and *b* is the expected maximum tissue loss in the centre of the range (50%). Mean tissue loss values were plotted for the 3 sampling days within each site. A point was considered to fall outside the constraint space (above the line) when its tissue loss exceeded the D_{max} value for that site. The sum of squared deviations (SS) from the constraint space was calculated for all points which exceeded their respective D_{max} values. Having calculated the observed SS, we then used a randomisation approach to rearrange the observed T_{loss} and RI values. The randomised data were plotted and, like the observed data, the SS was calculated for all randomised points which fell outside the constraint space. This process was repeated 10^4 times to generate a probability distribution of SS for the rearranged data. *Sargassum* tissue loss was considered to significantly increase or decrease from north to south if over 95% of SS values from the rearranged data sets were larger than the observed SS value.

To assess possible links between *Sargassum* tissue loss and herbivore biomass across the observed latitudinal range, the above analysis was subsequently repeated to examine the latitudinal trends in the biomass and density of the 15 most important macroalgal browsers observed in the study (based on mass standardised bites). If latitudinal variation in herbivore biomass was driving *Sargassum* tissue loss, we would expect to see concurrence between the shape of tissue loss and the shape of macroalgal browser biomass over the observed latitudinal scale. Note that because the current study does not cover the full latitudinal range of the observed macroalgal browsing species, the common hyperbolic species range distribution was not expected to be observed (cf. Enquist et al. 1995). For the analysis, fish species biomass and density were converted to relative biomass and density, by dividing the values for each site by the maximum values found at any site within the study.

Finally, the feeding propensity of the 4 dominant herbivores per site and day was plotted against RI to observe regional-scale trends in feeding behaviour. Feeding propensity versus RI was compared to the theoretical southwardly increasing or decreasing shapes (Fig. 1), following the methodology outlined above.
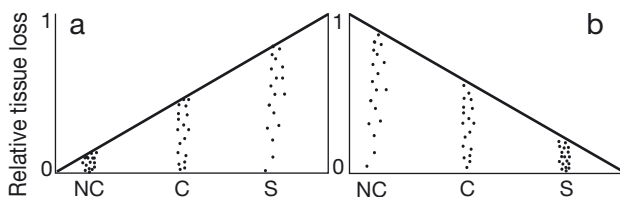

Fig. 1. Model distribution shapes that were compared with observed data using goodness-of-fit tests. Dots represent a hypothetical data set from each of the observed regions, fitting within (a) southwardly inclining and (b) southwardly declining constraint spaces. N: north, C: central, S: south

RESULTS

Benthic cover

Epilithic algae and soft coral communities dominated benthic cover on reef crests in both the north (34 ± 2% and 18 ± 2%, respectively, mean ± SE) and central regions (33 ± 3% and 24 ± 3%, respectively; Fig. 2). The most abundant hard coral growth form on northern reefs was massive hard corals, which accounted for 29 ± 3% of benthic cover, whilst the remaining hard coral growth forms represented approximately 18%. In the central region, branching coral occupied 24 ± 4% of reef area, with the remaining growth forms representing approximately 12% of total cover. No macroalgae were recorded on any of the transects in the north or central regions. By contrast, benthic cover in the southern region was dominated by macroalgae (40 ± 3%) and branching coral (42 ± 3%), with the remaining coral growth forms contributing approximately 8% to total benthic cover. Of the macroalgae present, *Lobophora variegata* was most abundant, representing between 31 and 100% of total macroalgal cover. Other taxa, including the brown macroalga *Dictyota* sp., were prevalent around Halfway Island, whilst the macroalgae *Asparagopsis* sp. (Rhodophyta) and *Caulerpa* sp. (Chlorophyta) were abundant at Olive Point. *Sargassum* was not recorded on the reef crest per se; however, it was abundant on the outer reef flat, 3 to 10 m from the crest (S. Bennett pers. obs.).
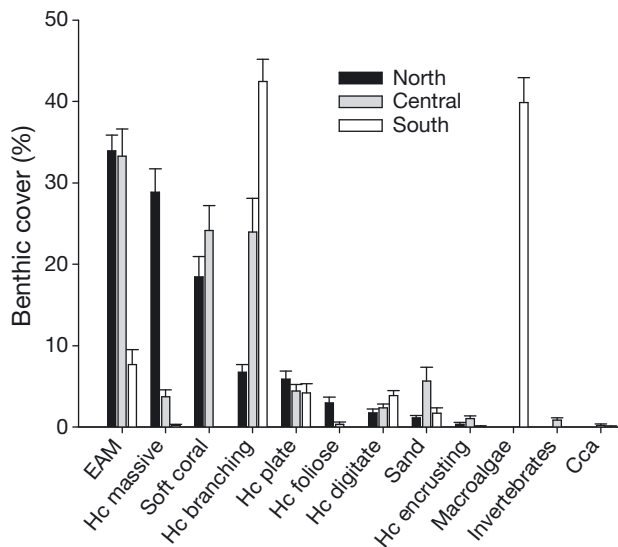
Macroalgal removal

