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Herbivory effects on benthic algal composition and growth on a coral reef flat in the Egyptian Red Sea

Christian Jessen*, Christian Wild

Coral Reef Ecology Group (CORE), Leibniz Center for Tropical Marine Ecology (ZMT) and University of Bremen, Fahrenheitstr. 6, 28359 Bremen, Germany

ABSTRACT: One of the major threats facing coral reefs is intense benthic algal growth that can result in overgrowth and mass mortality of corals if not controlled by herbivore grazing. Unlike the well-studied coastlines of the Caribbean, there is currently a lack of knowledge regarding the effects of herbivory on benthic communities in the Red Sea. This is particularly relevant today as the local impacts in the Red Sea are increasing due to growing population and tourism. Over 4 mo, this study investigated the impact of herbivory as a potential key factor controlling algal growth on a reef flat in the Egyptian northern Red Sea. The main experiment consisted of *in situ* deployment of exclosure cages in combination with quantification of sea urchins and herbivorous fish. When all herbivores were excluded, our findings showed a significant 17-fold increase of algal dry mass within 4 mo. Although herbivorous fish occurred in much lower abundance (0.6 ± 0.1 ind. m^{-2}; mean ± SE) compared to sea urchins (3.4 ± 0.2 ind. m^{-2}), they were 5-fold more efficient in reducing algal dry mass and 22-fold more efficient in reducing autotrophic production of nitrogen. A significant shift from benthic turf to macroalgae (mostly *Padina* sp. and *Hydroclathrus clathrathus*) was observed when grazers were excluded. These algae may serve as early warning indicators for overfishing. Findings suggest that herbivorous fish act as an important top-down factor controlling both benthic algal biomass and composition at the study location. Results also indicate the potential of rapid benthic community change at the study site if herbivory is impeded.

KEY WORDS: Herbivory · Benthic algae · Cage experiment · Reef flat · Red Sea · Sea urchin · Herbivorous fish

INTRODUCTION

Coral reefs belong to the most complex and diverse marine ecosystems in the world. The main reef ecosystem engineers are scleractinian corals which provide habitats for associated organisms and generate and transform inorganic and organic materials (Wild et al. 2011). Scleractinian corals stand in direct competition with algae for space and light. Algal development and occurrence in healthy coral reefs is usually impeded by low nutrient concentrations and the activity of herbivores (Burkepile & Hay 2006) that are beneficial to corals by controlling algae or promoting coral recruitment (Hughes et al. 2010).

In an intact reef, fish and echinoids are usually the most abundant herbivores (Jennings & Polunin 1996). The most important herbivorous fish groups in Red Sea coral reefs contain Siganidae (rabbit fish), Chaetodontidae (butterfly fish), Balistidae (trigger fish), Acanthuridae (surgeon fish), and Scaridae (parrot fish) (Vine 1974). The majority of sea urchins are omnivores, with algae as their preferred food source (Ruppert & Barnes 1994). Prolonged low levels of herbivory caused by overfish-

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*Email: christian.jessen@zmt-bremen.de

ing, together with natural disturbances, may result in phase shifts from coral-dominated reefs to a new state dominated by fleshy macroalgae (Hughes et al. 2010). High abundances of macroalgae do not only reduce suitable living space for herbivores (e.g. Underwood & Jernakoff 1981), but can also overwhelm grazing abilities of herbivorous fish when coral cover is low (Williams et al. 2001) or result in decreased grazing, since herbivorous fish avoid high abundances of macroalgae (Hoey & Bellwood 2011). This may lead to positive feedback loops that can further promote macroalgae-dominated reefs. Even though a recent study by Bruno et al. (2009) showed that the number of coral reefs that have been affected by phase shifts is smaller and rather restricted to the Caribbean, there are a few examples of reversed phase shifts (Hughes et al. 2010), and a key overall goal of reef management is to prevent these undesirable phase shifts (Mumby & Steneck 2011).

Actual scientific information on the effect of herbivory in the Red Sea is scarce, although the reduction of herbivores by means of overfishing is among the most dangerous of threats for coral reefs in the region (Wilkinson 2008). A recent study (Korzen et al. 2011) compared grazing effects of sea urchins and herbivorous fish, and 2 older studies examined the effect of herbivory on algal biomass (Vine 1974) and on algal species composition (Mastaller 1979). However, no studies exist focusing on reef flats that include a main areal of fringing reefs in the Red Sea and which act as a key habitat for a variety of species. Reef flats are particularly subject to anthropogenic impacts (e.g. fishing, watershed-based pollution and coastal development) due to proximity of the shore and easy accessibility.

The present study combines descriptive and experimental approaches to elucidate how the quantity (in terms of biomass development) and composition of benthic algae are affected by sea urchins and herbivorous fish of a typical reef flat in the Red Sea. We hypothesize that both herbivorous groups are key factors controlling benthic algal composition and biomass on this exemplary reef flat. We used fish and benthic invertebrate surveys to assess the abundance of herbivores and combined these observational data with experimental manipulations of herbivore access using exclosure cages.

MATERIALS AND METHODS

Study site

This study was carried out from October 2009 to February 2010 on the reef flat of the fringing reef close to the town of Al Qusayr in the northern Red Sea (26° 08′ 58″ N, 34° 15′ 24″ E; Fig. 1). Fringing reefs are very common in the Red Sea; the reef flat at the study site has a width of around 130 m, which is typical for the Red Sea (Head 1987). The study site was located adjacent to a hotel area, northwest and southeast of a swimming zone. Whereas swimming was not allowed outside the swimming zone, fishing was prohibited along the entire coastline of the hotel area (about 500 m in length). Outside this area, small-scale artisanal fishing occurred. The water depth on the reef flat where the cages were deployed ranged between 1.2 m at high tide and 0.7 m at low tide. The maximum tidal range was 0.6 m. All work was carried out by snorkeling.

