Herbivores strongly influence algal recruitment in both coral- and algal-dominated coral reef habitats

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ABSTRACT: Coral reefs can exist as coral- and macroalgae-dominated habitats often separated by only a few hundred metres. While herbivorous fish are known to depress the abundance of algae and help maintain the function of coral-dominated habitats, less is known about their influence in algae-dominated habitats. Here, we quantified herbivorous fish and benthic algal communities over a 6 mo period in coral-dominated (back-reef) and algal-dominated (lagoon) habitats in a relatively undisturbed fringing coral reef (Ningaloo, Western Australia). Simultaneously, we tested the effects of herbivorous fish on algal recruitment in both habitats using recruitment tiles and fish exclusion cages. The composition of established algal communities differed consistently between habitats, with the back-reef hosting a more diverse community than the *Sargassum*-dominated lagoon. However, total algal biomass and cover only differed between habitats in autumn, coinciding with maximum *Sargassum* biomass. The back-reef hosted high coral cover and a diverse herbivorous fish community, with herbivore biomass an order of magnitude greater than the lagoon. Despite these differences in herbivore composition, exclusion of large herbivores had a similar positive effect to foliose macroalgae recruitment on experimental tiles in both back-reef and lagoon habitats. Additionally, territorial damselfish found in the back-reef increased turf algae cover and decreased crustose coralline algae cover on recruitment tiles. Collectively, our results show that disparate herbivorous fish communities in coral- and algae-dominated habitats are similarly able to limit the recruitment of foliose macroalgae, but suggest that when herbivorous fish biomass and diversity are relatively low, macroalgal communities are able to escape herbivore control through increased growth.

KEY WORDS: Functional group · Recruitment · Macroalgae · *Sargassum* · Turf algae · Crustose coralline algae · Ecosystem function · Ningaloo

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INTRODUCTION

The replacement of corals by macroalgae is a relatively common occurrence in the degradation of coral reefs (Hughes 1994, Bellwood et al. 2004, Mumby et al. 2006). This shift from coral to macroalgal domi-

nance often occurs as a result of disturbance and mortality to the coral community (Done 1992, Hughes 1994), after which algae can proliferate through rapid recruitment, growth, and early dominance of newly available space (Littler & Littler 1999, Diaz-Pulido & McCook 2002, Connell et al. 2004). Two main pro-

cesses are often proposed to greatly influence macroalgal abundance in degraded systems: anthropogenic nutrient loading (bottom-up effects) and overharvesting of herbivore populations (top-down effects) (Burkepile & Hay 2006). In coral reefs, many studies have investigated the relative importance of these 2 processes (e.g. Diaz-Pulido & McCook 2003, McClanahan et al. 2003, Albert et al. 2008, Smith et al. 2010, Rasher et al. 2012), and a meta-analysis of 54 field experiments revealed that globally, herbivores have a greater effect on algal production and distribution than nutrient inputs (Burkepile & Hay 2006). Herbivores can directly influence algal abundance by consuming both algal recruits (Diaz-Pulido & McCook 2003) and adults (Hoey & Bellwood 2010a, Bennett & Bellwood 2011, Vergés et al. 2011), and their removal can cause algal proliferation that reduces juvenile and adult coral abundance and growth (Jompa & McCook 2002, Hughes et al. 2007, Birrell et al. 2008, O'Leary et al. 2012).

Functional group identity of herbivorous fish is particularly important when assessing algae-grazer dynamics (Cheal et al. 2010). Roving herbivorous fish are often classified into 3 major groups: grazers and detritivores (Acanthuridae, most Siganidae), scrapers and excavators (Scaridae), and browsers (e.g. *Naso* spp., Kyphosidae; Green & Bellwood 2009). Grazers and detritivores feed intensely on the epilithic algal matrix (EAM, which includes turf algae and detritus) (Wilson et al. 2003, Marshell & Mumby 2012), scrapers and excavators also feed on the EAM but remove part of the substrate as they feed (Bellwood & Choat 1990), and browsers feed on large, foliose macroalgae (Hoey & Bellwood 2010a, Bennett & Bellwood 2011, Vergés et al. 2012, Michael et al. 2013). Territorial herbivorous fish, including many Pomacentridae and some Acanthuridae, defend a defined area of reef substratum against other herbivores. Their behaviour promotes algal turf productivity and diversity, as well as altering successional trajectories of algal recruitment (Klumpp et al. 1987, Hixon & Brostoff 1996, Ceccarelli et al. 2001, 2005, 2006, Gobler et al. 2006, Hoey & Bellwood 2010b).