The SS of observed *Sargassum* cf. *myriocystum* tissue loss from the southwardly declining model was significantly lower than the 95% of SS distribution obtained using the randomisation approach, indicating a significant latitudinal decline in *Sargassum* removal by herbivores from north to south (p < 0.001, Fig. 3). The northern region was characterised by high levels of *Sargassum* tissue loss, between 42 ± 7 and 87 ± 3% (mean ± SE) removal of algal biomass over a 4.5 h period in all 6 sites (Fig. 4). The central region also generally displayed high rates of tissue loss, averaging between 63 ± 8 and 84 ± 6% in 4 of 6 sites (Hayman and Bird Islands), but only 5 ± 2 and 8 ± 3% for the remaining sites at Hook Island. The southern region, in contrast, was characterised by low rates of *Sargassum* removal, with 5 of 6 sites averaging between 3 ± 3 and 11 ± 4% tissue loss, with Olive Point being the exception with 53 ± 7%.

Bite rates

At a regional scale, the number of herbivorous fish species recorded feeding on the *Sargassum* assays declined from north to south (Fig. 5). In the northern GBR, 19 species took bites from the algae, compared with 14 species in the central region and just 7 species in the south. Of the species observed feeding on *Sargassum* assays, *Siganus doliatus*, *S. canaliculatus*, *Naso unicornis* and *Kyphosus vaigiensis* dominated, accounting for 91% of the 62 713 individual bites recorded in the study. In the northern region, 22 114 (82.6%) indi-
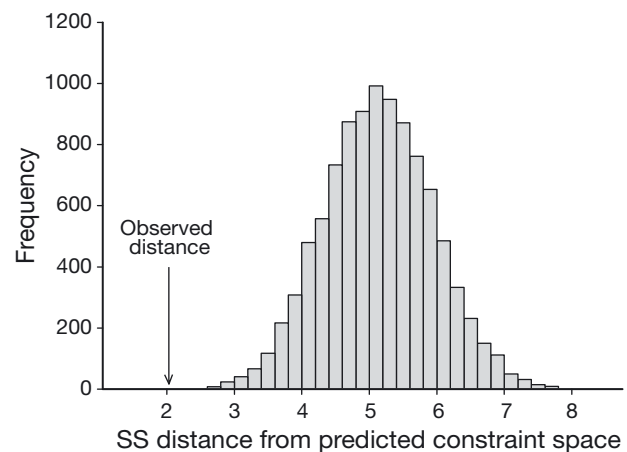

Fig. 2. Mean percentage benthic cover of 12 benthic functional groups. Bars represent mean values (± SE) from 24 replicate surveys (8 reef^{-1}) within the 3 respective regions. EAM: epilithic algal matrix, hc: hard coral, cca: crustose coralline algae, invertebrates: sponges and *Tridacna* spp. clams