Background parameters

Water temperature was measured with a dive computer (Gekko by Suunto®; accuracy: ±1°C) placed on the ground for a few minutes before temperature was recorded. A hand refractometer (Aqua Medic®) was used to quantify salinity (accuracy: ±1 unit). Water movement at each cage site was estimated using the plaster ball method described by Komatsu & Kawai (1992) during a complete tidal period (replication n = 4 site^{-1}; attached 30 cm above the seafloor using polyethylene ropes). Parallel to the coastline, 4 transect lines (20 m each) were placed on the reef flat at

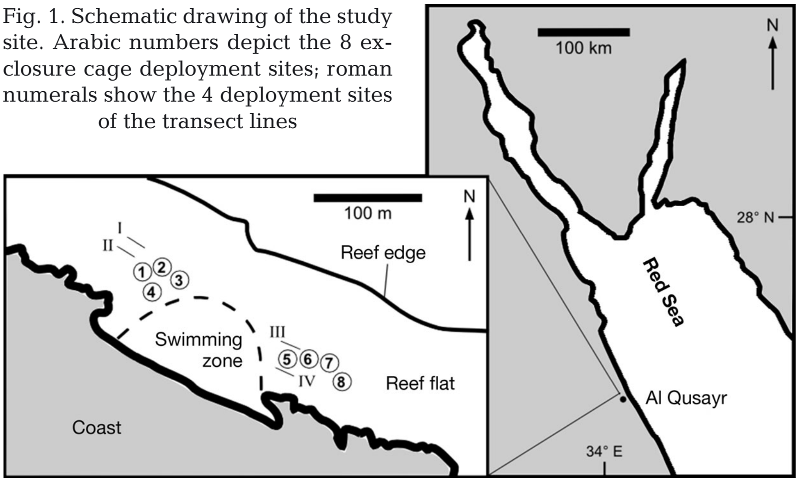

Fig. 1. Schematic drawing of the study site. Arabic numbers depict the 8 exclosure cage deployment sites; roman numerals show the 4 deployment sites of the transect lines

0.5 to 1.0 m water depth, 2 on each side of the swimming zone (see roman numerals in Fig. 1). Along these transects, reef rugosity was recorded using the chain-and-tape method as described by Risk (1972).

Benthic reef community composition

Along the 4 transects (20 m each), substrate cover was assessed using the linear point intercept (LPI) method described by Nadon & Stirling (2006), with 0.5 m intervals (40 points transect^{-1}). Categories were taken from the Reef Check manual (Hodgson et al. 2006) and included hard corals, soft corals, recently killed corals, nutrient indicator algae (all algae except coralline, calcareous [such as *Halimeda* sp.], and turf), sponges, rock, rubble, sand, silt/clay, and others.

Enumeration of herbivores

Along the same 4 transects, a visual fish survey was carried out after English et al. (1997), with slight modifications. For this study, we surveyed a total area of 60 m^2 (20 m length and 3 m width) at a water depth between 0.5 and 1.0 m. All observations were carried out at high tide (±90 min). To increase the accuracy of the survey, each transect was divided into four 5 m sections that were observed one after another for 2 min each, with the first minute spent observing the roving species and the next minute noting more stationary fishes while swimming slowly over the section. Preprinted data sheets were used to count and identify the fishes of all families, with the exception of camouflaged and hidden forms ('cryptic species'). Enumeration of fish abundance on each transect took place during 3 periods of the day: morning (06:00 to 08:00 h), midday (11:00 to 13:00 h), and afternoon (15:00 to 17:00 h), with 10 to 11 replicates at each time (making a total of 121 transects) between December 2009 until February 2010. Species identification followed Randall (1983), Debelius (2007) and Lieske & Myers (2009). Classifying fish into herbivorous and non-herbivorous groups was based on Randall (1983), Khalaf & Disi (1997), Lieske & Myers (2009), and our own observations (Appendix 1). We classified herbivores according to their ability to remove plant material from the reef (this also included facultative herbivores) and not on the ability for actual consumption or digestion of plant material (Choat et al. 2004).

The 4 transects described above were also used to quantify the abundance of sea urchins in the period from December 2009 to January 2010, but for these observations the transect width was reduced to 1 m (resulting observation area = 20 m^2). A single snorkeler identified and counted all sea urchins within the length of a 1 m plastic (polyethylene) bar over 4 periods of the day: morning (06:00 to 09:00 h), midday (11:30 to 14:30 h), afternoon (15:30 to 18:30 h), and evening (18:30 to 21:30 h). Replication was n = 4 for morning and evening and n = 3 for midday and afternoon (making a total of 56, with 4 sites, 4 periods of the day, and 3 to 4 replicates). Other herbivorous invertebrates (e.g. gastropods, crustaceans, and polychaetes) were not considered in this study, since they were rarely encountered on the investigated reef flat (C. Jessen pers. obs. from day and night surveys), and because herbivorous fish and sea urchins consume a great part of the algal production (Hatcher 1981, Carpenter 1986, 1988, Foster 1987), while microherbivores may be physically limited in their grazing abilities to certain algal species (Fauchald & Jumars 1979, Zimmerman et al. 1979, Howard 1982).

