

Identity and behaviour of herbivorous fish influence large-scale spatial patterns of macroalgal herbivory in a coral reef

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ABSTRACT: The functional role of macroalgae-consuming fishes is particularly important in coral reefs, as they can mediate the recovery of degraded systems when macroalgae become established. However, herbivory on coral reefs is often spatially and temporally variable, and the mechanisms that underpin variation in the consumption of algae are largely unknown. In this study, we examined local (within-reef, 100s of m) and broad-scale (regional, 100s of km) patterns of macroalgal herbivory along the spatial extent of Ningaloo Reef in northwestern Australia. Using underwater video cameras, we quantified the feeding rates of individual fish on a dominant macroalga *Sargassum myriocystum*, and we quantified social feeding behaviour to determine whether patterns in algal removal are influenced by whether fish feed as solitary individuals or as part of single-species or multi-species groups. While 23 fish species were observed biting macroalgae, spatial patterns in the intensity of herbivory were strongly driven by 3 species: *Naso unicornis*, *Kyphosus vaigiensis* and *K. bigibbus*. Feeding rates by individuals of these 3 species were always highest when individuals were part of monospecific groups, and we found a strong positive relationship between spatial patterns in the amount of macroalgae removed and the proportion of bites taken as part of groups, irrespective of fish size. This study highlights the importance of species-specific algae–herbivore interactions in coral reefs and shows that local variation in feeding behaviour is an important trait that contributes to explain spatial variability in macroalgal herbivory.

KEY WORDS: Herbivory · Macroalgae · Group feeding · *Naso unicornis* · *Kyphosus vaigiensis* · *Kyphosus bigibbus* · Ningaloo Reef

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INTRODUCTION

In coral reefs, herbivores are important for the persistence of healthy coral-dominated communities as they consume algae that can compete with corals for space (Connell et al. 2004, Hughes et al. 2007). Indeed, the removal of herbivores from coral reefs, be it

through overfishing (Jackson et al. 2001), disease (Hughes 1994) or experimental exclusion (Hughes et al. 2007), often results in the transition from a coral-dominated state to one dominated by stands of erect macroalgae (Done 1992, Ledlie et al. 2007, Hughes et al. 2007) and can have catastrophic effects upon ecological communities that depend on corals (Hughes

1994, Wilson et al. 2006, Pratchett et al. 2008, Paddock et al. 2009, Stella et al. 2011).

Herbivorous fishes are dominant primary consumers in coral reefs, but different species exhibit marked variation in feeding morphology (Bellwood & Choat 1990), behaviour (Fox et al. 2009), food choice (Choat 1991) and subsequent impacts on autotrophs and the underlying substrate (Bonaldo & Bellwood 2009). This variation can result in a suite of species playing different, but often complementary, roles (Burkepile & Hay 2008). Functionally, herbivorous fishes may be broadly classified into 2 distinct groups: 'grazers' and 'browsers' (Horn 1989). Grazing coral reef fishes include scrapers, excavators and detritivores (Bellwood & Choat 1990, Bonaldo & Bellwood 2009) that target various components of the epilithic algal matrix (EAM; sensu Wilson et al. 2003) and can therefore prevent the establishment and expansion of macroalgae via the removal of algal recruits. In contrast, browsers target large erect macroalgae and can therefore potentially reverse phase-shifts once algae become established (Bellwood et al. 2006, Hoey & Bellwood 2009).

In recent years, a focus on the varying feeding choices and feeding rates of different herbivorous fishes has provided new and useful insights on the role of these consumers in coral reefs (Mantyka & Bellwood 2007a, Burkepile & Hay 2010, 2011, Lefevre & Bellwood 2011). Using remotely-operated video cameras, these studies have provided important information on patterns of complementary feeding and redundancy among herbivorous fish species (Burkepile & Hay 2011) and have often revealed patterns different to those based on inferences from visual estimates of abundance by divers (Bellwood et al. 2006, Hoey & Bellwood 2009). Two of the most clear and interesting patterns emerging from these studies are that (1) even in high-diversity reefs such as the northern Great Barrier Reef (GBR), a subset of only 1–5 species are responsible for a disproportionate amount of the consumption of dominant algae such as *Sargassum*, although the identity of the species may vary from place to place (Bellwood et al. 2006, Mantyka & Bellwood 2007b, Fox & Bellwood 2008, Hoey & Bellwood 2009, Bennett & Bellwood 2011, Vergés et al. 2012), and (2) the total biomass of macroalgae consumed by herbivores varies widely among different coral reefs, even when they share apparently similarly communities of browsing herbivorous fish (Cvitanovic & Bellwood 2009, Hoey & Bellwood 2009, Bennett & Bellwood 2011). While the mechanisms that underpin variation in the consumption of algae among reefs are not yet fully under-

stood, local variation in feeding behaviour appears to play a significant role. For example, a recent study shows that differences in feeding propensity (i.e. whether a fish feeds given an opportunity) explain much of the latitudinal variation in algal consumption observed in the GBR (Bennett & Bellwood 2011). However, our knowledge about the effect of behaviour on feeding by herbivorous coral reef fishes has focused most strongly on species that feed on turf algae (Foster 1985, Reinthal & Lewis 1986, Wolf 1987), and we know comparatively less about how behaviour may influence consumers of macroalgae.

Group feeding is an important behavioural trait that strongly influences fish foraging rates. For instance, social foraging, as part of single species or multi-species groups, can enhance the ability of individual fish to locate and consume resources more rapidly, with successful foragers attracting other group members through behavioural cues associated with successful foraging (Pitcher & Parrish 1993, Lukoschek & McCormick 2000). In the safety of groups, individual fish can afford to spend less time in vigilance, and several studies show that grazers display greater foraging rates when feeding in a group compared to solitary feeding (Reinthal & Lewis 1986, Wolf 1987, Overholtzer & Motta 2000). Moreover, group feeding among grazing species can also allow access to preferred food resources by circumventing territorial attacks from aggressive competitors such as damselfish (Robertson et al. 1976, Foster 1985, Reinthal & Lewis 1986). While species that consume macroalgae, such as *Kyphosus* spp., *Naso unicornis* and *Siganus* spp., are known to display group feeding behaviour, we know little about how that behaviour may influence removal of macroalgae.