While it is clear that high levels of algal cover are a characteristic feature of degraded reefs, recent studies have challenged the view that intact reefs are coral-dominated habitats with small algal populations, and propose that some healthy coral reef ecosystems may instead be regarded as adjacent coral- and algal-dominated benthic communities (Wismer et al. 2009, Johansson et al. 2010, Vroom & Braun 2010). Herbivory varies dramatically among these adjoining habitats and is at least partly mediated by structural complexity, with the highest rates of algal consumption occurring in the more complex coral-dominated habitats (Hay 1981, Hay et al. 1983, Vergés et al. 2011). The use of long-term experimental herbivore exclusion cages has shown that herbivory is clearly one of the key processes that excludes large, foliose algae from coral-dominated habitats (Hughes et al. 2007, Burkepile & Hay 2010, Rasher et al. 2012) by limiting algal growth in both Caribbean and Indo-Pacific coral reefs (reviewed by Roff & Mumby 2012). Similarly, experiments assessing the impact of herbivore exclusion on algal recruitment in coral-dominated habitats also have demonstrated that high levels of herbivory can significantly reduce the recruitment of foliose algae to new substrata (Diaz-Pulido & McCook 2003, Burkepile & Hay 2006, Smith et al. 2010). In contrast to the well-established effects of herbivores on coral-dominated habitats, our knowledge about the influence of these consumers on habitats where algae dominate is limited. Herbivore populations and herbivory rates are generally low in these habitats (Fox & Bellwood 2007, Vergés et al. 2011), and it is thought that low consumption rates allow dense macroalgal stands to form. Once high-density patches of algae develop, positive feedback mechanisms inhibit further herbivory, facilitating algal growth and persistence (Hoey & Bellwood 2011). However, there is a lack of experimental evidence quantifying the effects of herbivores on algal recruitment in algal-dominated habitats.

Algal recruitment, in its broadest sense, incorporates the settlement and post-settlement survival and growth of algal propagules (sensu Diaz-Pulido & McCook 2003). Microscopic propagules are released into the water column from gravid adult algae; these disperse, settle, and then spend time in the EAM before developing into macroscopic individuals (Santelices 1990). Habitats with abundant adult algal populations may be expected to have higher algal recruitment due to higher propagule supply. For dominant brown algae such as *Sargassum* spp., dispersal is highly localised, with most propagules settling within 1 m from the adult (Kendrick & Walker 1995). The post-settlement survival of algal recruits is higher in areas with lower abundances of roving herbivores (Diaz-Pulido & McCook 2003) because algae experience little herbivory following recruitment to such areas (Lubchenco & Gaines 1981, Diaz-Pulido & McCook 2003). Thus, it may be expected that algal recruitment would be greatest in areas with less herbivores owing to (1) higher survival of microscopic settled propagules in the EAM, and (2) higher survival of recruits that reach critical size-escape thresh-

olds from predation (Lubchenco & Gaines 1981, Diaz-Pulido & McCook 2003), but this has never been tested.

In this study, we aimed to determine the effect of large herbivorous fish and habitat type on the recruiting algal community of a relatively intact coral reef ecosystem, Ningaloo Reef (Western Australia). Over a 6 mo period, we quantified changes in the benthic community and the herbivorous fish community in back-reef and lagoon habitats, 2 distinct neighbouring areas of the reef dominated by coral and algae, respectively, in terms of percentage cover of substratum. Simultaneously, we used settlement tiles and herbivore exclusion cages to test the effects of habitat and large herbivorous fish on algal recruitment. Based on a study by Vergés et al. (2011), which showed dominance of large macroalgae in the lagoon habitat and greater herbivore biomass and herbivory rates in the structurally complex coral-dominated back-reef habitat, our *a priori* expectation was that (1) algal recruitment would be greatest in the lagoon where algae are more abundant, and (2) algal recruitment would be reduced by herbivory, especially in the more structured back-reef.

MATERIALS AND METHODS

Study location

This study was conducted in the Ningaloo Marine Park, Western Australia (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m486p153_supp.pdf). Ningaloo is a coral reef system that has been managed as a marine park since 1987, and was rezoned in 2005 to include 33% of the park as no-take sanctuary zones (CALM & MPRA 2005). It is found in an arid zone that is free of any major anthropogenic threats and is generally considered relatively undisturbed (Johansson et al. 2010). Ningaloo Reef is the largest fringing reef in Australia and the only extensive fringing reef on the west coast of any continent (Collins et al. 2003). It is a narrow fringing reef approximately 270 km in length that forms a discontinuous barrier adjacent to the North West Cape, between the latitudes 21° 47′ S and 24° 00′ S. The back-reef habitat is situated a few metres inshore from the reef crest at a depth of 1.5 m at the spring low tide, and the lagoon habitat is situated further inshore at a similar depth. Both habitats are equally influenced by tidal movement, which has a maximum range of ~2 m during spring tides. The back-reef is dominated by tabulate *Acropora* and the lagoon is dominated by rubble, sand, and patches of foliose macroalgae (Cassata & Collins 2008).

We conducted our study from November 2008 until May 2009 in the Mandu no-take sanctuary zone (22° 08′ S, 113° 45′ E) within Ningaloo Marine Park (Fig. S1 in the Supplement). The Mandu Sanctuary Zone is approximately 8 km long by 2 km wide, and has a lagoon ~600 m wide and a back-reef ~400 m wide. We haphazardly selected 2 sites nested within each habitat (lagoon and back-reef), with sites between the lagoon and back-reef habitats separated by ~400 m, and each site nested within a habitat separated by ~400 m (Fig. S1 in the Supplement).