Deployment of exclosure cages

To simulate an overfished reef, we deployed 3 different cage treatments: closed cages, open-top cages, and controls (n = 8; Fig. 1). These cylindrical cages were constructed using metal-free plastic 'chicken wire' with a diameter of 40 cm, 30 cm height, and a mesh size of 2.5 cm. Closed cages were used to exclude large herbivores (e.g. fishes and sea urchins), while allowing access to smaller herbivorous fish and smaller predatory fish to prevent cages from being used as refuges for mesograzers (Lewis 1986). Open-top cages only allowed grazing by fishes, but prevented echinoids from entering (C. Jessen pers. obs.). Nearby locations (distance to cages <1 m) without any cage treatment served as controls. Further cage controls were not used, since previous studies have shown that a mesh size of 2.5 cm has little impact on algal community development, sedimentation rates, or water movement (Miller et al. 1999, Smith et al. 2001, Burkepile & Hay 2007). At each of the 8 sites, all 3 treatments were present, randomly distributed, and located within 1 m from each other. To assess the impact of herbivores on settling succession of benthic algae, 4 square terracotta tiles (each 256 cm^2) were installed horizontally in each cage and at control sites using cable ties. Cages were fixed to appropriate reef structures using plastic (polyethylene) ropes. Similar light levels between the treatments were assured by cleaning the cages from fouling organisms (mostly algae) every couple of days. To avoid excessive sedimentation, all cages and the controls were elevated by ca. 7 cm using installation of bricks underneath. The tiles were still accessible to echinoderms (C. Jessen pers. obs.).

Prior to the experiments, all tiles were preconditioned on the reef flat for 4 to 6 wk prior to the experiment to remove any interfering compounds that could have accumulated during tile production process. Before deployment, tiles were thoroughly wire-brushed to remove already settled turf algae, invertebrate recruits, and other organisms. Every 4 wk (on 28 November 2009, 26 December 2009, 24 January 2010, and 20 February 2010), 1 tile of each treatment was randomly removed to identify the functional groups of settled algae and to quantify algal biomass and sediment mass on the tiles. To minimize border effects, only the central area (92.2 cm^2) of each plate was used to determine algal mass and functional algal groups. To identify possible effects of temporal variations, a second time-shifted series of tile experiments was conducted in parallel by replacing every removed tile with a new (preconditioned) one, such that every treatment was always equipped with 4 settling tiles. The time-shifted series is marked in the text and graphs with an asterisk (e.g. 4 wk*). In total, 168 tiles were deployed and collected.

Immediately after the washing process, the algae were carefully scraped off with a spatula, and their wet mass was measured using a balance (accuracy: 0.01 g). Dry mass was obtained after air-drying the samples of algae for a few days until constant weight. For the N measurements, pooled algal material from each treatment (n = 8) from Week 16 were dried in the sun until constant weight, prior to analyzing the dry samples with a Thermo Flash EA 1112 elemental analyzer.

To estimate the relative influence of sea urchins and herbivorous fish on benthic algal growth, we used the following equations:

$$\text{Overall herbivore reduction} = [\text{algal growth}]_{\text{closed cage}} - [\text{algal growth}]_{\text{control}} \quad (1)$$

$$\text{Herbivorous fish reduction} = [\text{algal growth}]_{\text{closed cage}} - [\text{algal growth}]_{\text{open top}} \quad (2)$$

$$\text{Sea urchin reduction} = [\text{algal growth}]_{\text{open top}} - [\text{algal growth}]_{\text{control}} \quad (3)$$

Accumulated sediment from the tiles was separately collected underwater into sealable plastic bags and subsequently washed from the tiles using a fine water jet. The sediment dry mass was quantified using a balance (accuracy: 0.01 g) after removing salts by washing with fresh water and drying the sediment for 3 to 5 d in the sun until constant weight.

To quantify the proportional composition of functional algal groups, 100 points were randomly overlaid on the digital picture of the central area of each tile using the software Coral Point Count with Excel extensions (CPCe) 4.1 (Kohler & Gill 2006). The following categories were applied: filamentous algae, crustose coralline algae (CCA; calcareous encrusting forms), macroalgae (non-filamentous fleshy algae >1 cm), and 'no biotic cover'.

Statistical data analysis

All statistical tests were performed using STATISTICA v.9.0 (StatSoft). Temperature data were analyzed using the Wilcoxon matched pairs test; water movement using Kruskal-Wallis; and sedimentation data with a 1-way ANOVA for sites and each sampling time (for the 8 wk data set a square transformation was applied to meet parametric assumptions). Herbivorous fish and sea urchin abundances, as well as diversity (Shannon index), were analyzed using repeated-measures ANOVA (in the case of herbivorous fish, the data was log transformed to meet assumptions of sphericity that were tested with Mauchly's test). Algal dry and wet mass was analyzed with a 1-way ANOVA, though the latter data were log transformed to meet parametric assumptions. Comparison of algal differences between temporal stages was carried out with a *t*-test, and the data of algal N content was first log transformed to fulfill parametric requirements before analyzing with 1-way ANOVA and the Tukey HSD post hoc test.

RESULTS

Background parameters

Water temperature ranged between 23 and 27°C; the highest values were recorded during November and the lowest values at the end of January. No significant differences could be detected between the left and right sides of the swimming area (Wilcoxon matched pairs test: $Z = 0.28$, n = 16, $p = 0.78$). Salinity remained constant at 40.4 ± 0.2 (mean ± SE). Exposure to water movement (mass loss of plaster balls ranged between 16.3 ± 0.2% at Site 5 and 18.1 ± 0.4% at Site 3; mean ± SE) showed no significant differences between treatments or between the left and right side of the study area (Kruskal-Wallis tests—treatments: $H_{2,38} = 3.49$, $p = 0.17$; sites: $H_{1,38} = 0.49$, $p = 0.48$). Sedimentation (dry mass) on the settling plates did not differ between sites (1-way ANOVA: $F_{7,88} = 1.360$, $p = 0.233$) or between the treatments after 4, 8, 12, or 16 wk (Table 1). Reef rugosity values ranged between 1.12 and 1.36 for all transects.

