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REPORT

Small herbivores suppress algal accumulation on Agatti atoll, Indian Ocean

Nicole H. Cernohorsky[1] · Timothy R. McClanahan[2] · Idrees Babu[3] ·
Michal Horsák[1]

Abstract Despite large herbivorous fish being generally accepted as the main group responsible for preventing algal accumulation on coral reefs, few studies have experimentally examined the relative importance of herbivore size on algal communities. This study used exclusion cages with two different mesh sizes (1 × 1 cm and 6 × 6 cm) to investigate the impact of different-sized herbivores on algal accumulation rates on the shallow (<2 m) back-reef of Agatti atoll, Lakshadweep. The fine-mesh cages excluded all visible herbivores, which had rapid and lasting effects on the benthic communities, and, after 127 d of deployment, there was a visible and significant increase in algae (mainly macroalgae) with algal volume being 13 times greater than in adjacent open areas. The coarse-mesh cages excluded larger fishes (>8 cm body depth) while allowing smaller fishes to access the plots. In contrast to the conclusions of most previous studies, the exclusion of large herbivores had no significant effect on the accumulation of benthic algae and the amount of algae present within the coarse-mesh cages was relatively consistent throughout the experimental period (around 50 % coverage and 1–2 mm height). The difference in algal accumulation between the fine-mesh and coarse-mesh cages appears to be related to the actions of small individuals from 12 herbivorous fish species (0.17 ind. m^{-2} and 7.7 g m^{-2}) that were able to enter through the coarse mesh. Although restricted to a single habitat, these results suggest that when present in sufficient densities and diversity, small herbivorous fishes can prevent the accumulation of algal biomass on coral reefs.

Keywords Ecological redundancy · Diet specialization · Macroalgae · Phase shifts · Size-dependent processes

✉ Nicole H. Cernohorsky
nicole.cernohorsky@gmail.com

1 Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, Brno 61137, Czech Republic

2 Marine Programs, Wildlife Conservation Society, Bronx, NY 10460, USA

3 Department of Science and Technology, Coral Reef Research, UT of Lakshadweep 682555, India

Introduction

Coral reefs are losing coral cover from multiple stresses and frequently becoming dominated by various types of algae (Hughes 1994; Sheppard 2003; Graham et al. 2006; Bruno and Selig 2007; Hughes et al. 2010; Anthony et al. 2011). Whether these changes are permanent ecological phase shifts or temporary successional transitions is a topic of considerable debate (Dudgeon et al. 2010; Zychaluk et al. 2012; Mumby et al. 2013). Nevertheless, numerous similar changes or shifts have been documented in various terrestrial, freshwater, and other marine ecosystems (Steele 1998; Scheffer et al. 2001). On tropical coral reefs, the transition from coral- to macroalgal-dominated communities represents a fundamental change in the structure and function of the reefs, and the ecosystem goods and services they provide (Bellwood et al. 2006; Hughes et al. 2007; Graham et al. 2013). Consequently, it is increasingly important to understand the factors that influence and control the coral–algae balance.

Herbivores are viewed as key functional components of coral reefs that maintain the coral-dominated state of the ecosystem (Bellwood et al. 2004). Through their feeding activities, herbivores prevent algal proliferation, thus lower the competition between coral and algae (Rasher and Hay 2010), and facilitate coral recruitment by providing suitable substratum for the attachment of coral larvae (Hughes et al. 2007; O'Leary et al. 2013). With global climate change and the increasing occurrence of disturbances, such as coral bleaching, the maintenance of coral-dominated reefs will be increasingly reliant on functionally intact herbivore assemblages. The two main herbivorous groups responsible for keeping algae in check and promoting resilience on tropical coral reefs are fish and sea urchins, although fish are usually the most dominant herbivore on intact coral reef systems (Bellwood et al. 2004; McClanahan 2008). Although numerous studies have examined effects of herbivory on the coral–algal balance (Hay 1984; McCook 1996; McClanahan 2014), the role that different species or functional groups of herbivores play is only recently being appreciated (Hoey and Bellwood 2009; Hoey et al. 2013; Rasher et al. 2013; Hamilton et al. 2014; Humphries et al. 2014).

Larger herbivorous fish have been predicted to be more important than smaller herbivorous fish in terms of removing algae. Although small herbivorous fishes have been shown to have higher feeding rates and graze larger areas of the reef per unit body mass, most small fishes only crop the algae and do not remove it completely from the substratum (Bonaldo et al. 2014). In contrast, larger herbivores have slower feeding rates and larger bites and graze smaller areas per unit body mass, but remove the algae completely along with carbonate substratum, thus providing new open space for coral recruitment (Bonaldo and Bellwood 2008). Apart from this impact, total algal intake has also been shown to correlate positively with the fish body biomass (Bruggemann et al. 1994; Bonaldo and Bellwood 2008; Lokrantz et al. 2008). Therefore, large individuals and species are considered of prime importance in preventing algal dominance (Lokrantz et al. 2008; Norström et al. 2009; Edwards et al. 2014; Steneck et al. 2014). However, the term "large herbivores" may be context specific; for example, studies using exclusion cages have defined large herbivores as those unable to pass through chosen mesh sizes. The mesh areas used in experimental studies have, however, varied from 0.25 to 100 cm^2 (Hughes et al. 2007; Jayewardene 2009; Hoey and Bellwood 2010; McCauley et al. 2010; Trapon et al. 2013) and in some cases were not described. Variable definitions and cutoffs can, therefore, lead to ambiguity and result in different ecological responses to what can be interpreted as vague size-based management recommendations.

Most studies using exclusion cages to assess the impact of large herbivores on the benthos used small 1–9 cm^2 mesh (Smith et al. 2001; McClanahan et al. 2003; Hughes et al. 2007; Mörk et al. 2009). These cages exclude not only large herbivores but also nearly all size classes of herbivorous fish and sea urchins and allow only very small fishes and mesoherbivores (such as crustaceans) to enter the cages. In this study, we assessed the relative importance of large herbivores and define them as those unable to pass through 6-cm-wide meshes. We compared algal accumulation rates in various cages and meshes of an oceanic coral reef atoll of the Lakshadweep Islands, a largely unfished location. The remote location and reliance of the human population on tuna fishing provided an opportunity to reduce possible interactive effects between water quality, fishing, and body size that might otherwise confound studies in eutrophied or heavily fished reefs.