In this study, we used underwater video cameras to measure species-specific rates of herbivory on a dominant macroalga *Sargassum myriocystum* and to quantify group feeding behaviour of fish. Sampling was performed in 5 regions across ~300 km of Ningaloo Reef, Western Australia. Situated along the sparsely populated North West Cape, Ningaloo Reef is an arid-zone nearshore coral-reef system. This study addressed the following questions: (1) Is there variation in the identity and feeding rates of dominant consumers of algae among different sites (separated by 100s of m) and regions (separated by 10s of km)? (2) How prevalent is group feeding among species? (3) Does feeding rate increase with group participation and does that depend on whether they are single-species or multi-species groups? (4) Are regional quantitative differences in algal removal influenced by group feeding activity of the main species? In ad-

dition, the density of nominally herbivorous fish was estimated using underwater visual censuses, and this information was used to determine whether the observed feeding rates could be predicted by the biomass of the main consumers. Finally, since fish size can influence both feeding rates and social group membership, we also analysed the relationship between fish size, number of bites taken and whether fish were solitary or part of single-species or multi-species groups.

MATERIALS AND METHODS

Study site and structural complexity

This study was conducted during April and May 2009 on Ningaloo Reef, a fringing coral reef ~300 km in length (Fig. 1). Previous studies have indicated that recreational fishing influences fish assemblages at Ningaloo (Westera et al. 2003), so to minimise the potentially confounding effects of fishing on regional patterns, we selected 5 sanctuary (no-take) zones encompassing most of the latitudinal extent of the Ningaloo Marine Park (Bundegi 21° 51' S, 114° 10' E; Mandu 22° 05' S, 113° 52' E; Point Cloates 22° 44' S, 113° 39' E; Maud 23° 05' S, 113° 44' E; Gnaraloo Bay 23° 45' S, 113° 31' E). Within each region, sites were located at depths of 2–3 m in coral-dominated back-reef flat habitat (located a few meters inshore from the reef crest) since this zone supports the highest coral cover and is characterised by the highest herbivore biomass (Johansson et al. 2010, Vergés et al. 2011, 2012). Three sites were randomly selected within coral-dominated back-reef flat habitat at each region and spaced ~300 m apart (Fig. 1). Because structural complexity can strongly influence spatial patterns in fish herbivory (Vergés et al. 2011), a rugosity index ($n = 9$) was estimated at each site by laying a 10 m light chain along the substrate contour and measuring the equivalent straight line horizontal distance (Risk 1972). A 1-way analysis of variance using averaged rugosity values at each region confirmed there were no statistically significant differences in rugosity among regions ($F_{4,10} = 2.19$, $p = 0.14$).

Distribution of roving herbivorous fishes

The relative abundances of roving nominally herbivorous fishes (families Acanthuridae, Kyphosidae, Siganidae and tribe Scarinae within Labridae) from each site were quantified using timed visual cen-

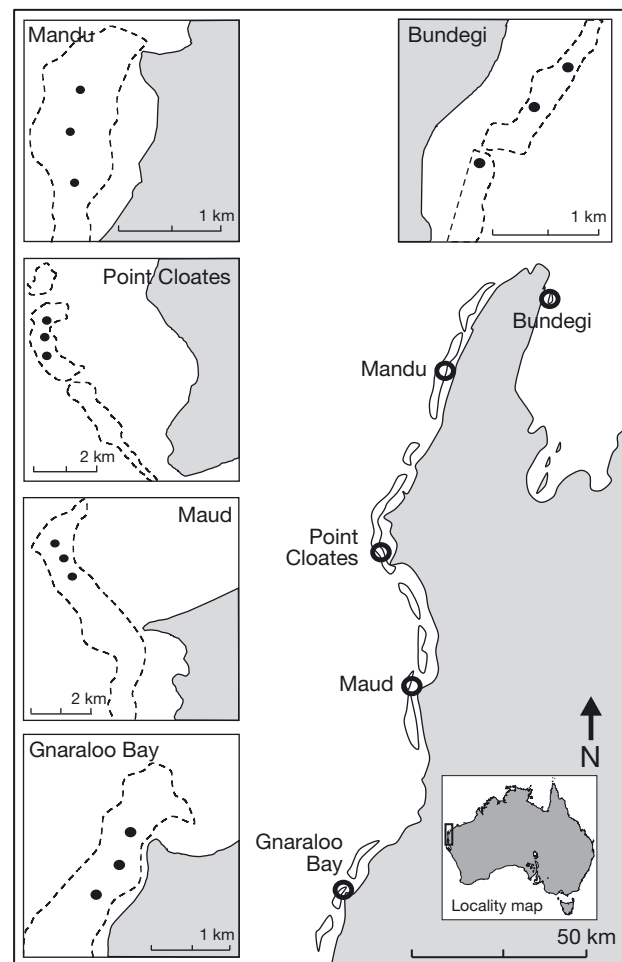


Fig. 1. Map of the Ningaloo Reef, Western Australia, indicating the regions (O) and sites (●) studied. Dashed lines show predominantly coral-dominated areas

suses. Underwater visual censuses (UVCs) were carried out on snorkel using 10 min timed swims parallel to the contour of the back-reef flat, encompassing the area of reef used for tethering experiments. The distance covered for each 10 min transect was measured by trailing an underwater measuring tape which was fixed to the reef at the starting point of each transect (mean distance of 100.7 ± 0.5 m). All nominally herbivorous fish species within a 5 m wide belt-transect, extending from the reef substratum to the sea surface, were recorded according to species, and sizes were estimated to the nearest 5 cm. All UVCs were conducted by the same observer (P. J. Michael). With the exception of the readily identifiable *Chlorurus sordidus* (Scaridae), all other dark coloured initial phase (I.P.) parrotfishes were recorded as a single group (*Scarus* I.P.). Similarly, mixed schools of fish that were likely to be a combination of *Acanthurus blochii* and *A. grammoptilus* (Acanthuridae) were

classified together as *Acanthurus* spp. due to difficulties in field identification. Two UVCs were carried out each of the 2 days that tethers were deployed at each site ($n = 12$ per region, see 'Materials and methods: Macroalgal tethers'), with a single UVC conducted immediately prior to the deployment of tethers, and another after the deployment period had ceased to minimise disturbance and any potential feeding deterrence to the herbivorous fish communities. Fish counts made from each of the UVCs were converted into densities (abundance) per unit area (ind. m^{-2}) using each individual transect area. Abundance estimates were then further converted into biomass estimates (g m^{-2}) using established length–weight relationships (Kulbicki et al. 2005).