Benthic reef community composition

Benthic cover was primarily rock (78.1 ± 4.4%; mean ± SE), followed by rubble (11.9 ± 2.6%), and hard corals (5.6 ± 3.3%). Sand, nutrient-indicator algae, and other substrates occurred only in small proportions (2.5 ± 1.8, 1.3 ± 0.7, and 0.6 ± 0.6%, respectively), while other categories were not present.

Enumeration of herbivores

During the fish surveys, 5446 individuals were observed, representing 66 different species (19 herbivores). Herbivorous fish abundance (0.6 ± 0.1 ind. m^{-2}; mean ± SE; Appendix 1) accounted for 79% of all observed fish (total abundance: 0.8 ± 0.1 ind. m^{-2}), but only 29% of the species were classified as herbivorous. From the view of fish families, Siganidae (primarily *Siganus rivulatus*) represented 55% the total individuals observed, followed by Pomacentridae (12%) and Chaetodontidae (9%). Fish diversity (Shannon index) ranged from 0.8 (Transect I) to 2.7 (Transect IV) and was highly correlated with rugosity (Pearson correlation: $r = 0.82$; $p > 0.05$).

Significantly higher abundance of herbivorous fish was observed in the morning with 0.9 ± 0.1 ind. m^{-2}, compared to 0.4 ± 0.1 for midday and afternoon (repeated-measures ANOVA: $F_{2,81} = 11.65$, $p = 0.003$; post hoc test Tukey HSD—morning vs. midday: $p = 0.009$, morning vs. afternoon: $p = 0.005$, midday vs. afternoon: $p = 0.89$).

During the sea urchin survey, 3596 individuals from 4 different species (*Heterocentrotus mammilatus*, *Diadema setosum*, *Tripneustes gratilla*, and *Echinometra mathaei*) were observed (3.4 ± 0.2 ind. m^{-2}); *E. mathaei* had the greatest abundance in most transects (2.0 ± 0.2 ind. m^{-2}). Whereas no significant differences were observed among sea urchin abundance in relation to diel patterns (repeated-measures ANOVA: $F_{3,18} = 0.06$, $p = 0.98$), there were large differences in abundance (repeated-measures ANOVA: $F_{3,18} = 12.05$, $p = 0.002$) and diversity (repeated-measures ANOVA: $F_{3,18} = 9.24$, $p = 0.004$) between the different transects. Abundance ranged from 1.7 ± 0.2 to 4.9 ± 0.4 ind. m^{-2}, and diversity (Shannon index) ranged from 0.5 to 1.1. Diversity was strongly linked to reef rugosity (Pearson correlation: $r = 0.90$; $p < 0.05$), whereas abundance was not ($r = -0.21$; $p < 0.05$).

Algal parameters

The analysis of functional algal groups on the tiles revealed a shift from mainly no biotic cover in the control treatments to filamentous algae in the open-top cages and macroalgae in the closed cage treatment (Fig. 2). In the control setup, 'no biotic cover' was the predominant functional group and applied to around 90% of the tile coverage (Fig. 2). The only algal group was filamentous algae, with a proportion of around 10%. In contrast, the 'no biotic cover' category evenly decreased from 94% (after 4 wk) to <50% (after 16 wk) in the open-top cages (Fig. 2). Filamentous algae were the first algae to colonize the tiles in the open-top cages, but after 16 wk, an average of 6% of the tiles was also covered by macroalgae. However, the highest increase of macroalgae was observed in the closed cage treatment, where they reached their highest abundance on the tiles after 16 wk, with 60% coverage. Contrary to the macroalgae, turf algae were the fastest settlers in the same treatment and proliferated after 4 wk, with a coverage of 8%. At the

Table 1. Sedimentation dry mass (mg cm^{-2}; mean ± SE) and results of 1-way ANOVA (df = 2) between the control, open-top cage and closed cage treatments and sampling times

	4 wk	8 wk	12 wk	16 wk
Control	3.53 ± 0.24	2.19 ± 0.22	2.40 ± 0.24	2.12 ± 0.32
Open-top cage	3.94 ± 0.20	2.60 ± 0.17	3.18 ± 0.29	2.60 ± 0.29
Closed cage	3.92 ± 0.13	2.76 ± 0.15	2.98 ± 0.37	2.42 ± 0.33
F	1.358	2.569	1.790	0.610
p	0.279	0.100	0.192	0.553