Materials and methods

Study area

Agatti atoll and its back-reef on the southwest side (Fig. 1a) were chosen for this study, due to the following characteristics: relatively large lagoon separating the reef from the populated island, high coral coverage, macroalgae being uncommon, and unfished reef fish populations because most fishermen from this island solely target pelagic fish, with few exceptions during the rough southwest monsoon. Agatti atoll is part of Lakshadweep Archipelago, situated off the west coast of India located between 8–12°N and 71–74°E. Lakshadweep forms the northernmost part of the Chagos–Maldives–Laccadive Plateau (Fig. 1a). It has a total of 32 km^2 of land made up of 27 islands, from which 11 are inhabited by a total of 64,000 people—the average density being $\sim$2000 individuals per km^2. Despite the high density of people on the island, their main sources of income are artisanal tuna fisheries and dried coconut production and no one was ever observed fishing on the coral reefs during our survey. This cultural habit of targeting skipjack tuna using the traditional pole and line fishing is common for the southern offshore islands of India and has left the reef and reef-associated species largely intact.

In 1998, the reefs experienced extensive coral bleaching and mortality. There are few reliable estimates of benthic reef communities for Lakshadweep reefs prior to 1998. Arthur et al. (2006) states that before the major bleaching event in 1998, benthic composition was similar to Maldivian and Chagos reefs, with estimates of 60–90 % coral cover, which are consistent with large-scale compilations of coral cover in this region (Ateweberhan et al. 2011). The recovery after the bleaching event was very site specific (Arthur et al. 2006); however, in many places, the recovery
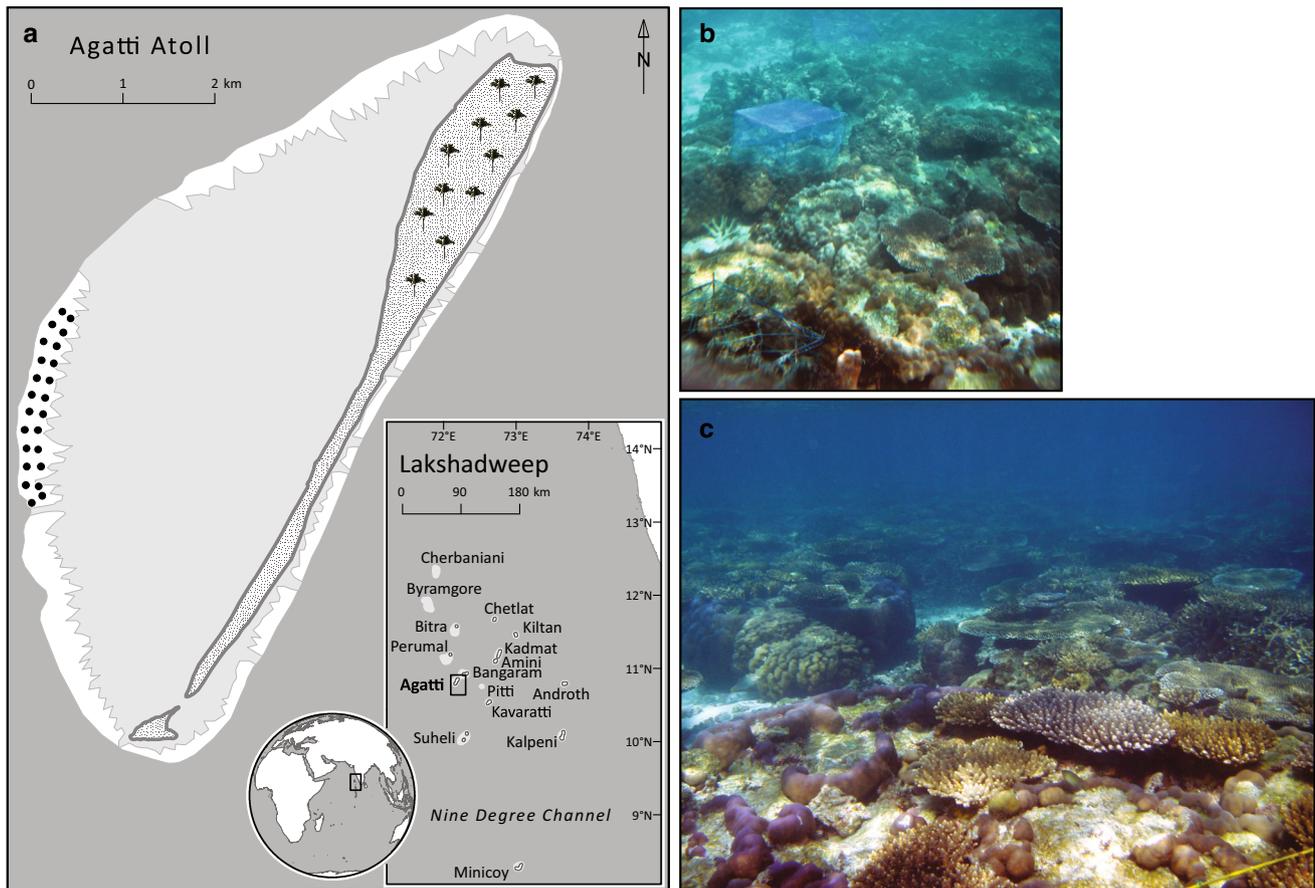
Fig. 1 Study location: **a** map showing the location of Lakshadweep islands, Agatti atoll (*gray* patterned area). The 24 sites (*black dots*) are situated in 12 pairs on the back-reef of the atoll starting from the main channel and distributed south along the atoll rim. Photographs of installed cages **b** and the back-reef habitat **c**; credit, N. H. Cernohorsky

was rapid. The back-reef of Agatti had an average of ~40–50 % coral cover during the study period and reached 80 % coral cover in some areas (NH Cernohorsky, pers obs; Fig. 1b, c).