Fig. 3. *Sargassum* cf. *myriocystum.* Results of the randomisation approach showing the sum of squared deviations (SS) of tissue loss from the constraint space for the southwardly declining shape. The arrow points to the distance of the observed value (SS = 2.033), whilst the histogram indicates the distribution of SS generated by randomly reorganising tissue loss data among latitudes, from 10^4 simulations (p < 0.001)
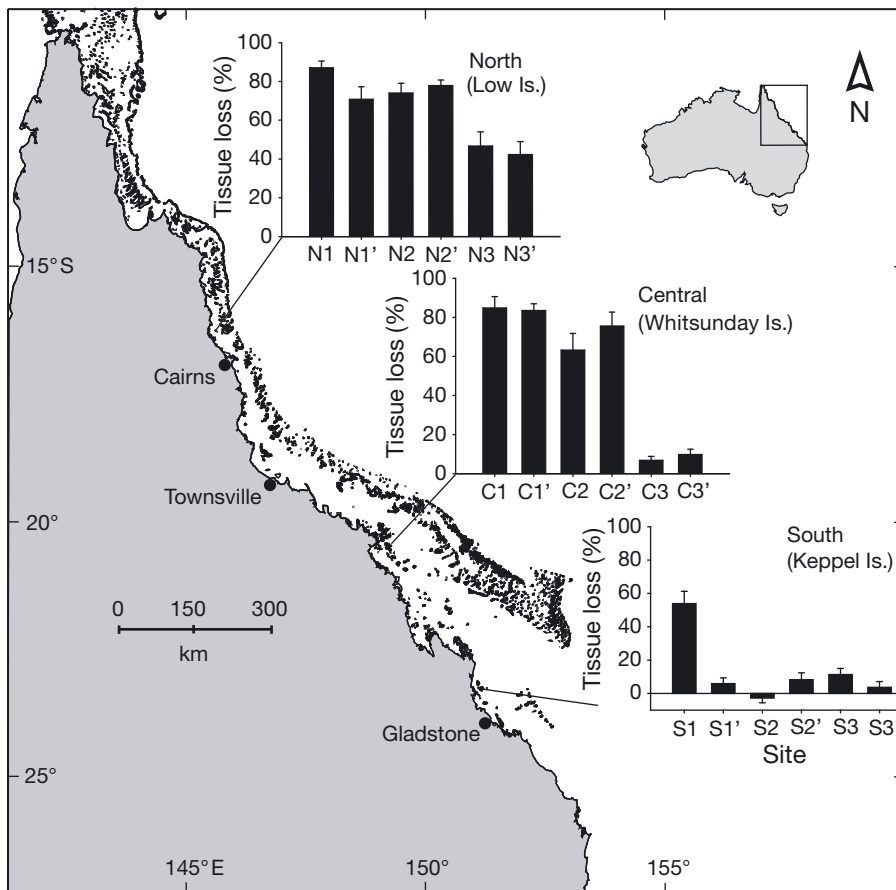
Fig. 4. *Sargassum* cf. *myriocystum.* Regional variation in herbivory on the Great Barrier Reef. Columns represent percentage decrease in mass ± SE averaged over 3 sampling days at each site (6 sites, n = 5 assays site^{-1} d^{-1}) for each region. Letters (A, B, C) labelling the horizontal axis represent the 3 locations (reefs) within each region. Apostrophised letters represent the second site within each location

vidual bites and 9610 (85.6%) mass standardised bites were recorded for the 4 dominant herbivores. In the central region, this rose to 34 176 (98.8%) and 16 514 (99.4%), then fell to 981 (95.8%) and 493 (98.4%) individual and mass standardised bites, respectively, in the southern region.

Herbivore biomass

A total of 22, 25 and 17 species of roving herbivorous fish were recorded on underwater visual censuses (UVCs) in the north, central and southern regions, respectively. From those species, UVC observations of the 15 most prominent *Sargassum* feeders found that just 4 species, viz. *Siganus lineatus, Pomacanthus sexstriatus, Scarus flavipectoralis* and *Siganus corallinus*, demonstrated a significant decline in biomass from north to south (p < 0.05, Fig. 6), whilst 3 species, *P. sexstriatus, S. lavipectoralis* and *Scarus niger*, demonstrated significant declines in density (p < 0.05, see Fig. S1 in the supplement at www.int-res.com/articles/suppl/m426p241_supp.pdf). All remaining species, including the 4 dominant feeders (*Naso unicornis, Siganus canaliculatus, S. doliatus* and *Kyphosus vaigiensis*) did not display any significant pattern (increasing or decreasing) in biomass or density across the observed inner GBR regions. None of these changes was significant when a Bonferroni corrected p-value of 0.003 was used.