Benthic community characterisation

Benthic community cover and algal biomass were surveyed at each site nested in the lagoon and back-reef habitats at 3 times of the year: spring (November 2008), summer (February 2009) and autumn (May 2009). Benthic community cover was sampled using a line intercept method following Fox & Bellwood (2007). A 10 m transect tape was laid haphazardly across the reef, and a diver recorded the nature of the substrate directly touching the tape measure at 1 m interval points and at points 1 m perpendicular to the right and left of the tape (total of 30 points per replicate). The substrate categories used were: live coral, crustose coralline algae (CCA), EAM (includes turf algae and detritus), foliose macroalgae (>1 cm height), and sand. We conducted a total of 6 replicate transects at each site in the lagoon and back-reef habitats.

Algal biomass was measured by clearing all macro-algae (thalli larger than 2 cm) in three 50 × 50 cm haphazardly placed quadrats at each site-habitat combination at every time point. Algal samples were bagged and returned to the laboratory, sorted to genus level where possible (a total of 17 genera were identified), rinsed with fresh water, oven dried at 60°C for ≥48 h, and weighed. Algal taxa that were unable to be identified were classified according to broad functional groups, including filamentous green, filamentous red, articulated coralline algae, and CCA.

Herbivorous fish community characterisation

Herbivorous fish abundance and biomass were characterised for each site nested in the lagoon and back-reef habitats at the same 3 times of the year

using the same transects in which benthic community cover and macroalgae were sampled (see above). A diver swam a 25 m transect at a constant speed and counted the abundance and size class (to 5 cm) of individual roving nominally herbivorous fish (sensu Choat et al. 2002, 2004) along 2.5 m on both sides of the transect line. Territorial damselfish abundance and size class were counted on the return swim along each transect, narrowing the width to 1 × 25 m length. At each site at each time period, 4 replicate transects were conducted; transects were separated from each other by at least 10 m. Abundance data were converted to biomass using the allometric length-weight conversions $W = a \cdot TL^b$, where W is weight in g, TL is total length in cm, and parameters a and b are constants obtained from Fishbase (Froese & Pauly 2005). Fish surveys were always conducted at least 2 h after sunrise and 2 h before sunset. Individuals were recorded from the 4 major roving herbivore families (Acanthuridae, Kyphosidae, Scaridae, Siganidae) and territorial damselfish (Pomacentridae) to the lowest possible taxa (generally to species, always to genus) (see Table S1 in the Supplement).

Algal recruitment experimental design

To assess the influence of large herbivorous fish on algal recruitment in habitats dominated either by macroalgae or coral, cages were installed to exclude herbivores at each site-habitat combination. We installed 6 plots per treatment per site, and these were scrubbed clean once a month throughout the experimental period. The cages were triangular in shape, and measured 50 × 50 × 50 cm. The corners were marked with rebar, to which PVC coated wire mesh was attached. The mesh size used was 2.5 × 2.5 cm, which excluded most herbivores but allowed some small fishes and invertebrates inside the cages. In the context of this study, large herbivorous fishes are therefore considered as those excluded by the experimental cage mesh size. In the caged plots, the wire material covered all sides and the top of the plots. A skirting edge on the sides of the cages was designed to prevent large benthic invertebrates from accessing the cages. Open (uncaged) plots were marked with the rebar, and partial cages were used as a control for cage artefacts and consisted of one side and a roof to maintain the potential influence of the cage while allowing access to all herbivores. Some of the plots (70%) from all 3 treatments in the back-reef habitat became inhabited by territorial damselfish. These fish were included in analyses as a covariate

owing to their influence on benthic algal communities (see review by Ceccarelli et al. 2001). Urchins are not abundant on the benthos in the back-reef or lagoon habitats (Johansson et al. 2010), and they were never found in the experimental plots.

In each plot, 2 recruitment tiles were installed in August 2008 and collected in February 2009. The tiles measured 10 × 10 cm and were made from PVC. Although PVC is not a natural substrate, long-term algal recruitment experiments have demonstrated that algal community composition on this material is similar to communities that recruit on tiles made of natural materials such as dead corals (Hixon & Brostoff 1996). The tiles were sanded to roughen the surfaces, which created irregular depressions to allow algal attachment (Hixon & Brostoff 1996, Smith et al. 2001, 2010). Recruitment tiles were attached to a piece of horizontal wire mesh, which was elevated 10 cm from the benthos in each plot. This standardised the attachment substrate and avoided smothering of the tiles by sediment.

In February 2009, 6 mo after deployment, the 2 tile replicates from each plot were carefully removed and placed in individual Ziploc bags *in situ*. After collection, the tiles were frozen until laboratory processing. In the laboratory, each tile was thawed and rinsed with seawater to remove any sediment, and any small invertebrates were removed with forceps. To determine the percent cover of the algal community on the top surface of each tile, a point-intercept method was used by placing a transparent plastic sheet with a grid of 25 dots on top of each tile. Using a dissecting microscope, the algae or substrata present beneath each point were classified into one of the following categories: bare tile, CCA, encrusting fleshy algae, turf algae (red, green, or brown), and foliose macroalgae (which included erect macrophytes such as *Dictyota*, *Laurencia*, *Lobophora*, *Padina*, and *Sargassum*).

Following classification, algae from the tile were scraped and oven dried at 60°C for ≥48 h, after which the algae were weighed to 10^{-4} g. To estimate fleshy algae biomass (including encrusting fleshy algae, turf algae, and foliose macroalgae), HCl (10%) was then added to the vials to remove any carbonate associated with coralline algae. Vials were again rinsed, placed in the oven at 60°C for ≥48 h, and reweighed.