Experimental design

We investigated the ecological impacts of using size-selective exclusion cages on the coral-dominated back-reefs of Agatti atoll (Fig. 1). We used two types of exclusion cages that differed in mesh size: (1) full cages with small 1×1 cm mesh (referred to as fine-mesh cages, *FM*) designed to exclude most visible herbivores such as fish and sea urchins, and (2) full cages with large 6×6 cm mesh (referred to as coarse-mesh cages, *CM*) designed to exclude only large fish (i.e., >8 cm body depth)—those from size classes that were demonstrated to be highly important in the consumption of macroalgae (Bellwood et al. 2006; Fox and Bellwood 2008; Steneck et al. 2014). Body depth is likely to be a better estimate of a fish's ability to pass through a mesh than body length, as found in

studies of fish that escape traps (Robichaud et al. 2000; Gomes et al. 2014). Consequently, we used published body depth–length relationships (http://www.fishbase.org) to convert total length estimates of each individual from visual surveys to body depth and their likelihood of entering the cages. Coincidentally, all fish larger than 8 cm body depth had total lengths greater than 22.5 cm and vice versa (Electronic Supplementary Materials, ESM, Table S1). We present this information here only for comparative purposes as most exclusion cage studies only report the lengths of fish unable to enter cages (Bellwood et al. 2006; Jayewardene 2009; McCauley et al. 2010); however, body length is not likely a good estimate of a fishes ability to enter an exclusion cage. This information combined with observations of fish entering the cages resulted in a list of species and size classes that were able to enter into the coarse-mesh cages and also confirmed that small fish were neither aggregating inside nor avoiding cages.

Apart from these two types of full cages, two partial cages were used: (1) cages with tops only (referred to as *T*)

constructed to check for the influence of shading, and (2) cages with sides only (referred to as *S*) to check for the influence of reduced water flow. Partial cages were only made of the 1 × 1 cm mesh as the wider spacing of the 6 × 6 cm mesh was expected to have little to no influence on algal community development, light, and water flow. Numerous studies using similar exclusion cages found no significant effects of the caging structure on the benthic community other than the exclusion of herbivores (Russ 1987; Hixon and Brostoff 1996; McCauley et al. 2010). Lastly, completely open plots were also established and served as the main controls (referred to as *C*). Thus, a total of five different treatments were used in this sampling design. All exclusion cages had dimensions of 40 cm width and length and 20 cm in height and were constructed of a metal frame and a mesh made of fishing net twine. They were affixed to the dead coral substratum using stainless steel nails and ties to keep the cages in place and ensure no unwanted incursions of fish.

The five treatments were replicated at each of our 24 sampling sites, resulting in a total of 120 experimental plots. Because foraging activity is known to vary among different parts of the reef (Robertson et al. 1979; Hoey and Bellwood 2008), we placed the sites (200 m apart) along a transect that followed the atoll rim, beginning from the main reef channel and ending at the next small channel. Half of these sites (12 sites) were placed on the leeward back-reef (inner back-reef) and the other half on the border of the back-reef and reef flat (outer back-reef), thus covering various back-reef habitats (Fig. 1). The distance between the inner and outer back-reef sites was 150 m. Treatment designations of specific cages were randomly determined at each site, but always ensuring that mainly dead coral heads were included in the cages. Average depth of the sites at low tide was 1.0–1.5 m.

The experiment ran for a total of 127 d from December 2009 to April 2010. Cages were visited every 10–14 d to be cleaned of algae and other settling organisms with a plastic brush. During those times, algae height was measured and benthic cover data were collected (with one exception toward the end of the experiment as weather conditions worsened) using in situ visual coverage estimates. Photographic images of the plots were also taken on each of these visits during the first 3 weeks and then every day after cage removal until plots were completely browsed. Benthic coverage data included coral, browsed substratum, other invertebrates, non-biological substratum, and algae identified to the lowest possible taxonomic level, but in majority of cases, only functional groups were ascribed as detailed identification in the field was not possible. Height measurements of algae were taken separately for each algal group using one measurement for each group, unless height seemed to vary within a group, then three measurements

were taken, and an average value was calculated. Algae was then pooled into the following groups for further analysis: macroalgae (upright fleshy and calcareous algae, such as *Gracilaria*, *Caulerpa*, and *Halimeda*, but also foliose algae such as *Dictyota* and *Padina*), fine low turf (short, around 1 mm, and sparsely distributed green/brown filamentous algae and microalgae), turf (higher denser turf made up of a mix of microalgae, filamentous algae, small macroalgae, and sediment), filamentous non-turf algae (filamentous algae sensu Steneck and Dethier 1994, and long strands of cyanobacteria often growing out from holes in the reef), crustose coralline algae (CCA—Corallinales, Rhodophyta, of crustose habit), and non-calcareous crustose algae (non-coralline algae of crustose habit, e.g., *Ralfsia*).

Herbivore surveys

For each of the 24 sites, sea urchin and herbivorous fish were censused using belt transects and visual counts. For the fish census, a 50-m transect rope was laid parallel to the reef crest at each site with cages situated in the middle part of each transect. After 5 min, allowing the fish to acclimate, timed swims (15–20 min) were conducted along the transect, counting all herbivorous fish 5 m on either side, thus covering an area of 500 m^2. Four to five fish counts were conducted at each site during various times of the day (0900–1700 h) evenly distributed between low and high tides. Water clarity exceeded 10 m during each of the sampling times. Censuses were done by a single person, NH Cernohorsky, who recorded the species, number of individuals, and estimated their total length. Fish lengths were recorded to the nearest centimeter for individuals <5 cm TL, to the nearest 5 cm for individuals between 5 and 40 cm TL, and to the nearest 10 cm for individuals >40 cm TL. Small juvenile parrotfish species were difficult to reliably identify to the species level in the field and were therefore grouped into the category *Scarus* spp. *Ctenochaetus* species were grouped into a *Ctenochaetus* spp. category due to difficulties in making reliable in situ identification.