Herbivore feeding behaviour

The combined propensity of the 4 dominant herbivores to feed on *Sargassum* assays displayed a significant regional (north to south) decline (p < 0.001, Fig. 7). In the north, the 4 dominant herbivores fed on 74.7 ± 2.1% (mean ± SE) of opportunities upon passing *Sargassum* assays, in comparison to 48.8 ± 12.8 and 17.9 ± 6.5% of occasions in the central and southern regions, respectively. At the species level, the feeding propensity of *Kyphosus vaigiensis* displayed a regional (north to south) decline (feeding in total on 75.0, 60.6 and 37.5% of occasions from north to south, respectively). A similar pattern was seen in *Siganus doliatus* (81.5, 54.2 and 35.9%). The pattern in *Naso unicornis* (70.5, 30.1 and 40.8%) and *S. canaliculatus* (80.8, 35.1 and 25.7%) was less clear, although consistently the southern reefs were consistently low and the north consistently high.
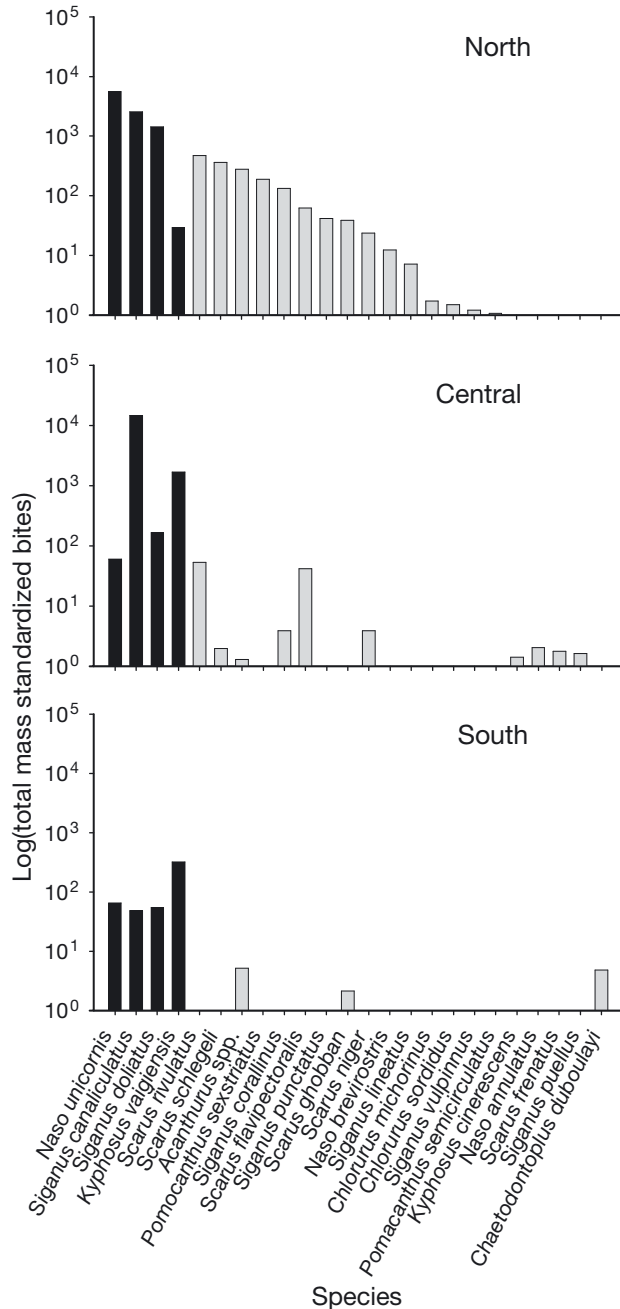
Fig. 5. Total number of mass standardised bites from (see 'Materials and methods: Feeding observations' for details) *Sargassum* assays by fish species, illustrating the regional decline in species feeding on *Sargassum* assays. Black columns highlight *Naso unicornis*, *Siganus canaliculatus*, *S. doliatus* and *Kyphosus vaigiensis*