Macroalgal tethers

Sargassum myriocystum was used to quantify variability in macroalgal removal by fishes. This species was selected because (1) it is the most abundant macroalga in Ningaloo Reef (Doropoulos et al. in press), (2) pilot studies indicated that it is highly palatable to herbivorous fishes, (3) it is readily identifiable in the field by a small conical disc holdfast giving rise to 3–6 main branches arranged spirally with spinous processes and no rhizoidal stolons (Modelo & Umezaki 1995), and (4) it is present in the adjacent lagoon habitats of most study regions. Importantly, *Sargassum* is the dominant genus following experimental exclusion of herbivores in many Indo-Pacific reefs such as the GBR (Hughes et al. 2007) and Ningaloo Reef (Webster 2007). *Sargassum* thalli were collected from lagoon habitats adjacent to the back-reef flat in each region, with the exception of Gnaraloo Bay where we did not find any large algal beds and thalli were instead collected from the closest region (Maud) where *Sargassum* occurred. Care was taken to minimise damage during collection by maintaining holdfasts intact. Thalli were transported back to the laboratory in catch bags and submerged in seawater in order to retain their moisture and turgidity. Prior to processing in the laboratory, the basal portions of multiple thalli were bundled with a rubber band to create the desired assay dimensions and excess water was removed using 10 standard spins (ca. 30 s duration) on a pull-cord salad spinner. The fresh weight of the tethers was then recorded using digital scales (mean \pm SE = 332.8 ± 2.8 g, $n = 360$) before being assigned a random identification label. Tethers were maintained in catch bags in the ocean overnight until deployment, and all plants were used within 18 h of initial collection.

Within each site, 6 replicate *Sargassum* tethers were haphazardly attached at least 5 m apart to bare substratum using plastic-coated garden wire. Wire and identification labels were concealed as much as possible. No tethers were placed within or near damselfish (Pomacentridae) territories, since territorial damselfishes can reduce the feeding rates and foraging effectiveness of other herbivorous fishes (Foster 1985, Hoey & Bellwood 2010b). A further 6 replicate tethers were deployed and protected from all herbivores by individual exclusion cages (50 cm L \times 50 cm W \times 75 cm H). A mesh size of 1.5 cm^2 was used to maximise water flow while fully restricting access by even small fishes. Each control tether was deployed near a treatment tether, forming a total of 6 paired treatment–control replicates for each sampling period. These 6 paired treatment–control *Sargassum* tethers were used to determine changes in biomass experienced by the algae over the deployment period due to factors other than herbivory (e.g. handling loss and abrasion). The physical proximity of each treatment–control pair was intended to account for potential variance in mass loss attributed to external factors jointly affecting both the control and the treatment algae (Prince et al. 2004). Deployment always occurred between 10:00 and 16:00 h, as this is the daily period when fish-grazing activity is highest in other coral reefs (Zemke-White et al. 2002, Fox et al. 2009). After 3.5 h, all tethers were retrieved and reweighed in the laboratory after removing excess water by spinning. This procedure was repeated on 2 different days at each of the 3 sites in all 5 regions of Ningaloo Reef ($n = 36$ treatment and $n = 36$ control tethers per region). The change in fresh weight of each treatment (uncaged) tether over the deployment time minus the change in fresh weight of its corresponding paired control (caged) tether provided us with an estimated measure of herbivory by fishes.

Video analysis: species-specific bite rates, fish size and group feeding behaviour

Stationary, high-definition video cameras were used to determine the contribution of herbivorous fish species to the consumption of the algal tethers, a technique that allows observations of feeding fishes without the potentially confounding effects of diver presence (Mantyka & Bellwood 2007a). Two video cameras (Sony-HDR SR12 in underwater housings) were simultaneously deployed at each site, each filming a randomly selected uncaged tether (i.e. 2 of the 6

deployed tethers were filmed). Video cameras were attached to concrete blocks and placed on the seabed 2–3 m from the selected tether, ensuring the entire tether could be viewed in the frame. During the initial seconds of filming, the camera focal length was calibrated using a scale bar of known length, which was later transposed onto the viewing monitor, where it was used as a reference scale to estimate the length of individual fishes. The cameras filmed continuously for the entire 3.5 h of deployment, which yielded 14 h of footage per site (i.e. 2 cameras \times 3.5 h \times 2 sampling days) and a total of 42 h of footage per region.

To quantify the bite rates of each fish species, we counted the total number of bites taken by individual fish on each filmed tether. All fish that were observed to bite on the tethered algae were identified to species level, with the exception of some indistinguishable I.P. scarids (family Labridae) that were classified together as *Scarus* I.P. A 'bite' was recorded only if the fish could be seen to apply its jaws to the tethered alga and close its mouth (following Mantyka & Bellwood 2007a). In those instances where individual bites could not be counted due to a succession of rapid bites without a discernable pause, the 'foray' was conservatively classed as a single bite event (Bellwood & Choat 1990). Bites from individuals >10 cm total length (TL) were tallied into 5 cm size-class categories. Fish sizes were converted into biomass, based on published length–weight relationships (Froese & Pauly 2005, Kulbicki et al. 2005) and using the midpoint of each size-class as the feeding individual's TL. Following Bellwood et al. (2006), bites were then converted into 'mass-standardised' bites (bite count \times feeding individual's body mass in kg) to account for differences in size, as larger individuals are likely to remove greater algal biomass per bite. This approach has limitations, as it assumes that bite volume scales directly with body size, and different species of similar size have the same bite volume, but is the most widely used approach in the literature to incorporate ontogenetic and interspecific variation in bite volume (Bellwood et al. 2006, Hoey & Bellwood 2009, Bennett & Bellwood 2011). Mass-standardised bite counts were expressed as bite rates (mass bites min^{-1}) by dividing the count for each species by the period when the algal tether was accessible for feeding. In those instances where the tether was grazed completely to its basal portions prior to the 3.5 h period, the available potential feeding time was adjusted to the time taken to complete feeding.

Group feeding behaviour was recorded during video analysis. A feeding observation was recorded every time a fish entered the video frame and took a

bite, and bites from each individual fish were counted until each individual left the video frame. If other fishes entered the video frame during that period, bites taken by other individuals were recorded as separate feeding observations. All bites taken by individual fishes were categorised into solitary, multi-species or single-species group feeding categories. Group feeding was considered to occur when 2 or more individuals from one or more species fed simultaneously (Lukoschek & McCormick 2000).

Algal cover

Since removal of algal biomass by fishes can be partially influenced by the abundance of macroalgae within the local area (Cvitanovic & Hoey 2010, Hoey & Bellwood 2010a, 2011), we measured algal cover at each site using 50 \times 50 cm photoquadrats positioned at 1 m intervals for 20 m, using 3 transects per site. Photos were analysed using Coral Point Count software (Kohler & Gill 2006), and 5 randomly assigned identification points per image were classified as either macroalgae or other substrata.

Statistical analyses

Variation in rates of consumption of *Sargassum* tethers ($n = 6$) was analysed with a 4-factor permutational analysis of variance (PERMANOVA), testing for differences for Region (fixed factor with 5 levels), Site (random factor with 3 levels nested within each region), Day (random factor with 2 levels nested within each site and region) and Camera (i.e. video camera presence; fixed factor with 2 levels). This last factor was included because the presence of a video camera on some of the assays could potentially influence fish behaviour and result in differences in algal biomass consumed. Analyses were based on the algal mass removed by fishes from the 6 tethered *Sargassum* replicates deployed each sampling day minus the mass loss by the controls. PERMANOVA, performed using 4999 unrestricted random permutations, was used to test for all univariate PERMANOVA analyses based on Euclidean distance measures, as estimates of sums of squares are equivalent to parametric ANOVA and permutations do not require the assumption of normality (Anderson et al. 2008).