Sea urchin numbers were assessed using the same belt-transect method. However, searches for urchins were performed over a much smaller area (20 × 6 m transect) and the observer meandered along the rope, crisscrossing the transect looking under coral heads and into all crevices. The method is time-consuming, and the mobility of sea urchins rather limited; consequently, the sea urchin count was carried out only once per site and only during the day. In each census, the species and number of individuals were recorded. Species of the genus *Echinostrephus* were grouped into the category *Echinostrephus* spp. because their identification characters cannot be seen in the field.

Data analysis

To obtain estimates of algal biomass, we calculated algal volume for each cage and each sampling time by multiplying algal cover (in cm^2) by algal canopy height (in cm; Steneck and Dethier 1994). Algal volume was standardized to an area of 1 cm^2 of dead coral substratum (i.e., without live coral) to eliminate variability caused by different proportions of live coral in different cages. To verify the accuracy of the benthic coverage data assessed by in situ estimates, we compared it with the coverage data obtained from the benthic photoquadrats and found that they produced similar coverage estimates. However, photoquadrats were less detailed in the sense that they were not very well suited for detecting less abundant algal taxa. Image analyses of the benthic photoquadrats to obtain benthic coverage data were completed using the program PhotoGrid 1.0.

Fish biomass estimates were calculated by converting total lengths (TL) of fish into biomass based on length–weight relations published in literature or available online (Kulbicki et al. 2005; http://www.fishbase.org). For the few species lacking specific allometric constants for the conversion, parameters from a closely related and similarly shaped species were used. Parrotfish species <3 cm of TL were excluded from the analyses, due to the fact that they were not likely to have undergone ontogenic changes from carnivores to herbivores (Bellwood 1988). The fish counts took place during the last month of the experiment when *Ctenochaetus* recruits were present on the reef in large numbers. These new, small recruits were also excluded from the analyses, due to their short-term episodic occurrence. As the relationships between individual species and ecosystem processes are still poorly understood, fish were analyzed as functional groups: grazers/detritivores, scrapers, excavators, and browsers (Steneck 2001; Bellwood et al. 2004; Green et al. 2009). Sea urchins were analyzed as a separate functional group within the herbivore guild, as their functional role in the ecosystem is abundance dependent (Carpenter 1981; McClanahan and Shafir 1990).

Differences in algal cover and height among treatments at the end of the experimental period were statistically tested. The data showed non-normal distribution and heteroscedasticity. We thus used Welch's analysis of variance (ANOVA) followed by Games-Howell post hoc test, as these methods do not assume homogeneity of variance (Games and Howell 1976; Brown and Forsythe 1974).

We explored the effect of excluding all herbivores or only large herbivores on algae accumulation using linear mixed-effects models (LME) because measurements of the response variable (i.e., algae volume) were not independent. The algae volume data were transformed by a decimal (base 10) logarithm to meet the normal distribution assumptions. The study uses a split-plot design with five types of cages (i.e., treatments) spatially clustered and with multiple observations for each cage. We used two levels of groupings (location and cage) to assess two possibly different random effects. The significance of the effect of the treatment (five types of cages), time (sampling occasions), and reef position (inner and outer back-reef) on algal volume was tested using the F test with a critical significance level established as 0.05. As no significant effect was found for the position (LME: $F_{1,22} = 1.0$, $p = 0.44$), the final model included only the treatment and time as fixed effects. This final model was also corrected for the heteroscedasticity by using the variance function (varIdent) with time as a covariate.

Several cages were lost during the experiment, and the losses increased after the ninth sampling interval (after the 93rd d), which resulted in an unbalanced number of observations among treatments. Therefore, we limited data for the LME modeling to the first nine sampling occasions, which were based on 88 samples from 110 cages of which most (70 %) were sampled during the whole period. All graphs and statistical analyses were done using R software (v. 3.1.3, R Core Team 2015).

Results

Herbivore abundance and biomass

A total of 38,538 herbivorous fish comprising 24 species in three families were counted and equated to an average herbivorous fish density of 0.23 individual m^{-2} ($\pm$ 0.01 SE) and an average biomass of 53.11 g m^{-2} ($\pm$ 7.66 SE). Grazers comprised 27 %, scrapers 41 %, excavators 28 %, and browsers 4 % of the total fish biomass (Fig. 2a). The herbivorous fish community was strongly dominated by *Acanthurus triostegus* (0.057 ind. m^{-2}) and juvenile parrotfish species (0.057 ind. m^{-2}). In terms of biomass, the dominant species were: *Chlorurus enneacanthus* (14.07 g m^{-2}), *Scarus rubroviolaceus* (12.72 g m^{-2}), *Acanthurus lineatus* (7.09 g m^{-2}), *Scarus prasiognathus* (5.32 g m^{-2}), and *Acanthurus gahm* (2.64 g m^{-2}). Fish abundances as well as biomass were higher at the outer than at inner back-reef sites (Fig. 2a, c, e). Fish were also less abundant near both the channels, and this gradient is shown by the good fit of a polynomial equation to the rim "transect" ranging along the atoll from sites 1 to 12 for abundance ($F_{2,9} = 9.69$, $p = 0.006$) and biomass ($F_{2,9} = 6.63$, $p = 0.017$; Fig. 2b, d, f).