DISCUSSION

Across the 3 observed inshore regions of the GBR, removal rates of *Sargassum* by herbivores exhibited a significant regional decline from north to south, driven primarily by changes in the behaviour of 4 dominant

herbivorous fish species, and to a lesser extent by a regional decline in herbivore feeding diversity. Four species, *Naso unicornis*, *Kyphosus vaigiensis*, *Siganus doliatus* and *S. canaliculatus*, consistently dominated feeding. Together, they accounted for 85, 99 and 98% of mass standardised bites within the north, central and southern regions, respectively. However, they recorded over an order of magnitude fewer bites in the south. Interestingly, this decline in bites and feeding diversity did not arise from lower herbivore biomass or density in the southern region. Rather, the major difference between fish herbivory among regions was in the feeding propensity of the 4 dominant feeders. This study demonstrates that whilst the relative importance of herbivorous species may remain the same over regional spatial scales, the magnitude of their ecosystem role can differ dramatically.

The high to moderate removal rates of *Sargassum* from the north and central regions is consistent with the existing body of literature on local-scale macroalgal consumption from inshore reefs around Orpheus Island (Mantyka & Bellwood 2007, Fox & Bellwood 2008, Cvitanovic & Bellwood 2009). Likewise, the generally low rates of *Sargassum* removal from the southern region observed in this study lend support to reports that herbivores play a reduced role in macroalgal removal on southern inshore reefs (Diaz-Pulido et al. 2009, Bennett et al. 2010).