Differences in Region, Site and Day for the mass-standardised bite rates of individual species on the filmed *Sargassum* tethers were examined using a 3-factor multivariate PERMANOVA with Region as a

fixed factor and Sites and Days as random nested factors. Analyses were conducted using Bray-Curtis dissimilarities to emphasise absolute differences and were based on square root-transformed data (to reduce the influence of abundant taxa on the analysis; Clarke & Warwick 2001) with 4999 unrestricted, random permutations of raw data. In order to identify the species that contributed most strongly to the removal of *Sargassum* biomass, we used a simultaneous multiple regression analysis. Mass standardised bite rates of the species responsible for >5% of bites in any region (7 species, see 'Results') were simultaneously regressed against the biomass removed from the corresponding filmed *Sargassum* tether. Species which accounted for <5% of bites in each region were pooled into higher taxonomic groupings for the analysis. Examination of partial correlations enabled us to identify the individual fishes (3 species, *Naso unicornis*, *Kyphosus bigibbus* and *K. vaigiensis*, hereafter referred to as the main browsers) that most influenced algal biomass loss. We then tested for differences in bite rates of these 3 species across Regions, Sites and Days using univariate ANOVAs. To determine whether levels of herbivory (expressed as removed grams of macroalgae) could be predicted by the biomass of the 3 main *Sargassum* consumers, as estimated by the UVCs, we used linear regressions averaging fish biomass and algae biomass variables at the Day level.

To establish the influence of group membership on the number of bites taken per individual fish by the 3 main browsers, we used univariate PERMANOVAs with social group category as a fixed factor (3 levels: single-species group, multi-species group or solitary). Bite counts from each filmed assay (each camera) were averaged for each social group category, and we combined data from all Sites and Regions for each species in the analysis. Similarly, the same design was used to determine the influence of social grouping on fish size. We used linear regressions to determine whether fish size could be used as a predictor of the number of bites taken per feeding observation by *Naso unicornis*, *Kyphosus bigibbus* and *K. vaigiensis*. In this regression analysis, we averaged the number of bites taken by each size-class in each filmed assay and combined the data from all Days, Sites and Regions. To determine spatial and daily variation in the number of bites taken as part of a group (single-species and multiple-species combined), we used ANOVA with Region as a fixed effect, Site as a random effect nested within each Region, and Day as a random effect nested on the interaction between Region and Site. Further, to

examine the influence of group feeding behaviour by the 3 main browser species combined on consumption of *Sargassum*, we used a regression analysis based on the proportion (%) of bites taken by the 3 browsers as part of a group (single-species and multi-species groups combined) within each filmed replicate and *Sargassum* biomass removed ($n = 59$, i.e. 12 filmed tethers per region minus 1 replicate loss due to camera malfunction).

Regional differences in algal cover were analysed using a 1-way ANOVA. We used linear regression to determine whether algal cover present at each site could predict levels of herbivory (expressed as grams of macroalgae removed). Both herbivory and percent cover of macroalgae were averaged at the Site level.

Prior to analyses, normality and equality of variances of the data were assessed by visual inspection of scatterplots and distribution of residuals, and where necessary data underwent transformation to improve assumptions. All data transformations are reported in the statistical tables of results. When overall significant differences were detected, a *posteriori* pairwise comparisons of means were performed using Tukey's HSD test (for univariate ANOVAs) or PERMANOVA's pairwise comparison tests (for permutational ANOVAs).

RESULTS

Consumption of tethered *Sargassum*

Rates of consumption of tethered *Sargassum* differed among regions of Ningaloo Reef (Table 1). *Sargassum* consumption in Point Cloates (245.6 ± 15.2 g) was higher than in any other region except Gnaraloo

Table 1. Results of ANOVA on biomass removed from *Sargassum myriocystum* tethers by fishes, testing for differences between Regions (50–300 km), Sites (<1 km), Days and video camera (Camera) presence. Parentheses indicate the levels each of the factors is nested within. **Bold** values indicate significance ($p < 0.05$)

Source of variation	df	MS	F	p
Region	4	167 000	6.585	0.008
Site (Region)	10	25 272	0.752	0.664
Day (Region × Site)	15	503 900	9.058	<0.001
Camera	1	56 550	11.584	0.012
Region × Camera	4	14 145	2.898	0.096
Site (Region) × Camera	10	4881.8	1.581	0.203
Day (Region × Site) × Camera	15	3087.8	0.833	0.643
Residual	120	3709		