The total number of sea urchins counted was 604 individuals comprising seven species in three families and revealed an average sea urchin density of 0.23 individuals per m^2. The two small-bodied urchins, *Echinostrephus* spp.
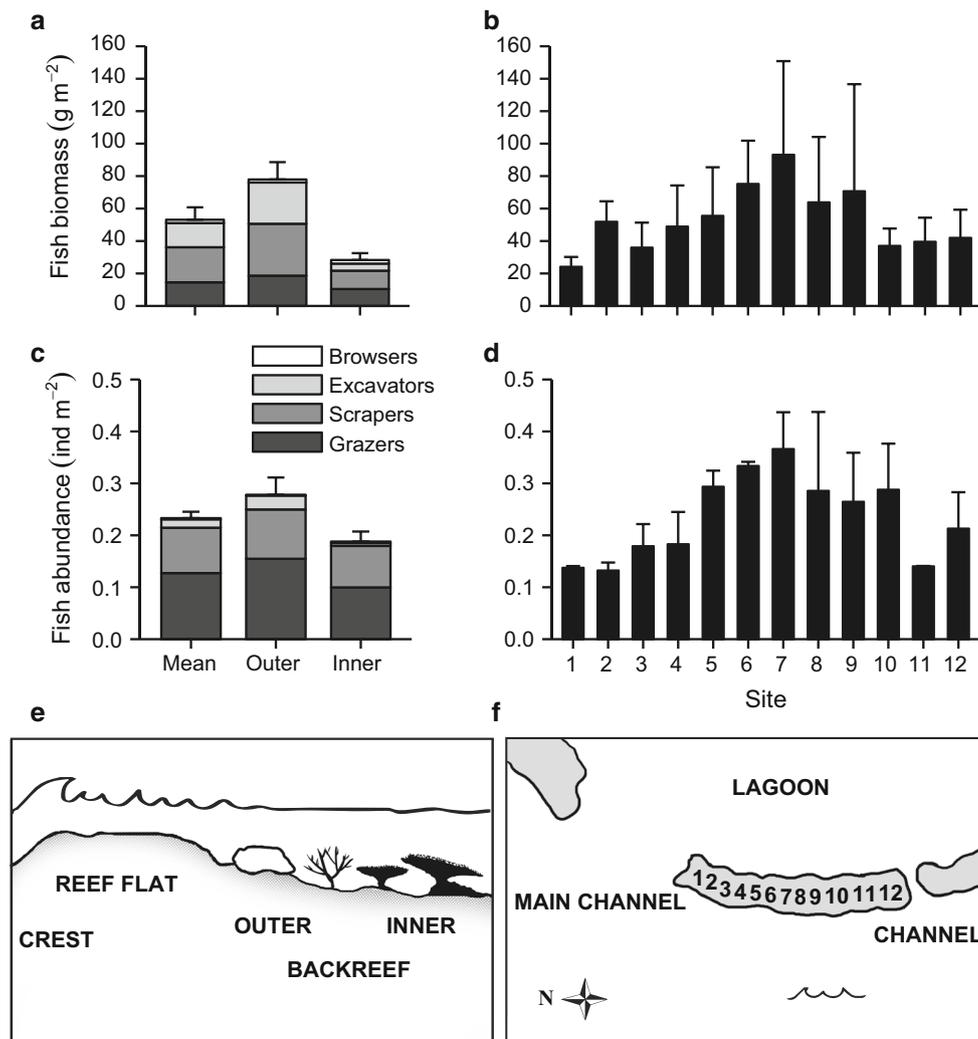
Fig. 2 Mean values of fish biomass (**a**, **b**) and abundance (**c**, **d**) in different reef habitats. Graphs on the *left side* show biomass and abundance at outer and inner back-reef sites **e** and the mean across all sites, showing different proportions of each functional group; *error bars* represent standard errors of the total mean (SE). Graphs on the *right* show polynomial distribution of fish abundance and biomass from the main channel, site 1, along the atoll rim to the small channel, site 12 (**f**); *error bars* represent maximum/minimum (as within sites only two replications were available)

and *Echinometra mathaei*, were the most abundant species accounting for 58 and 37 % of all counted sea urchins, respectively (Fig. 3).

Caging effects

The fine-mesh full (FM) cages were assumed to effectively exclude all herbivorous fish and urchins greater than ~1 cm body depth/diameter. Based on body depth–length relationships and the size of the mesh, the coarse-mesh full (CM) cages were assumed to effectively exclude only fish with a body depth greater than approximately 8 cm (which coincidentally corresponded to total body lengths greater than approximately 22.5 cm) and comprised most of the browsers, majority of excavators, some scrapers, and only

few grazers (Fig. 4; ESM S1). Fewer fish were capable of entering or observed entering the coarse-mesh full cage and were represented mainly by grazers and small, often juvenile, scrapers (Fig. 4). Overall, individuals from twelve fish species were potentially able to enter the coarse-mesh cages across all sites, with an average of eight species per site (Table 1). Although fish capable of entering the cages were present in much higher numbers than those excluded from the cages (0.17 ind. m^{-2}, 0.06 ind. m^{-2}, respectively), their total biomass was much lower (7.7 g m^{-2} vs. 45.44 g m^{-2}, respectively). Echinoidea were also capable of entering the CM exclusion cage, but were present on the reef in low numbers (Fig. 3). Further, the dominant species were *Echinostrephus* spp. and *Echinometra mathaei*, species mostly restricted to their burrows.
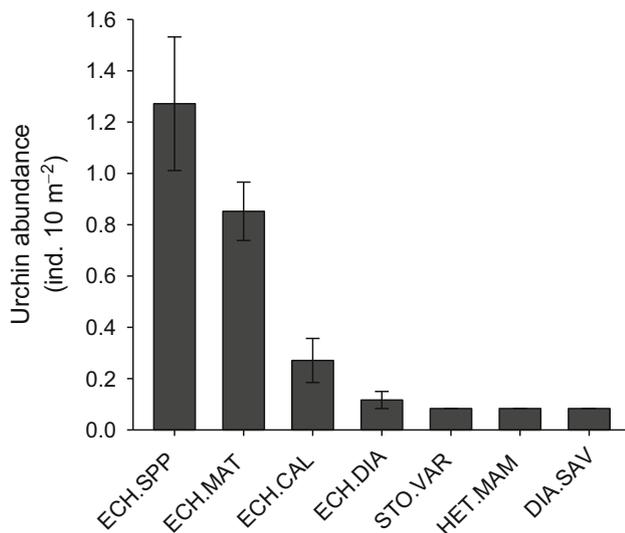
Fig. 3 Sea urchin species found on the back-reef and their mean background population densities. *Error bars* represent standard errors of the mean, ECH.SPP = *Echinostrephus* spp., ECH.MAT = *Echinometra mathaei*, ECH.CAL = *Echinothrix calamaris*, ECH.DIA = *Echinothrix diadema*, STO.VAR = *Stomopneustes variolaris*, HET.MAM = *Heterocentrotus mammillatus*, DIA.SAV = *Diadema savignyi*
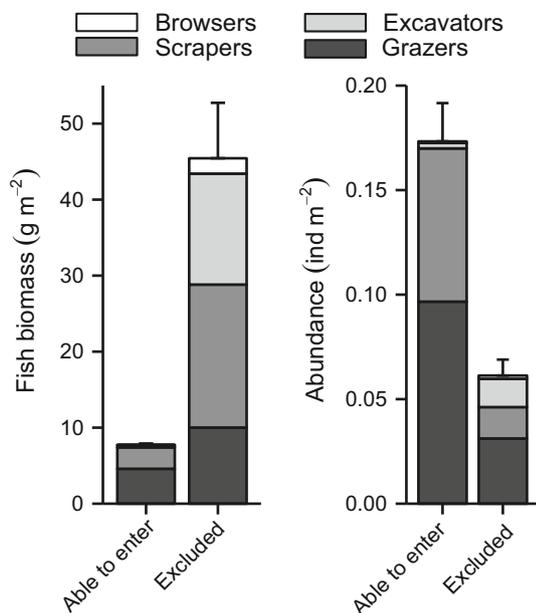