The repeated dominance of *Naso unicornis*, *Kyphosus vaigiensis*, *Siganus doliatus* and *S. canaliculatus* within each of the 3 regions examined in this study, over 900 km apart, provides evidence of a broader significance of the local-scale patterns of browser activity previously observed around Orpheus Island in the central GBR (Mantyka & Bellwood 2007, Fox & Bellwood 2008, Cvitanovic & Bellwood 2009, Lefèvre & Bellwood 2011), and the potential importance of these 4 species in maintaining macroalgal communities along the inshore GBR. In addition to these 4 dominant species, however, the minor browsing species, namely *Scarus rivulatus*, *Scarus schlegeli*, *Acanthurus* spp., *Pomacanthus sexstriatus*, *Siganus corallinus*, *Scarus flavipectoralis*, *Siganus punctatus* and *Scarus ghobban*, jointly took a relatively high number of bites in the northern region, recording over 4 times the total number of individual bites than all species combined in the southern region. The diverse feeding assemblage observed in the northern, and to a lesser extent, central regions of this study stands in contrast to the limited functional redundancy reported elsewhere such as far northern reefs (Hoey & Bellwood 2009). In the southern region, the low feeding rates and low functional redundancy observed came despite a relatively intact herbivore community. Notably, none of the dominant algal feeders declined. In fact, the 4 dominant feeders displayed
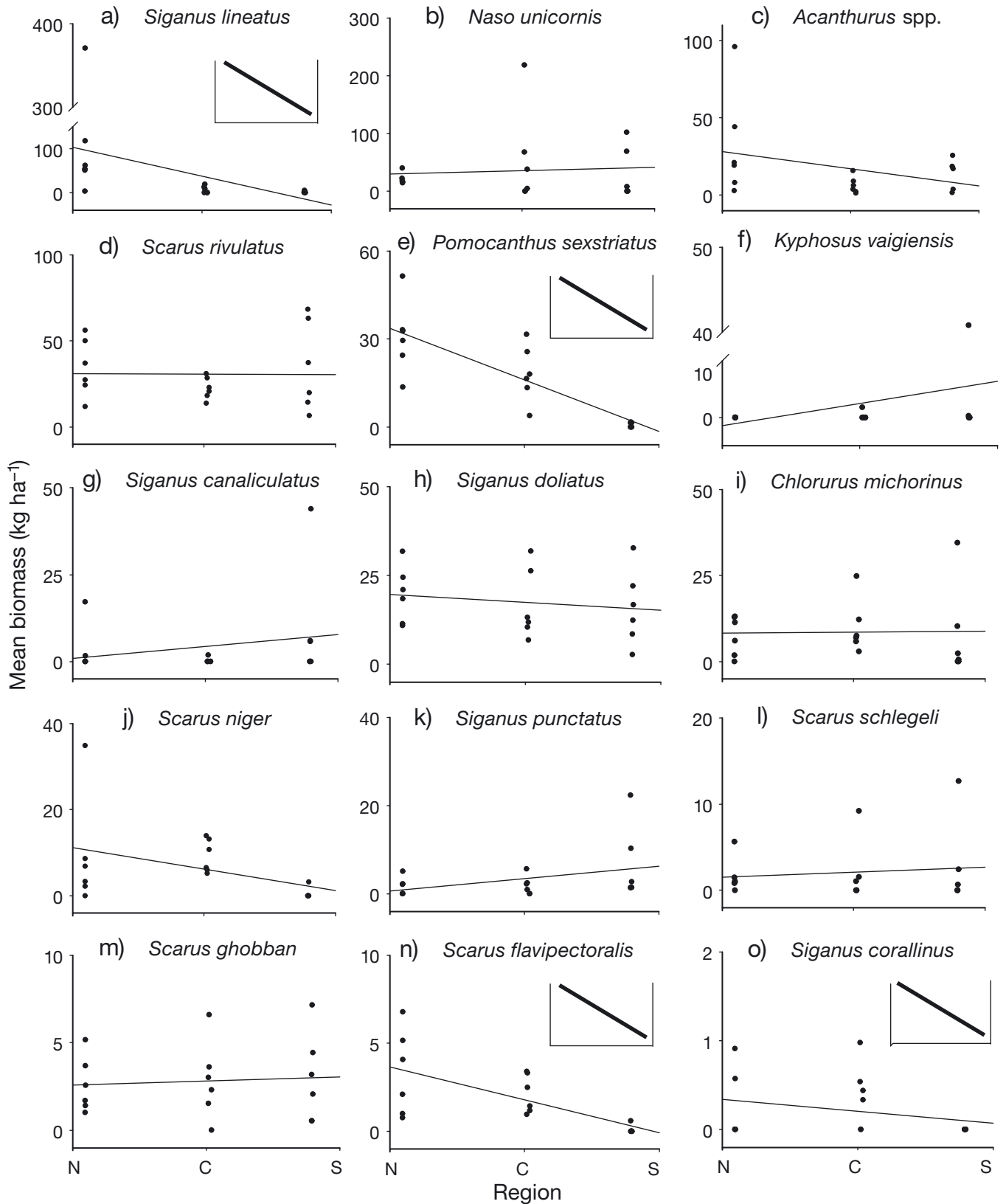
Fig. 6. Mean biomass of roving herbivores from 6 sites within the 3 latitudinal regions (n = 6 censuses site^{-1}). Species are ordered (a–o) to represent greatest to least biomass observed at any one site. Inset diagrams indicate the shape best fit by the goodness-of-fit test, for significant results (p < 0.05)
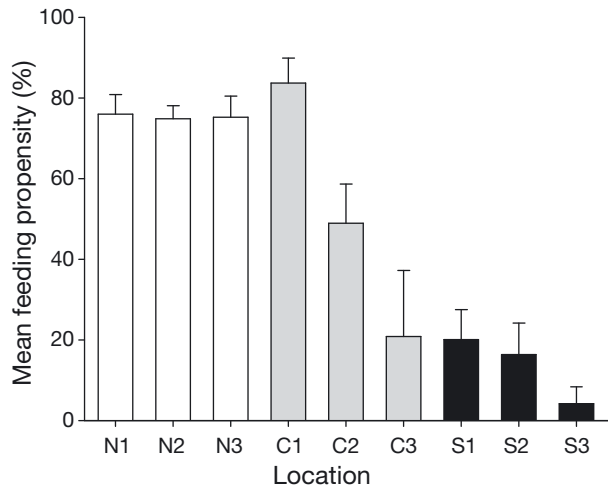
Fig. 7. Combined mean feeding propensity of *Siganus dolia-tus, S. canaliculatus, Naso unicornis* and *Kyphosus vaigiensis* per site. Feeding propensity = feeding entries/total entries (feeding + non-feeding) by fish into the camera frame. Each sites location represents 2 site with 3 × 1 h observations over 3 d. Feeding propensity significantly declined from north to south (p < 0.001). Error bars: ±SE