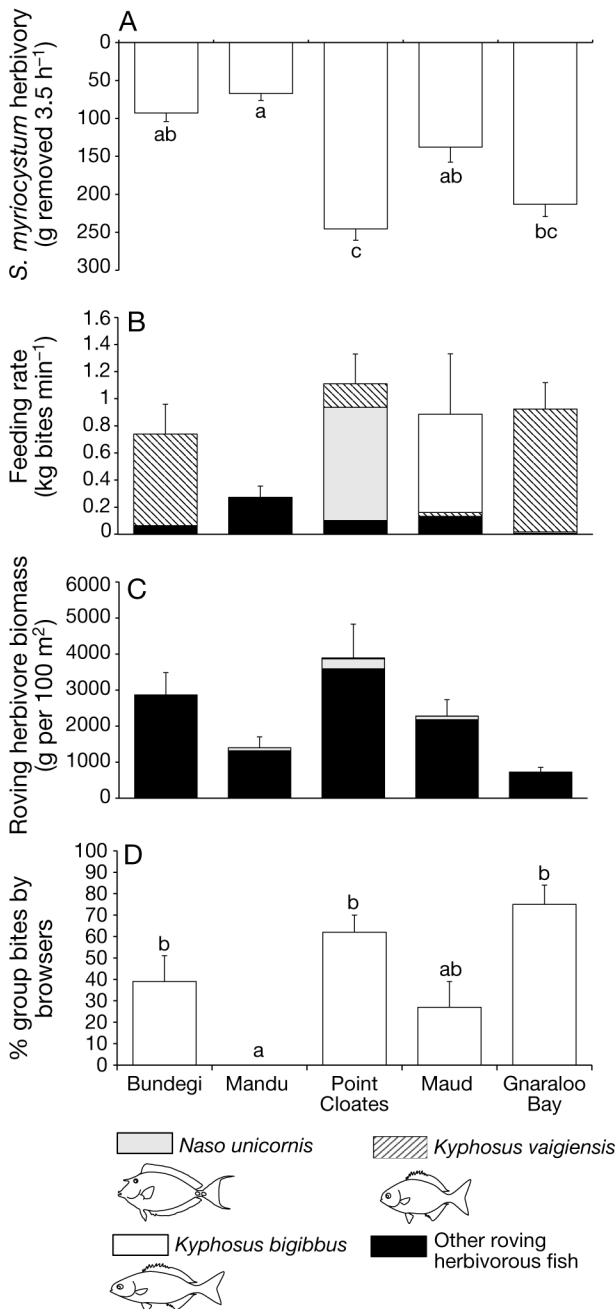


Fig. 2. Variation across the 5 regions of Ningaloo Reef for (A) herbivory on *Sargassum myriocystum* by fishes. Columns represent mean (\pm SE) biomass reduction from 36 replicate *S. myriocystum* tethers per region. Regional means sharing the same letter do not statistically differ. (B) Mean (\pm SE) feeding rate (kg bites min⁻¹) of herbivorous fishes recorded from video observations (n = 12 filmed replicates per region). (C) Mean (\pm SE) biomass (g per 100 m²) of the dominant macroalgal browsers and other roving herbivores (29 species pooled) encompassing the transplant experiment area (n = 12 underwater visual censuses per region). (D) Mean (\pm SE) proportion of bites taken by *Naso unicornis*, *Kyphosus vaigiensis* and *K. bigibbus* whilst part of a feeding group association (n = 12 filmed replicates per region)

Bay (213.2 ± 16.2 g) (Fig. 2A). *Sargassum* consumption rates also varied significantly between days (Table 1), but there were no consistent effects, i.e. consumption was sometimes greater on Day 1, and other times greater on Day 2. Variation among sites within regions was not statistically significant (Table 1); however, the presence of a video camera influenced consumption rates (Table 1), with filmed tethers losing on average ~20% less biomass than tethers that were not filmed (mean biomass consumed (\pm SE) in filmed tethers = 149.22 ± 14.86 g per 3.5 h, unfilmed tethers = 186.82 ± 9.64 g per 3.5 h).

Species-specific bite rates

Analysis of video footage yielded 32 395 bites from 23 fish species on the 59 filmed *Sargassum myriocystum* tethers (Fig. 3). There was significant regional and daily variation in the identity of the species observed feeding on the algal tethers, but not among

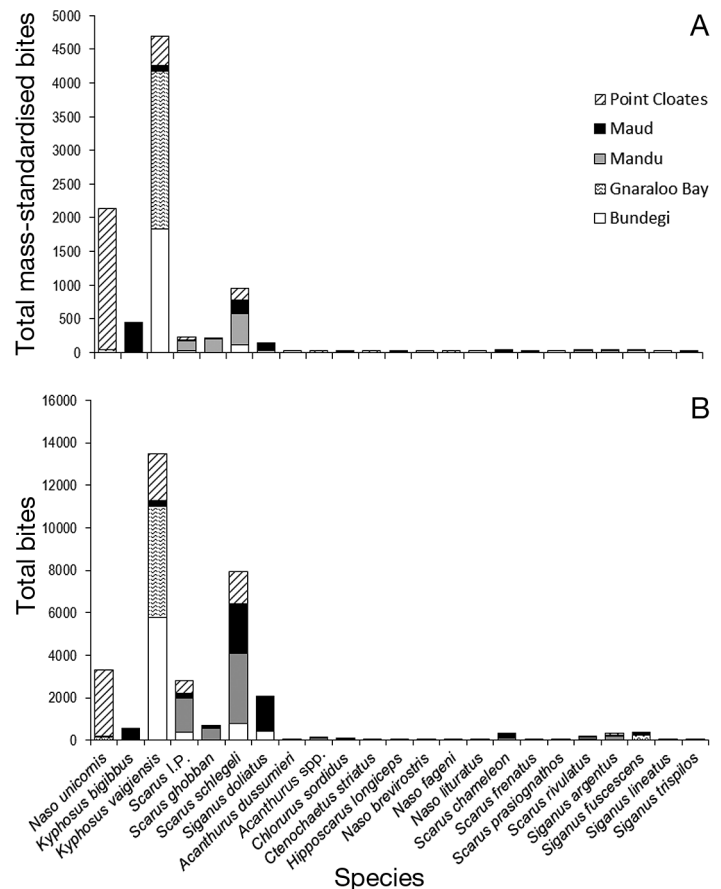


Fig. 3. Total number of (A) mass-standardised bites, and (B) raw bites, taken by fishes on the transplanted *Sargassum myriocystum* assays across 5 regions of the Ningaloo Reef, Australia. I.P.: initial phase

sites within region (Table 2A). *A posteriori* comparisons showed that species identity differed for each pairwise combination of regions (Monte Carlo $p < 0.05$), with the exception of Bundegi and Gnalaroo Bay, where a similar assemblage of fishes were observed feeding on the assays (Monte Carlo $p = 0.1770$). Seven species, namely *Naso unicornis*, *Kyphosus bigibbus*, *K. vaigiensis*, *Scarus* I.P., *S. schlegeli*, *S. ghobban* and *Siganus doliatus*, accounted for 95% of the bites (98% of mass-standardised bites). The bite rates of these 7 species explained approximately 73% of the variation in the loss of biomass from the filmed *Sargassum* tethers (Table 3; adjusted $R^2 = 0.73$). However, partial regressions indicated that, after accounting for autocorrelation in the data, only bite rates of *N. unicornis*, *K. bigibbus* and *K. vaigiensis* were significantly correlated with the reduction of *Sargassum* biomass from the filmed tethers (Table 3). The distribution of bites among these 3 taxa differed considerably across regions (Fig. 2B) and days (Table 2B). Point Cloates was characterised by the feeding of *N. unicornis*, which displayed significantly higher bite rates in this region (0.83 ± 0.19 kg bites min^{-1}) than elsewhere (Fig. 2B). Gnalaroo Bay and Bundegi displayed high bite rates of *K. vaigiensis* (0.90 ± 0.19 and 0.67 ± 0.21 kg bites min^{-1} , respectively; Fig. 2B). Maud was characterised by high bite rates of *K. bigibbus* (0.72 ± 0.46 kg bites min^{-1}), whereas Mandu was primarily characterised by higher rates of feeding by other species, comprising primarily parrotfishes (Fig. 2B).