Fig. 4 Mean abundance and biomass of fish excluded from the coarse-mesh cages (=excluded) and those potentially able to graze in coarse-mesh cages (=able to enter), showing different proportions of each functional group. *Error bars* are one standard error of the mean

Algal accumulation

There were no significant differences between plots (treatments) in the coverage of macroalgae, turfs, or corals

prior to the exclusion of herbivores (GLM: $p > 0.10$). Algal turfs dominated the Agatti back-reef algal communities and covered about 50–70 % of the dead coral substratum. Macroalgae cover was low across the back-reef habitat, usually <5 %. At the end of the experiment, coarse-mesh cages and controls were still dominated by very low turf, but the fine-mesh cages were dominated by macroalgae (Table 2).

We found significant effects of treatments (LME: $F_{4,82} = 54.4$, $p < 0.001$), sampling time (LME: $F_{1,772} = 58.1$, $p < 0.001$), and their interaction (LME: $F_{4,772} = 33.0$, $p < 0.001$) on algal accumulation. The exclusion of all herbivores by the FM cages had rapid effects on the benthos communities, and after the 127 d there was a significant increase in algal volume (Fig. 5). The increase in algal volume in the FM cages was significantly greater than in open or control plots throughout the experiment (LME: $t = 9.10$, $p \ll 0.001$). However, where only large herbivores were removed (CM cages), no difference in the increase in algal volume was observed when compared to controls (LME: $p = 0.829$). In the half cages (top only or side only) and control plots, no significant increase in algae was observed either (LME: $p > 0.177$). With exception of the FM cages, the amount of algae found in all these plots remained relatively constant throughout the experiment (Fig. 5).

Discussion

Our study is one of the few studies to experimentally examine the influences of different-sized herbivorous fish using exclusion cages with two mesh sizes (Jayewardene 2009; Steneck et al. 2014) and the only one to do so in the back-reef habitat of an oceanic atoll in the Indian Ocean. In contrast to most previous studies, which have shown that large herbivorous fish are likely the most important group of herbivores in preventing algal blooms (Bruggemann et al. 1996; Bonaldo and Bellwood 2008; Hoey and Bellwood 2010; McCauley et al. 2010; Steneck et al. 2014), we found no effect of removing large herbivores on algal accumulation. In these coarse-mesh, full cages and the side and top controls, the benthos did not undergo significant changes, indicating that small herbivores were sufficient to prevent algal accumulation at our study sites.

The ability of small fishes to prevent the accumulation of algal biomass was unexpected and highlights the importance of considering the local ecological context in influencing algal responses. In this study, it seems that small herbivorous fishes were present in sufficient numbers to maintain a low algal state. Other influential factors could include storms and sediment scouring, but given the clear conditions and the ability to maintain these cages intact for

Table 1 All censused herbivorous fishes present in the location, plus abundance and biomass values of those capable of entering (based on body depth) into the coarse-mesh cages and those excluded by the coarse-mesh cages (6 × 6 cm)

All herbivore fish species		Fish able to enter coarse-mesh cages		Fish excluded by coarse-mesh cages	
Species	Functional group	Ind. 500 m^{-2}	g 500 m^{-2}	Ind. 500 m^{-2}	g 500 m^{-2}
Acanthurus gahm	Grazer	1.06	89.06	2.48	1189.97
Acanthurus leucosternon	Grazer	6.28	119.24	–	–
Acanthurus lineatus	Grazer	2.73	11.05	11.62	3418.65
Acanthurus nigricauda	Grazer	0.45	12.91	0.97	179.67
Acanthurus tennentii	Grazer	–	–	0.06	18.41
Acanthurus triostegus	Grazer	28.49	1084.75	–	–
Chlorurus enneacanthus	Excavator	–	–	6.70	6979.26
Chlorurus sordidus	Excavator	1.29	153.39	–	–
Chlorurus strongylocephalus	Excavator	–	–	0.04	295.43
Ctenochaetus spp.	Grazer	8.56	953.01	–	–
Hipposcarus harid	Scraper	–	–	0.49	415.74
Naso brachycentron	Browser	–	–	0.08	304.19
Naso elegans	Browser	0.16	4.42	0.39	227.75
Naso spp.	Browser	0.10	0.56	–	–
Naso unicornis	Browser	0.12	0.85	0.27	453.70
Naso vlamingii	Browser	0.01	0.10	–	–
Scarus frenatus	Scraper	0.11	7.49	0.12	35.32
Scarus ghobban	Scraper	–	–	0.04	80.83
Scarus prasiognathus	Scraper	–	–	2.77	2630.25
Scarus quoyi	Scraper	–	–	0.02	3.47
Scarus rubroviolaceus	Scraper	–	–	4.06	6202.38
Scarus scaber	Scraper	7.76	364.50	–	–
Scarus spp.	Scraper	28.37	1019.20	–	–
Siganus lineatus	Grazer	0.19	1.67	0.14	57.87
Zebrasoma desjardinii	Grazer	0.02	3.30	0.24	115.95
Zebrasoma scopas	Grazer	0.35	6.82	–	–