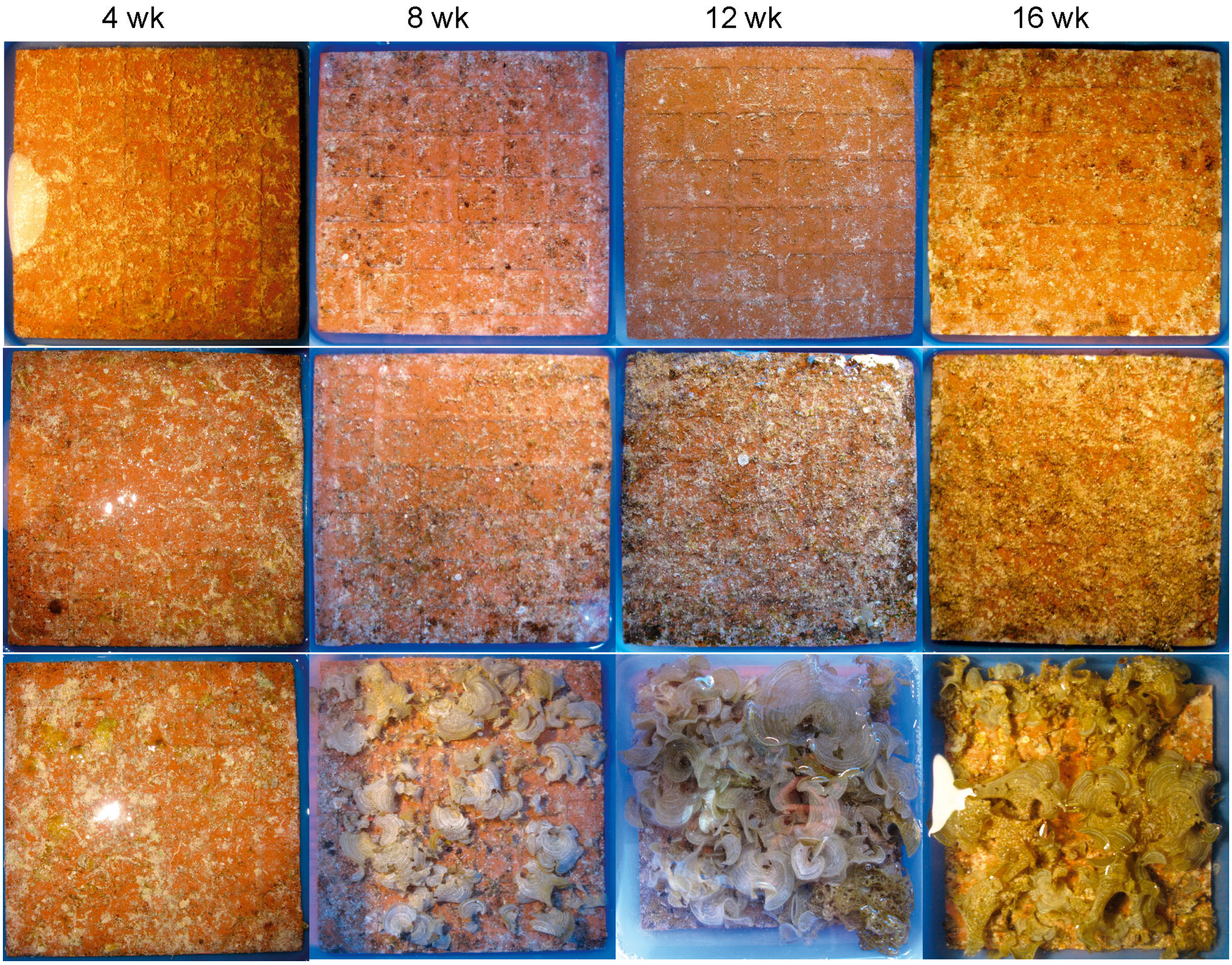

Fig. 2. Exemplary succession of algal growth on settling tiles in control (top row), open-top cage (middle), and closed cage treatments (bottom)

end of the study, relative cover of filamentous algae decreased again in favor of macroalgae.

The time-shifted series showed generally similar patterns, but the open-top and closed cage treatments exhibited increased proportions of filamentous algae after 4 and 8 wk. CCA coverage was not observed in any treatment during the entire study period (Figs. 2 & 3).

Exclusion of herbivores over 16 wk resulted in a significant 17-fold increase in algal dry mass (24-fold increase in wet mass) in the closed cages compared to control treatments (1-way ANOVA — algal dry mass: $F_{2,21} = 9.02$, $p = 0.001$; algal wet mass: $F_{2,20} = 20.55$ $p < 0.001$; Fig. 4). Algal wet mass in closed cage treatments almost doubled every 4 wk (Fig. 4). The time-shifted series of experiments supported the trend of increasing biomass (Fig. 4). It also showed that in the second half of the study period (8 wk* experiment series: Weeks 9 to 16) the closed cage treatments had significantly more algal wet mass than in the first half (Weeks 1 to 8) (*t*-test: $t_{14} = -2.23$, $p = 0.04$). Over all sampling times, no significant differences between sites were found for algal wet mass (1-way ANOVA: $F_{7,83} = 1.81$, $p = 0.10$).

The N content of algae on the tiles was lowest in the controls (8.1 ± 2.6 µg cm^{-2}; mean ± SE) and increased 6- and 27-fold, respectively, in the open-top cages (50.4 ± 14.0 µg cm^{-2}) and closed cages (216.1 ± 60.7 µg cm^{-2}). The closed cage treatment differed significantly from the other 2 treatments (1-way ANOVA: $F_{2,20} = 20.66$, $p < 0.001$; post hoc Tukey HSD — closed cages vs. control: $p < 0.001$, closed cages vs. open-top: $p = 0.009$).

Therefore, herbivorous fish removed algal biomass from the settling tiles 5 times more efficiently, in terms of dry mass, and 22 times more efficiently, in terms of N, than the benthic herbivores.