Herbivore abundance

A total of 31 herbivorous fish species from the 4 dominant families (Acanthuridae, Kyphosidae, scarids within Labridae and Siganidae) were observed throughout the study, with the composition of fishes being dominated by species other than macroalgal browsers (Fig. 2C). Collectively, *Naso unicornis*, *Kyphosus vaigiensis* and *K. bigibbus* accounted for only 1–7% of herbivorous fish biomass across regions, yet were responsible for 85–99% of the bite rates on *Sargassum* being quantified in these regions (except in Mandu, where browsers were depauperate; Fig. 2B,C). The intensity of herbivory could not be predicted

Table 2. Results of ANOVAs examining variation in mass standardised bite rates (kg bites min^{-1}) of (A) all feeding species, and (B) the dominant macroalgal browsers separately, for Region (50–300 km), Site (<1 km) and Day. Parentheses indicate the levels each of the factors is nested within. Bite rate data (B) was square-root transformed. **Bold** values indicate significance ($p < 0.05$)

Source of variation	df	MS	F	p
A) All species				
Region	4	22863	9.00	< 0.001
Site (Region)	10	2539.30	1.00	0.476
Day (Region × Site)	15	2530.70	2.53	< 0.001
Residual	30	998.75		
B) Macroalgae browsers				
<i>Naso unicornis</i>				
Region	4	1.57	179.23	0.012
Site (Region)	10	0.01	0.07	1.000
Day (Region × Site)	15	0.12	16.94	< 0.001
Residual	30	0.01		
<i>Kyphosus vaigiensis</i>				
Region	4	1.68	7.13	0.007
Site (Region)	10	0.24	1.34	0.287
Day (Region × Site)	15	0.18	5.97	< 0.001
Residual	30	0.03		
<i>Kyphosus bigibbus</i>				
Region	4	0.45	2.17	0.011
Site (Region)	10	0.21	0.75	1.000
Day (Region × Site)	15	0.28	47.49	0.002
Residual	30	0.01		

Table 3. Multiple regression analysis examining the relationship between feeding species mass standardised bite rates (kg bites min^{-1}) recorded from video observations and the corresponding biomass removed from filmed *Sargassum myriocystum* assays. Analyses were based on square-root transformed feeding rate data. Overall model adjusted $R^2 = 0.73$ ($R^2 = 0.77$), $F = 16.49$, $p < 0.001$. Significant ($p < 0.05$) variables are in **bold**. I.P.: initial phase

	Total bites	Partial coefficient	SE	t	p
Macroalgae browsers					
<i>Naso unicornis</i>	3299	192.28	25.19	7.63	< 0.001
<i>Kyphosus vaigiensis</i>	13443	157.90	20.19	7.82	< 0.001
<i>Kyphosus bigibbus</i>	565	151.25	22.56	6.70	< 0.001
Grazers					
<i>Scarus ghobban</i>	647	76.97	104.92	0.73	0.466
<i>Scarus</i> I.P.	2793	−1.96	126.23	0.02	0.987
<i>Scarus schlegeli</i>	7922	42.47	63.52	0.67	0.507
<i>Siganus doliatus</i>	2065	−107.95	103.37	1.04	0.301
Other broad taxa (pooled)					
Other acanthurids	228	−12.97	196.21	0.07	0.947
Other scarids	655	−61.49	181.00	0.34	0.735
Other siganids	777	65.62	162.42	0.40	0.688

based on the abundance of macroalgal browsers as no relationship was evident between the mass loss of *Sargassum* and the biomass of either *N. unicornis* ($R^2 = 0.06$, $F_{1,28} = 2.1$, $p = 0.2$) or *K. vaigiensis* ($R^2 < 0.01$, $F_{1,28} = 0.1$, $p = 0.9$). *K. bigibbus* was not observed during any UVCs.

Group feeding behaviour and size effects

Naso unicornis, *Kyphosus vaigiensis* and *K. bigibbus* were each observed feeding upon the *Sargassum myriocystum* tethers as a part of groups and as solitary individuals. For all 3 species, whether a fish fed as part of a group or alone significantly influenced the number of bites taken per feeding observation, and bite numbers were always highest when feeding in single-species groups (Fig. 4A–C; Table 4A).

Naso unicornis was recorded feeding 587 times across all regions except Bundegi. This species fed as a solitary individual in 39% of these observations, and as part of a single-species and multi-species group in 30 and 31% of instances, respectively. Pair-wise comparisons showed that the number of bites taken by *N. unicornis* was significantly higher when

Table 4. Results of ANOVAs testing the effect of social grouping (single-species groups, multi-species group and solitary feeding) on the (A) number of bites and (B) total fish size of the 3 main browsers. *N. unicornis*: *Naso unicornis*. Note that *Kyphosus bigibbus* was only observed in one region, observed as either single-species groups or as solitary individuals, and all specimens were roughly of the same size (30–35 cm; i.e. size test not appropriate). All data were log-transformed prior to analysis. Significant ($p < 0.05$) effects are in **bold**

Source of variation	df	MS	F	p
(A) Number of bites				
<i>N. unicornis</i>				
Social grouping	2	1.31	9.81	<0.001
Residual	33	0.13		
<i>K. vaigiensis</i>				
Social grouping	2	9.19	28.52	<0.001
Residual	73	0.32		
<i>K. bigibbus</i>				
Social grouping	1	16.99	32.41	<0.001
Residual	8			
(B) Size of fish				
<i>N. unicornis</i>				
Social grouping	2	0.05	0.75	0.480
Residual	33	0.07		
<i>K. vaigiensis</i>				
Social grouping	2	0.14	2.11	0.13
Residual	73	0.07		

it was part of a single-species group than when it was feeding alone ($p < 0.001$; Fig. 4A). *N. unicornis* tended to take more bites while in single-species groups than in multi-species groups and more bites in multi-species groups than alone, but these trends were marginally non-significant ($p = 0.08$). We recorded a total of 1608 feeding observations by *Kyphosus*