most of the study, these factors seem less likely to have influenced the outcome. Low nutrients could have also explained the absence of algal accumulation in the coarse-mesh cages, yet the fact that algal volume significantly increased in our fine-mesh cages supports the assumption that nutrients and sediments were not the main causes of the zero algal increase in the coarse-mesh cages (McClanahan et al. 2003). Sea urchins were likely to have little impact as well, as they were present on the reef in very low densities (Fig. 3) and were not observed to aggregate inside nor near the cages. Further, in wave swept and predator-abundant environments, the dominant urchins, *Echinometra mathaei* and *Echinostrephus* spp., are often restricted to their burrow and feed on algae that drift and settle into their burrows (Campbell et al. 1973; McClanahan and Kurtis 1991; Vanderklift et al. 2009). Patterns of low urchin numbers and their restriction to burrows and wave swept environments are expected for

high-fish-biomass reefs of this region (McClanahan et al. 1994, 2011).

Some caution should be applied when inferring the importance of small herbivorous fishes as the current study was spatially and temporally limited. Certainly, longer and larger spatial-scale studies and improved measures of potentially important grazing factors (numbers, biomass, feeding rates, and types) would better determine the exact effects of large-herbivore exclusion. According to the space availability model (Williams et al. 2001), if more space is available for the growth of algae, then the grazing capacity of herbivores may eventually become overwhelmed and macroalgae will be released from top–down control. Thus, the location of this study is consequential, as the back-reefs of Lakshadweep have relatively high coral coverage. However, shortly after the major bleaching event in 1998, when most of Lakshadweep corals bleached and died, space for algal growth was high. Nevertheless, no

Table 2 Comparison of mean (±SE) percent cover and height (mm) of different benthic groups in coarse-mesh cages (CM), fine-mesh cages (FM), and control plots (C) at the end of the experimental period (127 d)

Benthos groups	Coarse-mesh cages		Fine-mesh cages		Control		Welch (cover/height)		GH test (cover/height)		
	Cover	Height	Cover	Height	Cover	Height	Statistic	p	CM vs. C	FM vs. C	FM vs. CM
Macroalgae	4.3 (±2.0)	9.1 (±2.6)	24.4 (±3.8)	19.1 (±2.3)	3.1 (±2.1)	3.9 (±1.1)	$F_{2,22} = 17.5$/$F_{2,22} = 19.4$	***/***	–	***/***	***/***
Fine low turf	38.1 (±5.5)	1.29 (±0.1)	4.7 (±2.5)	2.1 (±0.4)	36.5 (±2.8)	0.9 (±0.1)	$F_{2,27} = 37.6$/$F_{2,24} = 1.0$	***/0.36	–	**/–	***/–
Turf	8.0 (±4.2)	3.4 (±0.7)	29.8 (±3.6)	5.8 (±0.7)	2.5 (±1.3)	3.0 (±0.9)	$F_{2,21} = 23.8$/$F_{2,23} = 18.9$	***/***	–	***/***	***/*
Filamentous non-turf algae	0.2 (±0.1)	18 (±11.14)	4.9 (±2.6)	13.2 (±2.4)	2.5 (±1.3)	35 (±17.6)	$F_{2,26} = 1.5$/$F_{2,29} = 0.6$	0.23/0.56	–	–	–
Crustose coralline algae	4.2 (±0.9)	–	2.9 (±0.9)	–	7.2 (±1.1)	–	$F_{2,30} = 4.4$/–	*/–	–	*/–	–
Non-calcareous encrusting algae	0.3 (±0.1)	–	2.0 (±0.8)	–	0.5 (±0.1)	–	$F_{2,25} = 2.0$/–	0.15/–	–	–	–
Browsed coral substrate	26.6 (±4.0)	–	0.7 (±0.6)	–	34 (±2.6)	–	$F_{2,22} = 89.8$/–	***/–	–	***/–	***/–
Other invertebrates	0.3 (±0.3)	–	1.9 (±0.6)	–	0.1 (±0.05)	–	$F_{2,19} = 4.1$/–	*/–	–	*/–	–
Non-biological	6.4 (±1.7)	–	12.9 (±1.9)	–	4.4 (±1.2)	–	$F_{2,27} = 6.8$/–	**/–	–	**/–	*/–
Hard coral	12.4 (±2.1)	–	15.9 (±2.5)	–	12.9 (±1.6)	–	$F_{2,27} = 0.6$/–	0.54/–	–	–	–

Welch's ANOVA test followed by Games-Howell post hoc test (GH test) was used to test the differences in cover and height; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. CM = 6×6 cm, FM = 1×1 cm mesh openings
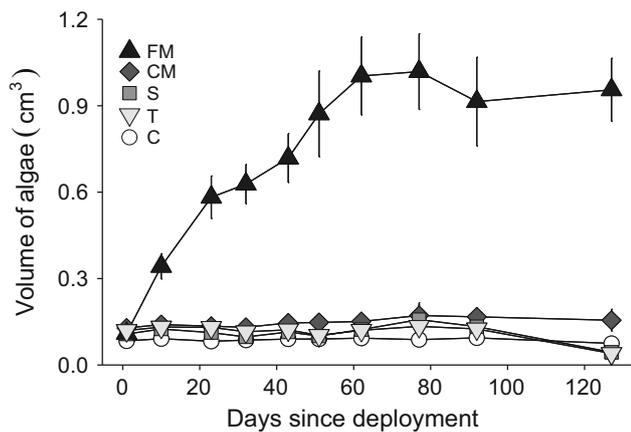
Fig. 5 Algal accumulation over 127 d at 24 back-reef sites of Agatti atoll for each treatment type (*FM* fine-mesh cages, *CM* coarse-mesh cages, *S* partial cages with sides only, *T* partial cages with tops only, *C* controls). Algal abundance expressed as mean volume (±SE) for a standardized area of 1 cm^2 of dead coral substratum

macroalgae blooms were reported despite this rapid increase in available space (Arthur et al. 2006), which suggests considerable capacity for herbivores to compensate for the increased algal production.