Data analyses

Separate principal coordinate analyses (PCO) were conducted to visualise differences in benthic

community cover, algal community composition, and fish community composition. Vector plots using Spearman rankings based on correlations >0.6 were overlaid on PCO plots to visualise relationships between variables and the ordination axes. Differences in total biomass of fleshy algae, roving herbivorous fish, and damselfish were tested using mixed effects analysis of variance (ANOVA) with habitat (2 levels) and time (3 levels) as fixed factors and site (2 levels) included as a random factor nested in habitat. Benthic cover and biomass of algal communities and roving herbivorous fish were used to assess patterns in their compositions using separate mixed effects permutational multivariate analysis of variance (PERMANOVA) with the same model design described above.

Mean percent cover on the top surface of the tiles was used to analyse the composition of the recruiting algal community. Data collected from the replicate tiles within each plot were averaged, and the averaged data used as the residuals for all analyses (i.e. at the plot level). We used a mixed effects permutational multivariate analysis of covariance (PERMANCOVA). Habitat (2 levels) and herbivory (3 levels) were included as fixed factors, with site (2 levels) included as a random factor nested in habitat. *Pomacentrus alexanderae* (damselfish) were included as a covariate because they established territories in 70% of the experimental plots in the back-reef. Following this, the mean percent cover of each individual functional group and total fleshy algal biomass were analysed using permutational ANCOVA using the same model.

All data were evaluated using p-values generated from 9999 permutations using Primer-E v6 (Clarke & Gorley 2006) with the PERMANOVA+ add-on package (Anderson et al. 2008). When the number of unique permutations was low, the Monte Carlo asymptotic p-value was used to assess statistical significance (Anderson 2005). Interaction or main effect terms were pooled when they were highly non-significant (p > 0.25) (Underwood 1997), and significant differences (p < 0.05) were investigated with pair-wise comparisons. Euclidean distance was the metric used to create resemblance matrices for all univariate data analyses and Bray-Curtis similarity was the metric used to create resemblance matrices for all multivariate data analyses. When necessary, the data were transformed to meet the assumptions of homogeneity (permutational analysis of multivariate dispersion, PERMDISP). Transformations for relevant data analyses are outlined in Tables S2–S6 in the Supplement.

RESULTS

Benthic community cover, algal biomass, and algal community composition

Multivariate analysis of the benthic community cover revealed a significant distinction between the lagoon and back-reef habitats, and between summer and autumn in both habitats (Table S2a in the Supplement at www.int-res.com/articles/suppl/m486p153_supp.pdf). The community composition was separated on the PCO1 axis (Fig. 1a), which explained 91.5% of the total variation (eigenvalue 49834), and the PCO2 axis explained 8.4% of the total variation (eigenvalue 5498). Spearman correlations indicated that differences between habitats were clearly driven by the dominance of foliose macroalgae and sand in the lagoon, and by dominance of live coral and EAM in the back-reef (Fig. 1a). The lagoon had an average of 29% macroalgae, 63% sand, and <4% live coral, EAM, and CCA cover, while the back-reef had an average of 48% live coral, 28% EAM, 16% sand, 5% macroalgae, and 2% CCA cover.

Total algal biomass showed a significant Habitat × Time interaction (Table S2b), with biomass greater in the lagoon compared with the back-reef during autumn only (Fig. 2a; Table S2b). There was a marked increase in algal biomass in the lagoon from 168 g DW (dry weight) m^{-2} in spring and summer to 748 g DW m^{-2} in autumn. Benthic algal community composition displayed significant differences between the lagoon and back-reef habitats (Table S2c). Spearman correlation indicated that *Sargassum* was highly correlated with the lagoon, while no particular algae were correlated with the back-reef (Fig. 1b). Throughout the study, foliose algae in the lagoon were dominated by *Sargassum* (88% algal community biomass) followed by *Hypnea* (9%). In the back-reef, *Sargassum* contributed 46% to the total algal community biomass, 25% *Turbinaria*, 13% articulated coralline algae, 6% *Lobophora*, and 4% *Dictyota*.