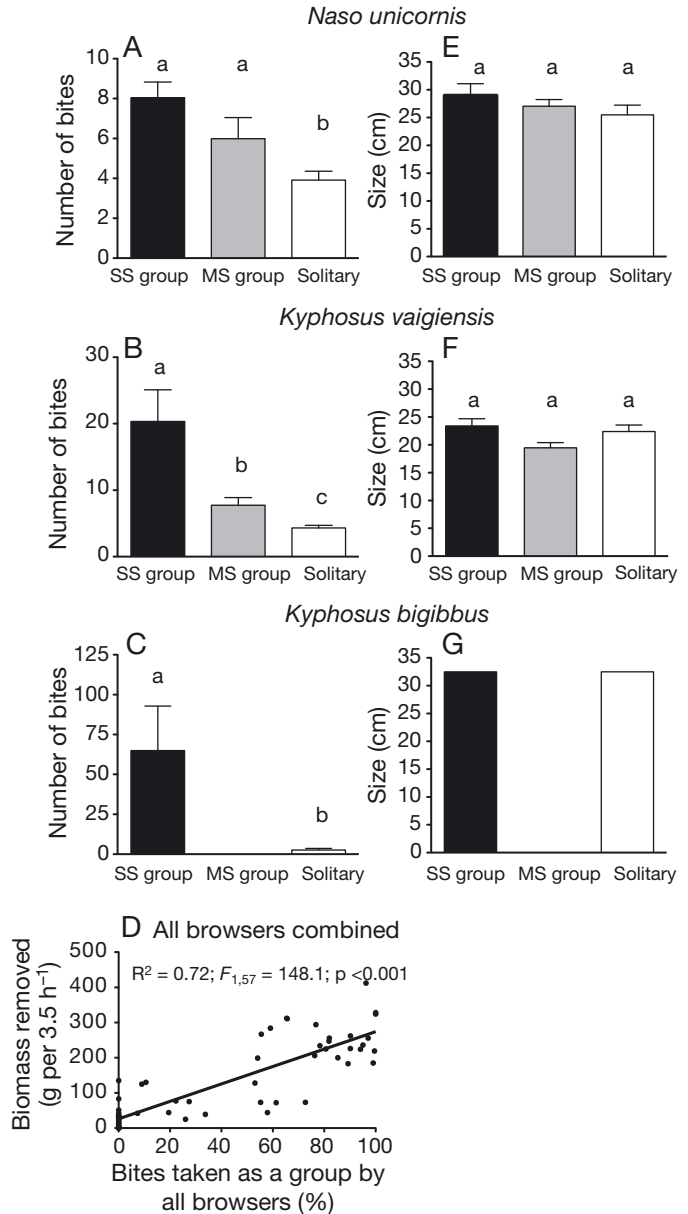


Fig. 4. (A–C) Mean number of bites (\pm SE) taken per individual fish by the 3 main browsers as a function of group feeding behaviour (SS = single-species group, MS = multi-species group, or solitary.) Note the different scales in the y-axis for the 3 browser species. (D) Relationship between proportion of bites taken as part of groups and *Sargassum myriocystum* biomass consumed. (E–G) Mean size (\pm SE) of fish as a function of group feeding behaviour. Means sharing the same lowercase letter do not statistically differ

vaigiensis across all 5 regions. In most instances, *Kyphosus vaigiensis* was observed feeding alone (57% of observations), followed by feeding in single-species (29%) and in multi-species (14%) groups. When feeding in single-species groups, the number of bites per feeding observation (i.e. per individual fish) for *K. vaigiensis* was roughly double that taken when feeding in multi-species groups, which was also significantly higher than when feeding alone ($p < 0.001$ for all pairwise comparisons, Fig. 4B). Finally, we recorded 29 feeding observations by *K. bigibbus*, all of them in Maud. In 76% of these instances, *K. bigibbus* fed as solitary individuals, while at other times it was observed feeding in single-species groups (we never observed this species feeding in multi-species groups). The number of bites taken by individual fish when feeding in single-species groups was significantly higher than when feeding alone ($p = 0.01$; Fig. 4C, Table 4A).

We found no significant differences in fish size among the different social groupings for any of the 3 browsers (Table 4B, Figs. 4E–G). Fish size did not influence the number of bites taken per feeding observation by *Naso unicornis* ($R^2 = 0.017$, $F_{1,34} = 0.58$, $p = 0.45$), or *Kyphosus vaigiensis* ($R^2 = 0.012$, $F_{1,78} = 0.93$, $p = 0.34$). All *K. bigibbus* individuals observed in the feeding assays were of the same large size (~32.5 cm, Fig. 4G), and this species was therefore not considered in any size analyses.

Group feeding (multi-species or single-species simultaneous feeding) occurred in all regions except in Mandu, where no group feeding was recorded by any of the 3 dominant browsers (Fig. 2C). Group feeding by the 3 main browsers was highest in Gnarlou Bay, Point Cloates and Bundegi, broadly reflecting regional patterns in *Sargassum* consumption (Fig. 2 & Table 5). We detected a significant positive relationship between the proportion of bites taken as part of a feeding group (including both multi- and

single-species groups) by these 3 species and *Sargassum* biomass removed ($R^2 = 0.72$, $F = 148.1$, $p < 0.001$; Fig. 4D).

Algal cover

There were significant differences in algal cover among regions ($F_{4,10} = 6.16$, $p = 0.009$, arcsine-transformed data). Post-hoc pairwise comparisons showed that algal cover was higher in Mandu and Maud (6 and 15% cover, respectively) than elsewhere (SNK $p < 0.05$). However, there was no relationship between the cover of macroalgae and rates of *Sargassum* removal ($F_{1,13} = 1.3$, $p = 0.31$).

DISCUSSION

Our study demonstrates high regional and daily variability in the rates of removal of macroalgae and in the identity of the main herbivorous fishes across the back-reef flat habitat of Ningaloo Reef. We identified 3 key taxa that dominated macroalgae consumption patterns (*Naso unicornis*, *Kyphosus vaigiensis* and *K. bigibbus*), all of whom displayed the highest feeding rates when foraging in single-species groups. Furthermore, we found a strong relationship between regional variation in the proportion of bites taken as part of groups and the biomass of macroalgae removed.

The social feeding behaviour of *Naso unicornis*, *Kyphosus vaigiensis* and *K. bigibbus* ranged from solitary to single-species and multi-species group feeding, as has been observed in other surgeonfishes and kyphosids (Eristhee & Oxenford 2001, Meyer & Holland 2005). Feeding rates by the 3 dominant consumers of macroalgae were always higher when individuals were part of a group, and this is consistent with the behaviour displayed by EAM grazing fishes (Reinthal & Lewis 1986, Wolf 1987, Overholtzer & Motta 2000). Moreover, the highest number of bites was generally taken by individuals that were part of single-species groups. Such monospecific social foraging is thought to increase the food intake of individuals by enhancing their ability to locate specific food items, especially when these are either scarce or patchily distributed (Krebs et al. 1972). Indeed, macroalgae are usually present in low abundances in healthy coral-dominated habitats and tend to be patchily distributed (Wismer et al. 2009, Vergés et al. 2011). This type of social facilitation in foraging is particularly well-known for flocking birds (Krebs

Table 5. Results of ANOVA on percentage of bites taken as a group by the 3 main browsers (*Naso unicornis*, *Kyphosus vaigiensis* and *K. bigibbus*) testing for differences between Regions (50–300 km), Sites (<1 km), and Days. Percentage group feeding data were arcsine transformed for the analysis. Parentheses indicate the levels each of the factors is nested within. **Bold** values indicate significance ($p < 0.05$)

Source of variation	df	MS	Pseudo-F	p
Region	4	10186	6.418	0.007
Site (Region)	10	1587	0.9	0.562
Day (Region × Site)	15	1755	5.693	<0.001
Residual	30	308.3		

et al. 1972), and our results suggest that it may also be an important strategy for macroalgae-consuming fishes. While group feeding can confer substantial benefits to individuals, associated costs also need to be acknowledged, as increased competition for limiting resources is likely to be most intense in single-species groups due to greater niche overlap (Powell 1989). Consistent with this, aggressive territorial behaviour was observed in this study, as juvenile *K. vaigiensis* often chased other herbivorous fishes from the filmed tethers during feeding (P. J. Michael pers. obs.), and this type of behaviour has been identified for other macroalgae consuming kyphosids (Hamilton & Dill 2003). We note that since the trade-off between the costs and benefits of group membership varies as a function of group size (Hoare et al. 2004), the size of feeding aggregations may therefore also influence feeding rates. However, group size was not measured in this study.