A further unexpected result was the lack of differences between habitats in the accumulation of algae within the coarse-mesh cages despite large differences in fish biomass and abundance (Fig. 2). The impact of various levels of herbivory was likely to have been offset by other factors, such as depth, coral cover, or wave and current intensity, which also differed between the different habitats. Furthermore, they differed such that where herbivore levels were low, depth and either coral cover or water motion were greater, and vice versa—thus likely compensating for the expected effects on algae. Other studies show that spatial dynamics of herbivorous fish can cluster within reef habitats (Fox and Bellwood 2014) with herbivore intensity varying among locations at distances < 100 m apart (Cvitanovic and Bellwood 2009; Hoey and Bellwood 2010; Bonaldo and Bellwood 2011). The degree to which herbivore clustering is a stable or a transient behavior will influence estimates of herbivory and thresholds for preventing macroalgal dominance.

The amount of algae removed by herbivores and its regrowth is likely to be dependent, not only on herbivore biomass, but on other factors including feeding mechanisms, such as sucking, nipping, and scraping, but also herbivore diversity and the functional makeup and redundancy of the herbivore community (Cheal et al. 2010; Thibaut et al. 2012). We found no buildup of algae, even though the biomass of herbivorous fishes was relatively low in the coarse-mesh cages (7.7 g m^{-2}). This suggests some need to reassess the roles of different functional

groups. For example, among the four main herbivore functional groups, browsers are considered the main group responsible for removing macroalgae (Green et al. 2009). Yet, due to their large body depths, only the very smallest browsers were capable of entering the coarse-mesh cages, leaving grazers and scrapers as the main groups responsible for cropping algae inside the coarse-mesh cages. We therefore conclude that browsers, particularly large-bodied ones, played little role in the suppression of macroalgae and this observation may apply to reefs more broadly.

Recent studies reveal that some herbivore species from non-browser functional groups also consume macroalgae, despite some taxa being unpalatable to many herbivores (Ledlie et al. 2007). In the Seychelles, for example, *Sc. rubroviolaceus* and *A. triostegus* have been observed to forage on macroalgae (Ledlie et al. 2007), in Fiji *Ch. sordidus* was observed to be responsible for the removal of red macroalgae (Rasher et al. 2013), and in the Line Islands some species of grazers and scrapers were found to predominantly graze on non-turf algae (Hamilton et al. 2014). There is also some evidence that suggests that feeding habits of some parrotfishes (Nash et al. 2012), surgeonfishes, and rabbitfishes (Chong-Seng et al. 2014) can change in response to changing reef ecology. Consequently, we suggest that other non-browser species may have been responsible for removing macroalgae from our experimental coarse-mesh cages. However, macroalgae were scarce at the back-reef study sites relative to the epilithic algal matrix (EAM; Wilson et al. 2003), which is preferred by most herbivores. The EAM consists of algal turfs, microalgae, macroalgal germlings, detritus, sediment, and other small organisms, which may mean that herbivores that feed on EAM will tend to graze unselectively. Consequently, they are likely to consume or damage macroalgae germlings in the process, which will prevent germlings from growing into mature thalli (Lewis 1986). The failure of macroalgae to increase in our coarse-mesh cages is likely caused by an abundance of EAM-feeding herbivores in Agatti back-reef (Fig. 4). Since the species responsible for controlling algae were not monitored in the experimental plots, the various species-specific roles remain uncertain.

Reefs with low human impacts, such as Agatti, may simply have more potential functional redundancy and more dietary overlap than presumed from species-specific diet studies (Johansson et al. 2013). Many recent studies have suggested limited dietary overlap and functional redundancy among herbivores, but these studies have focused mostly on excavators (Bellwood et al. 2003, 2012), or browsers in the presence of macroalgae (Bellwood et al. 2006; Cvitanovic and Bellwood 2009; Hoey and Bellwood 2009). Many macroalgal taxa are, however, generally scarce on coral-dominated reefs where EAM and coralline

algae dominate. Herbivore resistant taxa, such as *Amphiroa* and *Turbinaria*, will develop adult thalli when the EAM is intensely grazed, but few other macroalgal taxa were observed in this remote atoll. In such cases, only a limited number of species from the overall herbivore community will actually feed on or make macroalgae an important part of their diet (Johansson et al. 2013).

Low macroalgal diversity on coral-dominated reefs could force species to adapt to feeding on the more abundant EAM and hide the full herbivore functional specialization. In contrast, herbivores on reefs with high and diverse macroalgal cover may utilize their diet specialization potential, which would create an impression of limited functional redundancy. Distinguishing and understanding these types of adaptations and complex interactions between the state of the algae and feeding behavior and diet specialization are difficult. Nevertheless, assuming more adaptation potential than found in time- and space-limited studies is expected to reconcile the many contradictory studies (Robertson and Gaines 1986; Hamilton et al. 2014). In our case, the removal of large herbivores did not result in algal accumulation as may have been expected, and thus there must have been considerable functional redundancy between the large and small herbivores. Large herbivores, however, play other ecological roles, such as bioerosion (Bruggemann et al. 1996; Bellwood et al. 2012), which is especially common on atolls and low-lying islands, such as Lakshadweep. Small herbivores are unlikely to be able to equal or compensate for the role of large herbivores in bioerosion. Nevertheless, we show that smaller herbivores play an important role in reef ecosystems, especially because they are much less susceptible to fishing. Consequently, we suggest that they provide an important component of functional redundancy when disturbances, such as coral bleaching events or selective fishing pressure, are common. Furthermore, this study stresses the importance of ecological context and herbivore plasticity when assessing potential impacts of fishing and management on changes in herbivory, algae, and coral.

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