Herbivorous fish biomass and community composition

We recorded a total of 15 species of roving herbivorous fish from the Acanthuridae, Kyphosidae, Scaridae, and Siganidae families (see Table S1 in the Supplement). Initial phase parrotfish were recorded as a single group (*Scarus* IP). Four species of territorial Pomacentridae that feed on benthic algae were
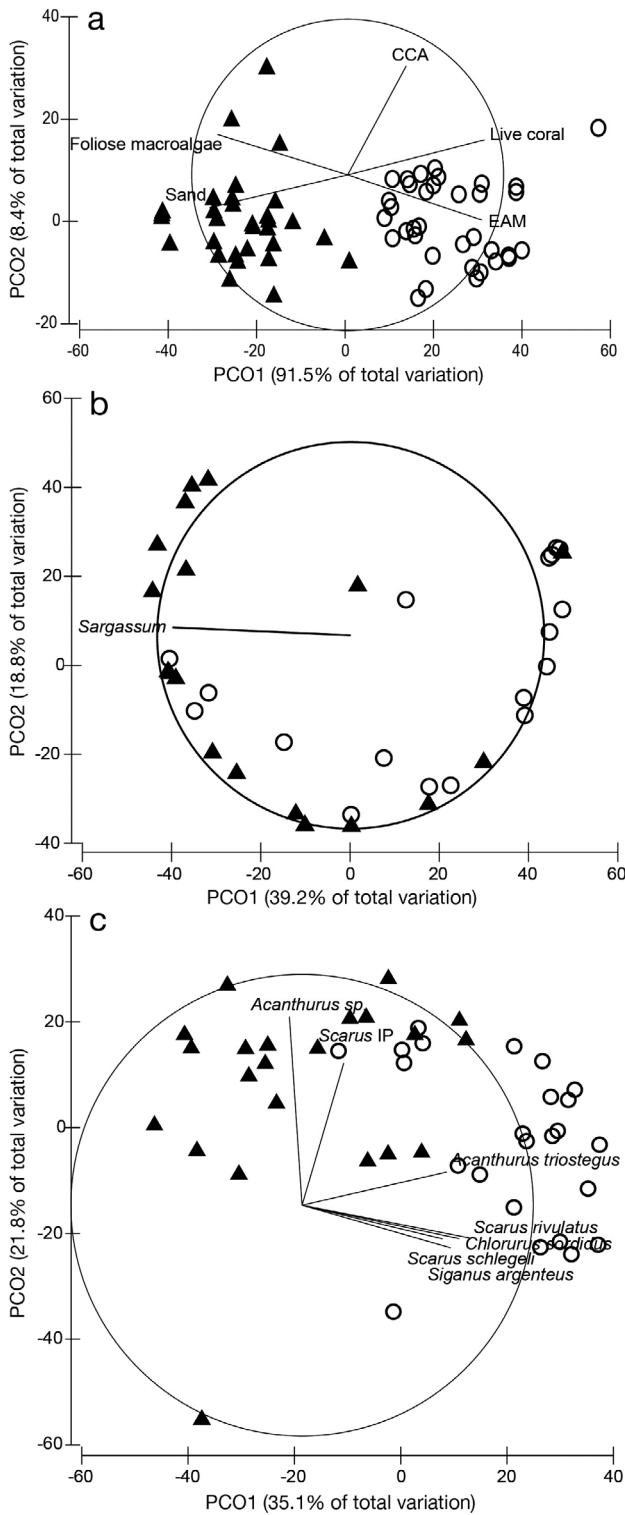
Fig. 1. Principal coordinate analyses (PCO) of (a) benthic community cover, (b) algal community composition, and (c) herbivorous fish community composition from lagoon and back-reef habitats at Ningaloo Reef. (▲) lagoon; (O) back-reef. Vector overlays represent correlations >0.6 based on Spearman ranking. CCA, crustose coralline algae; EAM, epilithic algal matrix
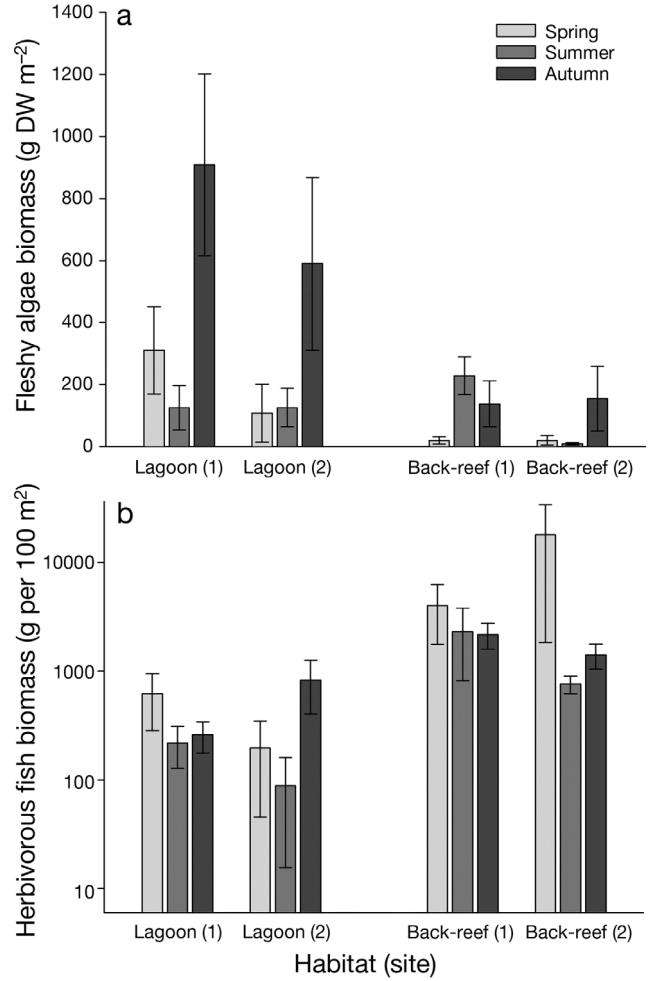

Fig. 2. Mean biomass (± SEM) of (a) fleshy algae and (b) herbivorous fish in the lagoon and back-reef habitats during spring, summer and autumn at Ningaloo Reef. Note the logarithmic scale on the *y*-axis for herbivorous fish biomass

recorded: *Hemiglyphidodon plagiometapon*, *Pomacentrus alexanderae*, *Stegastes fasciolatus*, and *S. obreptus*.