We found a strong relationship between social feeding behaviour by *Naso unicornis* and *Kyphosus* spp. and the amount of algal biomass removed in the different regions, and this was independent of the total number of simple bites taken by fishes. For example, *Sargassum* mass loss was nearly 2 and a half times greater in Gnaraloo Bay than in Bundegi even though the overall number of bites taken by the dominant browser *K. vaigiensis* did not differ between the 2 regions. At Bundegi, kyphosids took more than half the total bites whilst feeding as individuals, whereas schools of up to 15 simultaneously feeding fishes took on average 80% of the bites in Gnaraloo Bay. This increase in the number of bites taken by individuals when they are in a group is presumably due to factors such as decreased time invested in vigilance when feeding socially, as described for other species (Pitcher & Parrish 1993). These results suggest that the extent to which feeding behaviour alters efficiency in macroalgal consumption can explain some of the variability that is regularly recorded in macroalgal removal across space and time. In turn, a number of factors may be mediating regional variation in the formation of groups. For instance, individual fish modify their choice of groups in response to ecological factors such as food availability and predation risk (Hoare et al. 2004). Although we did not measure predator abundance or predation risk, the regional differences recorded in group feeding are broadly consistent with the theoretical prediction that group feeding will be less favoured in the presence of relatively abundant macroalgae, as the number of bites taken as part of a group was lowest in the 2 regions with greatest algal cover (Mandu and

Maud). The formation of groups may also be influenced by fish abundance (i.e. species may be more likely to school at higher densities), but we found no consistency between the biomass of the main browsers (as measured using UVCs) and group feeding. Fish size can also influence group membership and feeding rates among grazers (Bruggemann et al. 1996), but this was not observed on the 3 main browsers in this study. Finally, stochastic and uncertain elements in the foraging environment are also likely to influence feeding behaviour. This was reflected in our study by significant daily variation in all variables measured, i.e. the amount of algae removed, the number of bites taken by fish (both collectively or by the key browsers), and the percentage of bites taken as part of a group.

Despite observing 23 species feeding on *Sargassum* across Ningaloo Reef, patterns in macroalgal removal were largely due to just 3 species: *Naso unicornis*, *Kyphosus vaigiensis* and *K. bigibbus*. The dominance of *N. unicornis* and kyphosids in this west-continental coral reef system supports and extends previous findings from Ningaloo and other Indo-Pacific reefs such as the inner- and mid-shelf GBR, which have also identified these taxa as responsible for a disproportionate amount of algal consumption (Bellwood et al. 2006, Mantyka & Bellwood 2007b, Fox & Bellwood 2008, Cvitanovic & Bellwood 2009, Hoey & Bellwood 2009, Bennett & Bellwood 2011, Vergés et al. 2012). Other roving herbivorous species played only a minor role in the removal of macroalgal biomass, despite high bite counts by several species, especially the parrotfishes *Scarus schlegeli*, *Scarus* I.P. and *S. ghobban*. These scarids were observed taking small, rapid bites when feeding (i.e. small and fast opening and closing of the jaws) and appeared to be feeding on epiphytes or surface detritus. These findings are consistent with other studies that also record minor effects by these groups of grazing fishes on macroalgal tethers in this same coral reef system (Vergés et al. 2012) and elsewhere (e.g. Bellwood et al. 2006, Fox & Bellwood 2008, Fox et al. 2009) and is supported by studies based on jaw morphology and field observations that identify these scarids as scrapers (Bellwood & Choat 1990). In contrast, the success of *N. unicornis* and kyphosids in consuming tethered *Sargassum* is not surprising, since these fishes are among a small group of coral reef fishes that are morphologically and physiologically capable of consuming furoid macroalgae (Clements & Choat 1997, Choat et al. 2004, Crossman et al. 2005).

The removal rate of *Sargassum* was not related to the biomass of macroalgal browsers observed in

UVCs. In fact, one of the main consumers of tethered *Sargassum*, *Kyphosus bigibbus*, was never detected during visual censuses, yet in the absence of divers (as shown by video) they fed in groups of greater than 15 individuals and had a dramatic impact on the *Sargassum* tethers. Conversely, although *Naso unicornis* was observed during UVC in Bundegi and Mandu, it was not shown to feed in these regions at all. These results highlight the fact that species critical to the healthy functioning and resilience of reef systems may go unnoticed through the single-handed use of underwater visual observations of fish communities, as has been shown in various other studies (Fox & Bellwood 2008, Cvitanovic & Bellwood 2009, Hoey & Bellwood 2009).

In this study, we detected a significant bias in algae biomass removed that was due to the presence of video cameras. Filmed algal assays lost about 20% less biomass than neighbouring algal assays that were not filmed, which suggests that the feeding rates quantified using video footage represent a slight underestimation of real consumption rates. Although in recent times there has been a plethora of studies using video cameras to quantify species-specific rates of herbivory in coral reefs (Bellwood et al. 2006, Mantyka & Bellwood 2007b, Fox & Bellwood 2008, Bennett & Bellwood 2011, Vergés et al. 2012), few studies have formally investigated the potential effects of video camera observations (Hoey & Bellwood 2009), and it is therefore possible that this bias applies to other studies. The use of recently developed smaller, less intrusive video cameras in future studies might reduce this bias, but our results highlight the need to include all potential sources of variation in statistical analyses so that biases can be identified.

Given the unprecedented worldwide decline in coral reef health in recent decades (Gardner et al. 2003, Pandolfi et al. 2005, Bruno & Selig 2007), and subsequent urgent calls for process-oriented research and management (Hughes et al. 2003, 2005, Folke et al. 2004), understanding variation in ecological processes such as herbivory that promote the ability of coral reefs to recover from disturbances is essential. We are currently moving beyond just recognising the importance of the entire herbivorous guild in shaping benthic communities to acknowledging the species-specific quantitative nature of these algal–herbivore interactions. In this study, the use of remote video cameras has provided an insight into the highly variable patterns of macroalgal herbivory, whereby species identity and the relative amount of group versus solitary feeding explained much of the variation in rates of herbivory observed.

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