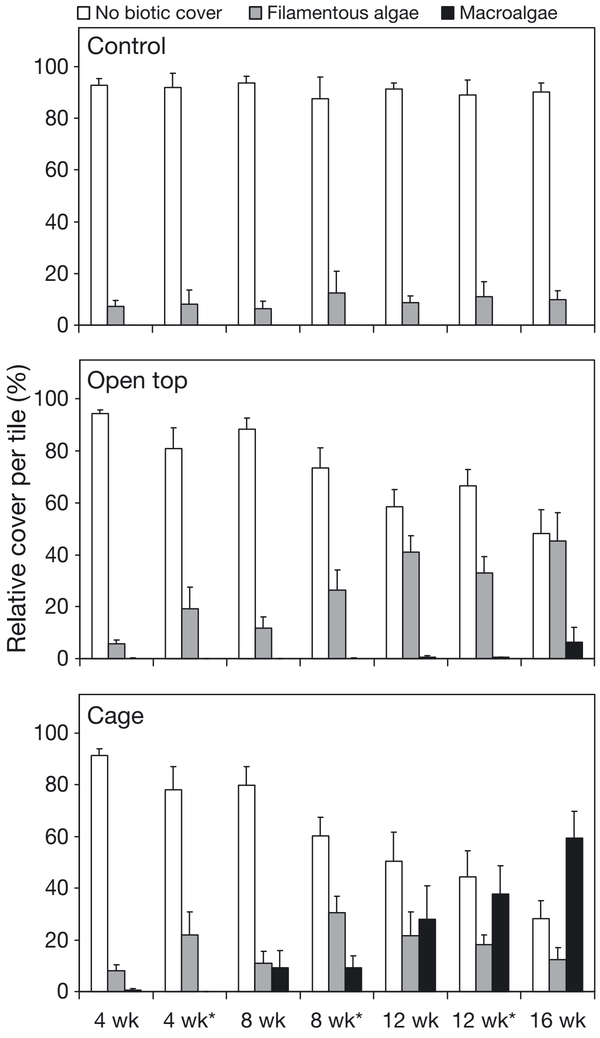

Fig. 3. Succession of functional algal groups in each treatment. Mean (±SE) percentage cover is shown of 3 functional groups ('no biotic cover', 'filamentous algae', and 'macroalgae') in 3 treatments (control, open-top cages, and closed cage) over 16 wk. Sample times marked with an asterisk are the time-shifted second series of experiments (see 'Materials and methods'). n = 8 for each treatment at each sampling time

DISCUSSION

This study characterizes herbivorous fish and sea urchin abundance and their effects on benthic algal development on a coral reef flat in the Red Sea. Exclusion of herbivores led to intensive growth and elevated biomass of macroalgae (closed cages) and filamentous algae (open-top cages) compared to controls. Furthermore, herbivorous fish were clearly more efficient than sea urchins in controlling algal biomass.

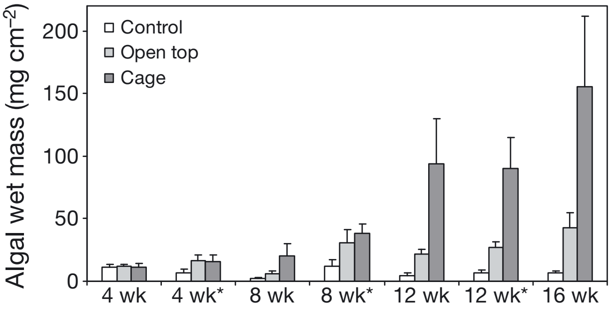

Fig. 4. Development of algal biomass (wet mass; mean ± SE) of the 3 treatments (control, open-top cages, and closed cage) over 16 wk. Sample times marked with an asterisk are the time-shifted second series of experiments (see 'Materials and methods'). n = 8 for each treatment at each sampling time

Distribution of fish and sea urchin

The number of fish species on the reef flat in our study was low compared to that in studies conducted at greater water depths and in larger study areas of the Red Sea (Table 2), however studies from similar water depths observed even lower species numbers (Table 2). This indicates that larger study areas and greater water depths, with potentially more feeding and refuge places, possibly influenced the observed differences. Previous observations from non-quantitative comparisons, without transects, between the reef flat (84 species counted) and the fore-reef wall (136 species) support this view (C. Jessen unpubl. data). Particularly larger herbivores from the families Acanthuridae and Scaridae were only present in the deeper part of the reef (data not shown).

Herbivorous fish abundance in the Red Sea is highly understudied, with previous studies revealing a lower abundance than that found in the present study, even at greater water depths (Table 2). Notably, herbivorous fish were 2 times more abundant in the morning than at other times of the day. Likely the fish exploited food sources early in the day and escaped increasingly unfavorable conditions (increased temperature, salinity, predation, or UV radiation) during the course of the day.

The high variations in abundance found in the present study are similar to results in older studies from the Gulf of Aqaba (Benayahu & Loya 1977, Mastaller 1979). Sea urchin diversity was strongly linked to reef rugosity (values here were relatively low, see Alvarez-Filip et al. 2009). However, it was not linked to fish predator abundance (Balistidae and Tetraodontidae; data not shown) which is generally considered one of the major factors (besides competi-

Table 2. Comparison of fish surveys in the Red Sea. Data are only shown for water depths similar to the present study (≤12 m). Some studies reported only pooled data from various water depths (curly brackets). *Values were estimated from graphs; **herbivores fish abundance was calculated from numbers of the families: Scaridae, Acanthuridae, and Siganidae; ?: missing or unclear information; GoA: Gulf of Aqaba