Total biomass of roving herbivorous fish differed significantly between the lagoon and back-reef habitats, where the biomass in the back-reef was at least an order of magnitude higher than the lagoon (Fig. 2b; Table S3a). In contrast to the benthic algal community, we detected no significant differences in total herbivorous fish biomass among times or sites (Table S3a). The herbivorous fish community composition also differed significantly between the lagoon and back-reef habitats, and we also detected differences among sites, but not among the times of the year (Table S3b). Although there was some overlap, the separation of fish communities between the

lagoon and back-reef habitats was clustered pre-dominantly on the PCO1 axis (Fig. 1c), which explained 35.1% of the variation (eigenvalue 31923). The second PCO axis explained 21.8%, and the third axis explained 13.6% (eigenvalues 21084 for PCO2 and 12520 for PCO3). *Acanthurus triostegus*, *Chlorurus sordidus*, *Scarus rivulatus*, *S. schlegeli*, and *Siganus argenteus* were correlated with the back-reef, while *Acanthurus* spp. and *Scarus* IP were correlated with both habitats.

Total damselfish biomass differed significantly between habitats ($F_1 = 282$, p = 0.003), but no significant differences were found among time or sites. Total damselfish biomass per 100 m^2 averaged 18 g in the lagoon and 369 g in the back-reef. *Pomacentrus alexanderae* was the only damselfish observed establishing territories in our experimental plots in back-reef habitats, and was observed indiscriminately establishing territories in all cage treatments (open, partial, closed).

Recruitment tile algal community composition and biomass

The community composition of the algae growing on the recruitment tiles was not significantly influenced by habitat, but was instead strongly affected by the experimental herbivore exclusion treatments (Table S4). Algal community composition was significantly different between tiles excluded from roving herbivores (closed treatments) compared with those exposed to roving herbivores (open and partial treatments; post-hoc analysis Closed ≠ Open = Partial). These differences were characterised by significantly higher cover of foliose macroalgae (Fig. 3b) and bare tile (Fig. 3a) in the roving herbivore exclusion treatment in both habitats (Table S5). The presence of *Pomacentrus alexanderae* damselfish significantly affected the community composition of the algae present on the recruitment tiles (Table S4). *P. alexanderae* territories were only established at plots in the back-reef sites, where their presence significantly increased turf cover (Fig. 3d) and decreased CCA cover (Fig. 3c) irrespective of roving herbivore exclusion treatment (Table S5). There was significant variability among sites in the multivariate analysis (Table S5) and for the CCA, turf, and foliose macroalgae cover in the univariate analyses (Table S5).

Following a similar pattern to total algal cover, the biomass of fleshy algae was significantly higher on tiles excluded from roving herbivores (closed treatments) compared with those exposed to roving herbi-vores (open and partial treatments; post-hoc analysis Closed ≠ Open = Partial) in both lagoon and back-reef habitats (Fig. 3f; Table S6). We found no significant differences in total algal biomass between habitats, and high variability among sites within each habitat (Table S6).

DISCUSSION

Our study has highlighted 3 important aspects of algal dynamics in a relatively intact coral reef ecosystem. First, contrary to our first hypothesis, we found no habitat effects on the recruiting algal community. Our *a priori* expectation was that algal recruitment on the experimental tiles would differ between habitats due to large differences in the benthic community and herbivorous fish assemblages described in Vergés et al. (2011). Instead, we found similar recruiting algal communities in the 2 habitats despite large differences in the adult, established communities of macroalgae. Given the close proximity of the 2 neighbouring habitats, and the water movement between the habitats that supports the exchange of particulate matter from the back-reef to the lagoon (Wyatt et al. 2010), this similarity in recruitment is likely to be due to a comparable supply of propagules. Second, in partial support of our second hypothesis, algal recruitment was highly influenced by herbivores, but this effect was surprisingly similar for algal communities in both lagoon and back-reef habitats despite major differences in their respective herbivorous fish communities, with back-reef herbivorous fish biomass being an order of magnitude greater than in the lagoon. Finally, although we detected clear and constant differences between lagoon and back-reef algal community composition, differences in algal biomass and cover were restricted to certain times of the year.