subtle, albeit non-significant, increases in apparent biomass and density from north to south. These observations are consistent with previous reports describing herbivore biomass and density based on UVCs to be poor predictors of the realised functional role of species (Bellwood et al. 2006, Cvitanovic & Bellwood 2009), particularly browsing herbivores (Fox & Bellwood 2008, Hoey & Bellwood 2009).

Behavioural observations of feeding propensity provide an explanation for the discrepancy between UVC observations and functional impact. The dominant 4 herbivores jointly displayed a strong difference in feeding propensity among regions. The dominant southern herbivores only fed on 17% of opportunities when passing *Sargassum* assays, markedly less than observed in the northern and central herbivore locations where these species fed on 74 and 48% of total feeding opportunities, respectively. The large difference in feeding propensity by herbivores, on *Sargassum*, provides a mechanism that may explain the observed disparity in feeding and algal removal rates. The question which arises from this study is therefore: Why does the feeding propensity of herbivore communities vary so greatly among regions of the inshore GBR? One potential cause of these differences is temperature.

Temperature has been identified as the primary cause of reduced herbivore feeding rates in the western Atlantic (Floeter et al. 2005), and along latitudinal gradients in general (Harmelin-Vivien 2002). To minimise temperature variation, the current study was staggered, working north to south to coincide with the

warming months from October to December. Temperature data from multiple sites within the 3 regions indicated that during the southern field trip, water temperatures were, on average, warmer (26.97 ± 0.08°C, mean ± SE) than in the north (26.51 ± 0.07°C) or central field trips (26.47 ± 0.04°C, Australian Institute of Marine Science: www.aims.gov.au/docs/data-centre/seatemperatures.html; see Fig. S2 in the supplement at www.int-res.com/articles/suppl/m426p241_supp.pdf). Although long-term temperature variation cannot be discounted, temperature per se does not appear to be the primary driver of differences in feeding propensity among reefs.

A second mechanism which may have contributed to the low feeding rates on certain reefs could have arisen through a decrease in preference for the transplanted algae, driven either by the availability of an alternate resource, or an increase in deterrent effects of the transplanted algae. By only using small-leaf *Sargassum* (cf. *S. myriocystum*) for assays, potential feeding preference effects between different species of *Sargassum* were minimised. Nevertheless, nutritional quality and secondary metabolite defences can vary between plants of the same species (Arnold et al. 1995). Intraspecific chemical defences can also vary locally, and have been reported to influence herbivory between nearby populations of *Sargassum* sp. (Taylor et al. 2003). The low removal rates of *Sargassum* in the south, however, are inconsistent with previous findings that higher-latitude plants are less chemically defended than lower-latitude conspecifics (Bolser & Hay 1996). Therefore, whilst intraspecific variability in defence may potentially explain some of the local variability in removal rates, the relationship with the observed regional-scale patterns in *Sargassum* removal is unclear. Other species of fleshy macroalgae, primarily *Lobophora variegata*, occupy reef crests of the southern region, which may have provided an alternate food source for herbivores. However, this is a relatively unpalatable macroalga (Pillans et al. 2004, Weidner et al. 2004, Bennett et al. 2010), and the high densities observed in the southern region grow predominantly within the framework of branching *Acropora*, making it largely inaccessible to roving herbivores (Bennett et al. 2010) and unlikely to present a preferred alternative. However, the effect of other algae at larger, among-habitat, scales may be important. The presence of *Sargassum* on the adjacent reef flat of southern reefs may present an alternative to the assays and make them less desirable. A comparable decline in the 'attractiveness' of assays to herbivores on inshore reefs of the northern GBR has been related to local macroalgal abundance (Hoey & Bellwood 2010). Herbivores may be responding to among-habitat rather than within-habitat patterns of algal abundance.