Location	Water depth (m)	Transect size (width × length) (m)	Transects per site	Sites	Replicates	Area (m^2)	Species (N)	Diversity index (H')	Total fish abundance (ind. m^{-2})	Herbivorous fish abundance (ind. m^{-2})
Qusayr, Egypt[1]	1	3 × 20	4	1	12	7380	66	0.8–2.7 (= 2.1)	0.75	0.59
Qusayr, Egypt[2]	5	5 × 50	6	1	1	1500	111	1.3–1.8?	0.5–1.4?	?
Qusayr, Egypt[2]	10	5 × 50	6	1	1	1500				
Dahab, Egypt[3]	2–6	8 × 9	2	1	11	1584	77	?	?	?
GoA, Egypt[4]	1	10 × 100	3	3	4	36000	27	?	0.09	0.08**
GoA, Egypt[4]	3	10 × 100	3	3	4	36000	41	?	0.22	0.18**
GoA, Egypt[4]	10	10 × 100	3	3	4	36000	35	?	0.15	0.11**
Egyptian Red Sea[5]	5 + 10	2 × 2	10	?	130?	40 × 130?	261	?	?	?
South Sinai, Egypt[6]	3	10 × 50	4	9	1	18.000	65	2.5	0.17	?
South Sinai, Egypt[6]	10	10 × 50	4	9	1	18.000		2.6	0.13	?
GoA Eilat, Israel[7]	?–15	2 × 50	3	4–5	4	16800	235	2.1–3.2	1.4–10.5	?
GoA Eilat, Israel[8]	5	2 × 25	0–4	3	1	350	159	?	4.3	0.18**
GoA Eilat, Israel[8]	10	2 × 25	0–3	3	1	300		?	3.9	0.06**
GoA Eilat, Israel[9]	1	2 × 25	2?	2	1	200	?	?	?	0.7–2.0*
GoA Eilat, Israel[9]	5	2 × 25	3?	2	1	300	?	?	?	0.1–0.4*
GoA Eilat, Israel[9]	10	2 × 25	3?	2	1	300	?	?	?	<0.05–0.2*
GoA Eilat, Israel[10]	4–7	3 × 15	1	1	5	225	95	2.7*	1.3*	0.4
GoA, Jordan[11]	0.5–1	5 × 200	2	1	1	2000	10**	?	?	0.15
GoA, Jordan[11]	2	5 × 200	2	1	1	2000	17**	?	?	0.23
GoA, Jordan[11]	5	5 × 200	2	1	1	2000	15**	?	?	0.08
GoA, Jordan[11]	10	5 × 200	2	1	1	2000	12**	?	?	0.11
GoA, Jordan[12]	6	5 × 50	3	5	1	3750	198	2.1–2.8*	1.9–4*?	?
GoA, Jordan[12]	12	5 × 50	3	5	1	3750		1.7–2.4*	3–8*?	?
Saudi Arabia[13]	1	5 × 200	1	4	1	4000	24*	?	0.55*	0.17*?
Saudi Arabia[13]	1.5	5 × 200	1	4	1	4000	32*	?	2.28*	0.24*?
Saudi Arabia[13]	6	5 × 200	1	4	1	4000	36*	?	1.33*	0.21*?
Saudi Arabia[13]	12	5 × 200	1	4	1	4000	39*	?	0.70*	0.12*?

[1]Present study; [2]Kochzius (2007); [3]Zajonz et al. (unpubl. data from 2006); [4]Ashworth & Ormond (2005); [5]Pilcher & Abou Zaid (2000); [6]Tilot et al. (2008); [7]Brokovich et al. (2006); [8]Brokovich et al. (2008); [9]Brokovich et al. (2010); [10]Rilov & Benayahu (2000); [11]Bouchon-Navaro & Harmelin-Vivien (1981); [12]Khalaf & Kochzius (2002); [13]Roberts & Ormond (1987)

tion, see Hay & Taylor 1985) determining sea urchin abundance (e.g. McClanahan & Shafir 1990, Harborne et al. 2009). However, Young & Bellwood (2011) recently proposed that only a few individuals of specific predator species may control sea urchin abundance.

Effects of herbivory on algal biomass and composition

The exclusion of sea urchins alone (open-top cages) and, even more, the combined exclusion of sea urchins and herbivorous fish (closed cages) resulted in significantly more algal growth than in the controls. This indicates that herbivorous fish removed significantly more algal biomass than did sea urchins.

In addition to the increased abundance of algal biomass, the absence of herbivores also affected algal composition. The most apparent change in algal composition on the settling tiles was the growth of filamentous algae and macroalgae in both caged treatments (open-top and closed cages) compared to the controls (Fig. 3). Both algal groups increased in cover on the settling tiles in the absence of herbivores. The high proportion of empty substrate in the controls demonstrates 2 important roles of herbivores: they (1) generate space, e.g. for settling coral larvae, and (2) prevent algal settlement, which otherwise may negatively impact coral recruitment (Kuffner et al. 2006, Birrell et al. 2008, Rasher & Hay 2010). However, none of the herbivores were able to completely prevent filamentous algae from growing, since these algae still accounted for ~10 % coverage in the control treatments. This may represent natural levels and may be due to the fast growth rates of this algal group (Airoldi 1998) rather than be an indication that the reef is overfished, since (low) algal biomass in the controls did not accumulate in the course of the study. Similar experiments from the Saudi Arabian Red Sea by C. Jessen et al. (unpubl.) confirm these growth patterns.

Fishes with access to the open-top cages successfully prevented macroalgae from growing on tiles for almost the entire study period, although filamentous algae developed in these treatments. This indicates a number of possible scenarios: e.g. either grazing by herbivorous fish alone was not sufficient to keep algae cover at low levels, or secondary metabolites of the algae deterred grazing fish (Paul et al. 2007, Hay 2009, Fong & Paul 2011) or fishes did not graze as much in the open-top cages as in the controls.

Macroalgal cover increased when all herbivores were excluded, but was mostly absent in the other treatments where herbivorous fish had access. This clearly demonstrates the role of herbivorous fishes in keeping the tiles clear of macroalgae. These results correspond with studies from other reefs (reviewed by Hay 1991, Burkepile & Hay 2006), and with the study by Mastaller (1979) from the Red Sea, who also observed an increase in macroalgal cover (e.g. *Hydroclathrus clathrathus* and *Padina* sp.) in response to exclusion of all kinds of herbivores, but did not distinguish between grazing by herbivorous fish and sea urchins.