Similar to other recruitment studies that have identified the role of roving herbivores in limiting foliose macroalgal abundance in coral-dominated habitats (Belliveau & Paul 2002, Diaz-Pulido & McCook 2003, Burkepile & Hay 2006, Albert et al. 2008), large herbivores significantly influenced early algal community structure in both lagoon and back-reef habitats of Ningaloo Reef. Even though roving herbivore abundance was significantly lower in the lagoon compared with the back-reef, when herbivores were allowed access to graze the recruitment tiles there was no difference in algal cover or biomass between habitats; and when large roving herbivores were excluded, macroalgal cover and biomass similarly
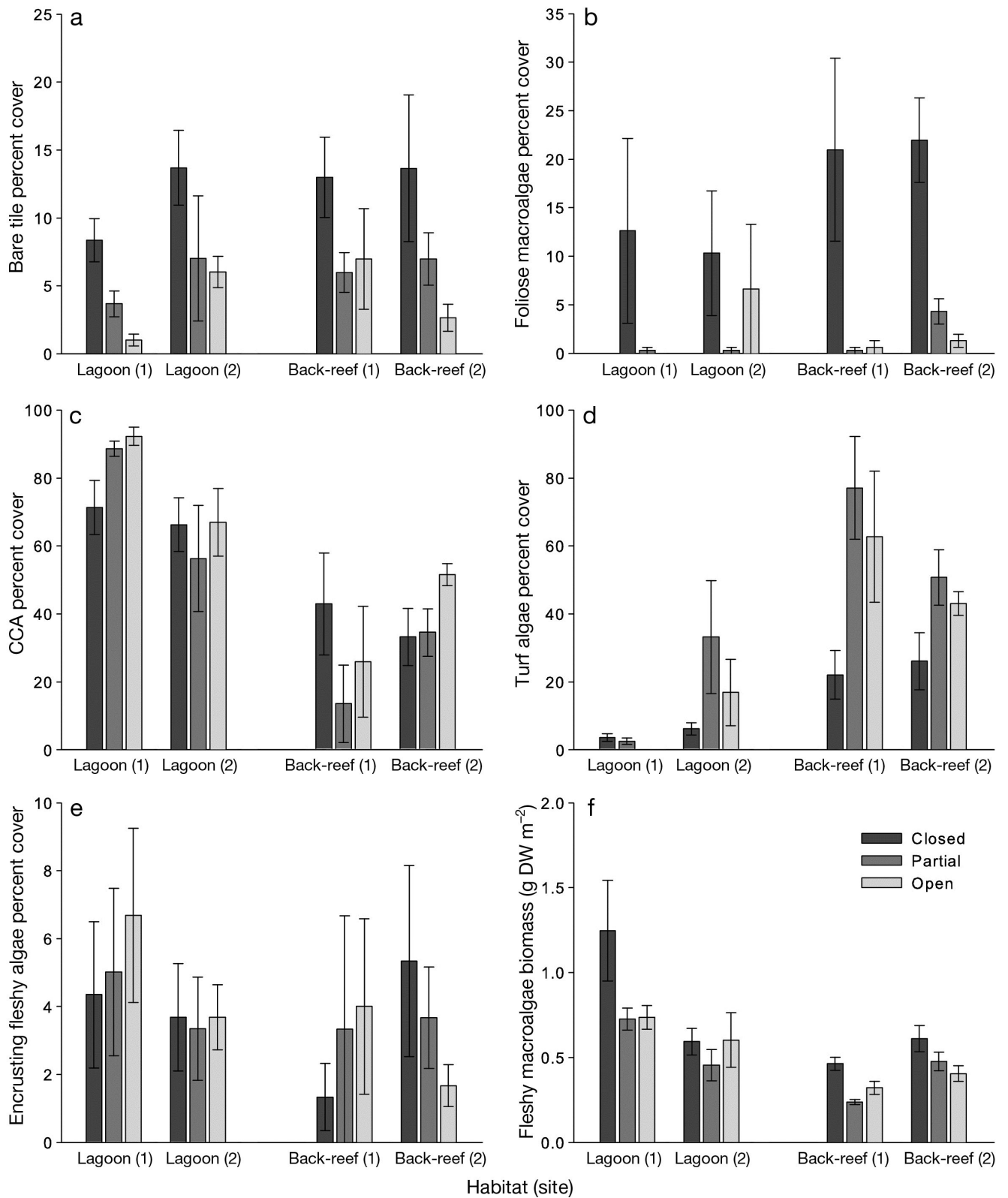
Fig. 3. Mean percentage cover (± SEM) of (a) bare tile, (b), foliose macroalgae (c) crustose coralline algae (CCA), (d) turf algae, and (e) encrusting fleshy algae, and (f) the mean biomass (± SEM) of fleshy macroalgae on recruitment tiles after 6 mo in lagoon and back-reef habitats depending on herbivore exclusion treatments. Note the different scales on the *y*-axes for each functional group. Closed = herbivores excluded; partial = cage with lid and one side only; open = no cage.

increased in both habitats. Although there was a trend towards higher biomass of foliose algae on the recruitment tiles in the lagoon, this was not statistically different at this early stage of development. The amount of bare space was higher when herbivores were excluded, suggesting that perhaps the foliose algae found on the recruitment tiles limited the growth of other algae (e.g. encrusting algae, CCA, turf). This may be due to competitive forces such as abrasion or shading, as has been demonstrated when temperate kelp limits algal understory growth (Kendrick et al. 1999). Our study clearly demonstrates that large herbivorous fish play an important role in structuring the community composition of algal recruits in both herbivore-rich and herbivore-depauperate coral reef habitats.