Finally, feeding propensity may not have been shaped by the algae per se, but rather by fish behaviour in relation to topographic complexity. The high feeding rates on the reef crest of central and northern reefs are, among other things, reported to be strongly influenced by the provision of benthic structural complexity for protection (Fox & Bellwood 2007). On inshore reef crests of the northern and central GBR, structural complexity is achieved by a diversity of coral functional groups, of which massive *Porites* colonies are dominant, both as living colonies and as a base for soft corals and turf algal communities. In contrast, southern inshore fringing reef crests are dominated by monospecific stands of branching *Acropora* coral, with high densities of the macroalgae *Lobophora variegata* growing within the branching framework (Bennett et al. 2010). Large areas of closely-branched *Acropora* sp. provide small-scale (<10 cm) topographic complexity, yet medium-scale (1 to 10 m) topographic homogeneity. In contrast, functionally diverse coral communities provide a higher degree of small-scale habitat homogeneity, due to the relatively planar surfaces of massive, foliose and even plate growth forms, yet medium-scale habitat complexity. For large roving herbivores, the small-scale complexity of branching habitats provides a far less preferred feeding habitat than the planar surfaces described above (Bennett et al. 2010). It may be that the difference in the scale of cover is a significant factor underpinning the observed patterns of herbivory and algal growth among regions. Southern reefs have extensive beds of branching corals that deter herbivores but encourage algal growth, while northern reefs have less complexity at a scale that encourages algal growth but more complexity at a scale suitable for herbivores.

The current study has revealed reduced rates of herbivory on southern reefs, in a system containing a relatively intact herbivore community. This finding stands in marked contrast to other systems where herbivory is low, such as those impacted by the removal of herbivores through over-fishing (Hughes 1994, Mumby et al. 2006), or cold water marine systems (Harmelin-Vivien 2002, Floeter et al. 2005). The current finding does, however, display similarities to parts of the Atlantic where an intact but relatively depauperate herbivore community is unable to reduce established macroalgae from the reef (Paddack et al. 2006). Unlike in Paddack et al. (2006), however, all the reefs observed in the current study retain relatively high coral cover and represent some of the 'healthiest' reefs within their respective inshore regions. It is therefore unlikely that the high rates of herbivory observed in the north and central reefs can be generalised across all inshore reefs in those regions. Rather, these results should be treated as the 'best-case scenarios' of macro-

algal herbivore resilience within the 3 respective regions. Furthermore, whilst northern and central herbivore communities displayed relatively high rates of herbivory, it remains unclear what volume of macroalgae these communities can consume and therefore what level of disturbance they can insure against. Nevertheless, the very low rates of observed herbivory on the southern reefs reflect the limited capacity of some components of the herbivore community to provide resilience following disturbance events. Future studies should focus on how these rates of herbivory relate to algal production rates within the 3 respective regions. Macroalgal accumulation is a result of the balance between growth and removal, and in this respect, regional variation in algal growth rates may be important in shaping the observed patterns of macroalgal cover.

The limited role of herbivory on southern reefs has demonstrated that the role of functional groups can be constrained without the loss or harvesting of important species. Whilst the nature of macroalgal herbivory appears to be relatively consistent (i.e. the same species dominate feeding) across regional scales, the magnitude of the activity varies dramatically between reefs along the length of the GBR. Therefore, just because 2 reefs have intact and structurally comparable herbivore communities, it does not necessarily follow that the 2 communities will have the same realised functional impact on the reef. In order to understand the effective contribution of functional groups to ecosystem processes on reefs, it may be necessary to directly investigate functional groups in the specific ecological context of the local ecosystem. The current study cautions against the dangers of extrapolating local-scale understanding of functional groups to broader spatial scales.

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