We also observed the macroalgae *Hydroclathrus clathrathus* and *Padina* sp. exclusively inside the caged treatments (open-top and closed cage) during our study period. This suggests that this *H. clathrathus* can be used as an early warning indicator for reduced herbivory possibly triggered by overfishing, as proposed by Littler & Littler (2007), who suggested fleshy algae as early warning indicators of reef degradation, because of their fast growth and turnover rates. While other studies did not report the appearance of *H. clathrathus* in the Red Sea under natural conditions before March (Fishelson 1973, Benayahu & Loya 1977, Mastaller 1979), we found it as early as January. The exact reasons that trigger the appearance of macroalgae are not yet known, but the biomass of some species of macroalgae seems to be controlled by seawater temperature (Ateweberhan et al. 2006, Ferrari et al. 2012). However, the Gulf of Aqaba, the study site used by Fishelson (1973), Benayahu & Loya (1977), and Mastaller (1979), undergoes strong seasonal changes in temperature and inorganic nutrient concentrations (Wolf-Vecht et al. 1992, Genin et al. 1995) that may differ from the values at our study site. More research is needed to unravel the parameters that trigger growth and the occurrence of *H. clathrathus*, *Padina* sp., and other macroalgae in the Red Sea.

Since CCA serves as an important settling substrate for coral recruits (Harrington et al. 2004, Arnold et al. 2010), it is interesting that CCA coverage was never detected on the settling plates throughout the entire study period, regardless of the treatment. This stands in contrast to other studies in which CCAs appeared no later than 4 (Smith et al. 2010) and 8 wk after the herbivores were excluded (Belliveau & Paul 2002). The lack of CCA coverage in the present study may be explained in 2 ways: either sedimentation rates were too high, creating anoxic conditions, and thereby reducing CCA survival and recruitment (Fabricius & De'ath 2001, Figueiredo &

Steneck 2001, Steneck 1997) or CCA was outcompeted by filamentous algae. Our own observations in the Saudi Arabian Red Sea (authors' unpubl. data) showed that CCA were absent on light-exposed tiles with and without dense filamentous algae cover. Instead, non-coralline crusts partially covered the light-exposed tiles, while CCA started to grow on light shaded tiles after 4 wk, where filamentous algae were lacking.

Importance of sea urchins and herbivorous fish grazing

Our results are in line with previous studies (e.g. Vine 1974, Wanders 1977, Hay 1981a,b, Tribble 1981, Hay et al. 1983, Morrison 1988) which determined that herbivorous fish play a major role in structuring communities of algae. We could show by direct comparisons that, on the individual level, herbivorous fish were 22-fold more efficient than sea urchins in reducing autotrophic production of N and 5-fold more efficient in reducing algal dry mass on the reef flat. This points out the high ecological importance of herbivorous fish and indicates that this group deserves special consideration in management plans. Experiments by Korzen et al. (2011) at a water depth of 5 m in the Gulf of Aqaba support our findings. Korzen et al. (2011) carried out algal assays over 3 d using remotely deployed video cameras to evaluate herbivorous fish (observed mostly at daytime) and sea urchin (mostly at nighttime) grazing and found that fish were mainly responsible for removing algae. In contrast, a previous study in the same area by Benayahu & Loya (1977) suggested that sea urchins (i.e. *Diadema setosum*) largely regulated the cover of turf algae. Some early studies from the Caribbean also found sea urchins, especially *D. setosum*, to be a very important herbivore (Ogden et al. 1973, Sammarco et al. 1974, Sammarco 1980), though Hay (1984) related these findings to overfished reefs, while herbivorous fish were comparatively more important on reefs with little fishing pressure. The same patterns seem to be valid for the Red Sea.

The importance of (obligate) herbivorous fish in our study is likely underestimated, since facultative herbivores were also included in the herbivorous fish group. Open-top cages can alter grazing by herbivorous fish (e.g. McClanahan et al. 2002), therefore making our estimates of the relative role of fish grazing conservative. Furthermore, it has to be taken into account that fish in the open-top cages did not compete against sea urchins (Hay & Taylor 1985), and may have grazed relatively more than in the controls where echinoids were also able to graze. This may have resulted in some overestimation of the importance of herbivorous fish, adversely to the underestimation suggested before.

CONCLUSIONS

In times of global warming, ocean acidification, increased coral bleaching and pollution, overfishing poses an additional threat to coral reefs. The present study clearly demonstrated the high potential of benthic macroalgal growth when grazing by herbivores is reduced. This underlines herbivory as an important top-down factor at the study site. In comparison to sea urchins, herbivorous fish showed a much higher efficiency in removing algal biomass and N generated by algae. In particular, in the absence of fish, the macroalgae *Hydroclathrus clathrathus* appeared and prospered. Hence, our findings suggest that *H. clathrathus* could serve as indicator alga for overfishing in the Red Sea.

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Appendix 1. List of counted herbivorous fishes and their proportion of the total herbivorous fish count

Family	Species	Percentage of total herbivorous fish
Acanthuridae	*Acanthurus nigrofuscus*	2.5
	Acanthurus sohal	0.3
	Zebrasoma desjardinii	2.9
Chaetodontidae	*Chaetodon auriga*	4.9
	Chaetodon fasciatus	5.9
	Chaetodon paucifasciatus	0.4
	Chaetodon semilarvatus	<0.1
Kyphosidae	*Kyphosus bigibbus*	0.1
Pomacanthidae	*Pomacanthus imperator*	0.1
Pomacentridae	*Abudefduf sordidus*	2.2
	Plectroglyphidodon leucozonus	4.7
	Stegastes nigricans	5.2
Scaridae	All species	<0.1
Siganidae	*Siganus luridus*	0.8
	Siganus rivulatus	69.4
	Siganus argenteus	0.1
Tetraodontidae	*Arothron hispidus*	0.3

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