While large roving herbivorous fish similarly affected the cover and biomass of fleshy macroalgal recruits on the experimental tiles in both habitats, composition of algal recruits on the tiles was differentially influenced in the lagoon and back-reef by the presence of smaller territorial damselfish in the experimental plots located in the back-reef. The presence of territorial damselfish (*Pomacentrus alexanderae*) increased turf algal cover, however we cannot distinguish whether this was caused by direct (i.e. consumptive) or indirect (e.g. through increased nutrient supply via faeces) effects. Other studies have demonstrated that large roving herbivores have a significant influence on the broad benthic algal community structure (Mumby et al. 2006, Paddack et al. 2006, Fox & Bellwood 2007, Wismer et al. 2009, Vergés et al. 2011), while the farming practices of territorial damselfish can instead influence turf productivity and diversity at smaller scales (Klumpp et al. 1987, Ceccarelli et al. 2005, Gobler et al. 2006, Hoey & Bellwood 2010b). Territorial damselfish often chase away larger roving herbivores to protect the turf algal communities that they farm, influencing patterns of algal recruitment and succession (Hixon & Brostoff 1983, 1996, Ceccarelli et al. 2001, 2006). The farming behaviour of damselfish also generally reduces the establishment of large foliose macroalgae, through their selective removal from the EAM (e.g. Hixon & Brostoff 1996, Ceccarelli et al. 2001, Gobler et al. 2006, but see Hoey & Bellwood 2010b). Although we did not quantify their effect on the established algal community, the presence of territorial damselfish in the back-reef sites presumably influenced the high EAM cover in that habitat. These patches add to the spatial heterogeneity of algae in coral-dominated reef habitats, providing an important source of nutrition that supports a large portion of the secondary production in reef systems (Smith et al. 2001, Wilson et al. 2003).

Although benthic algal community composition differed markedly between habitats throughout the 6 mo period, total algal biomass and algal cover only differed between habitats during the autumn, which was characterised by a major increase in macroalgae in the lagoon. Similar to studies from the Great Barrier Reef that find seasonal increases in algal cover in autumn (Schaffelke & Klumpp 1997, Lefevre & Bellwood 2010), the increase of macroalgae found in the lagoon at Ningaloo Reef was dominated by *Sargassum*. However, the patterns observed in adult algal communities are not what we expected based on the results from our recruitment experiment. It appears that, although the herbivorous fish found in the lagoon were able to limit the recruitment of foliose algae in experimental plots, they were not able to prevent the marked increase in *Sargassum* biomass observed in autumn. This may be due to a number of reasons. On the one hand, algae may be escaping herbivory through size effects: as recruits grow into adult algal thalli they may become tougher, harder, less nutritious, or more easily recognised as unpalatable (Duffy & Hay 1990). Indeed, a previous study from the same location shows that herbivores have negligible effects on dominant adult algae such as *Sargassum myriocystum* and *Lobophora variegata* in lagoon habitats (Vergés et al. 2011). On the other hand, the inability of lagoon herbivores to constrain the periodic increase of adult foliose algae may be due to a 'resource saturation' effect comparable to the predator-saturation hypothesis that explains mass seeding events in plants (Janzen 1974, 1976). Under conditions of high algal productivity, herbivores may become satiated and unable to control algal growth, a process that has also been suggested to explain the limited role of herbivores in marginal coral reefs with high algal densities (Bennett et al. 2010). In contrast, the abundance and diversity of the herbivore community found in the back-reef habitat appears sufficient to consistently limit macroalgal growth. Therefore, it appears that while the herbivorous fish community in the lagoon was capable of limiting foliose algae on the settlement tiles, there was a periodic increase in algal growth that escaped this top-down effect.

It is interesting to note that while the intense herbivory found in the back-reef at Ningaloo Reef (Johansson et al. 2010, Vergés et al. 2011) consistently limited macroalgal abundance throughout the period of this study, it may also drive the higher algal diversity found in that habitat compared with the

lagoon. Although algae were only identified at a coarse taxonomic level (genus or functional group), we were nevertheless able to identify clear differences in diversity among habitats, with 12 macroalgal taxa inhabiting the coral-dominated back-reef versus only 7 in the lagoon. The enhanced algal diversity found in the back-reef is likely to be driven by the intense herbivory of roving herbivores and abundant damselfish, following the intermediate disturbance hypothesis (Hixon & Brostoff 1983, 1996). Additionally, many of the taxa found in the back-reef have physical or chemical defences (e.g. coralline algae, *Dictoyota, Lobophora, Turbinaria*) (Steinberg & Paul 1990, Mumby et al. 2005, Bittick et al. 2010), as a means of deterring grazing from roving herbivorous fish.

In our study, algal communities varied in lagoon and back-reef habitats at different spatial and temporal scales. Surprisingly, despite large differences in the herbivorous fish communities between lagoon and back-reef habitats at Ningaloo Reef, we found that grazing from large roving herbivores equally affected algal recruitment in both habitats. This suggests that relatively depauperate herbivorous fish communities such as those found in marginal or overfished coral reefs may be enough to control algal recruitment to the same levels as found in communities characterised by diverse and abundant herbivorous fish. However, our results show that, when herbivorous fish biomass and diversity are low, algae that are established within a habitat are able to escape herbivore control during periods of maximum algal growth. In this context, the role of browsers, i.e. herbivorous fishes that are able to consume adult macroalgae, emerges as particularly important in the prevention of shifts towards macroalgal dominance. Our findings are therefore consistent with a growing number of studies that recommend the development of coral reef management and conservation programmes that aim to specifically protect dominant browsing fishes (e.g. *Naso unicornis*, *Kyphosus* spp.) (Hoey & Bellwood 2009, Vergés et al. 2012, Michael et al. 2013).

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