Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia, 9-13 July 2012
11A Ecology and macroecology: general session

Top-down and bottom-up effects on Red Sea coral reef algae

Christian Jessen[1], Cornelia Roder[2], Javier Villa Lizcano[2], Christian R Voolstra[2], Christian Wild[1]

[1]Coral Reef Ecology Group (CORE), ZMT Bremen, Fahrenheitstr. 6, 28359 Bremen, Germany
[2]Red Sea Research Center, KAUST, 23955-6900 Thuwal, Saudi Arabia
Corresponding author: christian.jessen@zmt-bremen.de

Abstract. Overfishing and eutrophication can lead to a reduction in herbivory and an increase in algae growth, respectively. Therefore, they are among the most significant local pressures on coral reefs. In particular Red Sea coral reefs, with their high degree of endemism, are increasingly threatened by effects of coastal development and overfishing. Here, we evaluated the independent and combined effects of the top-down factor herbivory and the bottom-up factor inorganic nutrient availability in an offshore reef of the Central Red Sea. We deployed exclosure cages and fertilizer sources *in situ* over 4 months (with 5 temporal samplings) to study development of dry mass and functional groups of algae on installed terracotta tiles. Our findings indicate that exclusion of herbivores had a stronger impact than eutrophication alone, and the combined treatment had the highest impact. The effect of elevated nutrients alone had no impact on composition of functional algae groups, dry mass, and the development of organic carbon (C_{org}) and nitrogen (N) on the tiles. However, when larger herbivores were excluded, tile surface cover changed drastically from patchy non-coralline crusts to filamentous algae. Dry mass increased up to 300 times, and with additional nutrient enrichment up to 500 times, though strong successional patterns could be observed. Our study is the first from the Red Sea that evaluates top-down and bottom-up factors on algae development and underlines the importance of addressing both of these factors in management measures to preserve the local coral reef resources.

Key words: Red Sea, Herbivory, Cage experiments, Eutrophication, Settlement tiles.

Introduction

Today coral reefs are threatened in many ways. Besides global stressors, such as climate change with resulting ocean warming and acidification, local factors are also negatively affecting coral reef health. Among the most important of these are eutrophication and overfishing. Since coral reefs mostly occur in oligotrophic environments, where algae growth is restricted by inorganic nutrient limitations, increased levels of these nutrients can have dramatic impacts on the reef ecosystem. Elevated nutrient concentrations can directly affect scleractinian corals, as ecosystem engineers (Wild et al. 2011), in a positive or negative way (Lough & Cooper 2011). Yet corals are mainly harmed indirectly (Lapointe 1997). Beneficiaries of eutrophication can be crustose coralline algae (CCA; Belliveau & Paul 2002), an important settlement substrate for corals (Harrington et al. 2004), but also turf and macroalgae that can prevent coral recovery (Schaffelke et al. 2005), inhibit coral recruitment (Schaffelke et al. 2005), or directly outcompete corals (Hughes et al. 2007).

Overfishing is another important local factor and can cause reef decline. A healthy herbivorous fish community supports a higher resilience of coral reefs since it limits growths and establishment of algal communities (Hughes et al. 2007). Both factors, nutrient enrichment and overfishing, together with climate change can lead to phase shifts (Hughes et al. 2007), a change from coral-dominated reefs to alternative stable states controlled by algae. Once the predominant algae are established, not only herbivory can be impeded (Hoey & Bellwood 2011), but availability of settlement space can be reduced, and frequency and intensity of interactions between corals and algae may increase (Done 1992). This leads to reduced coral recruitment, polyp growth (Mumby et al. 2007), and reduced habitat complexity (Mumby & Steneck 2011).

To our knowledge, no studies from the Red Sea are published that evaluated the separate and combined effects of artificially increased nutrients and simulated overfishing. This is particularly important, because both named threats pose the highest risk to Red Sea coral reefs (Burke et al. 2011). Therefore, we used manipulative in situ experiments with artificial nutrient enrichment and herbivore exclusion to answer the question how bottom-up and top-down factors contribute to development of benthic algae diversity and dry mass.

Material and Methods

Study site

The herbivore exclusion and nutrient enrichment experiments were carried out at Al-Fahal reef about 13 km off the Saudi Arabian coast in the Central Red Sea (N22.18.333, E38.57.768; Fig. 1) from June to September 2011.

Cage setups

Sixteen PVC frames were deployed in the reef at 5-6 m water depths along a 70 m transect. Each frame was equipped with 6 terracotta tiles of 100 cm² surface area. Prior to the start of the experiment, the tiles were autoclaved to remove any interfering compounds that could have accumulated during tile production and transported to the study site in a sealed plastic bag to avoid contamination. Tiles were installed at an angle of 45 degrees to fit reef contour and avoid excessive sedimentation approximately 10 cm above the ground using stainless steel screws. We applied four different treatments on the frames (each with a replication of n =4): control (only the equipped frame), fertilizer tubes (see nutrient enrichment section), cage (hemispherical metal cages with a mesh size of 3 cm), and combination of cage and fertilizer tubes. One tile per frame was collected on each of the five sampling events, after 1, 2, 4, 8 and 16 weeks.

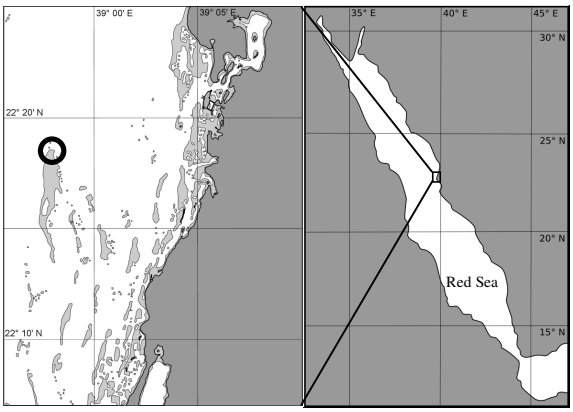

Figure 1: Study site. Right panel shows position of the study area in the Red Sea. The circle on the left panel indicates study site at the Northern tip of Al Fahal-reef about 13 km off the Saudi-Arabian coast.

Nutrient Enrichment

Nutrient enrichment was simulated by deploying four fertilizer tubes around the frame, consisting of perforated PVC tubes filled with Osmocote fertilizer (Scotts, 15 % total nitrogen (in form of nitrate & ammonium), 9 % phosphate (phosphoric pentoxide), and 12 % potassium oxide) embedded in 3 % agarose. Fertilizer was deployed once with regular monitoring of nutrient concentrations assuring a constant release rate.

Response variables

On each sampling date, pre-scored tiles (n=16) were divided in half (each 50 cm^2; an area which had been chosen from the asymptote of species-area curves by Hixon & Brostoff 1996). Half-tiles were then wrapped in sterile ziplock bags and brought onboard where one half was stored in liquid nitrogen for subsequent microbial analyses (results reported elsewhere), while the other half was kept on ice until further processing.

Tiles were photographed with a digital camera, subsequently rinsed with fresh water to remove salt and attached sediment prior to removal of all algae cover using a spatula. Then the cover was dried in an oven at 37 °C to constant weight and dry mass (not decalcified) was measured with a precision balance (Mettler Toledo XS205, accuracy: 0.01 mg).

In order to quantify the proportional coverage of functional groups on the tiles, 100 points were randomly overlaid on the digital picture of each tile using the software Coral Point Count with Excel extensions (CPCe) 4.1 (Kohler & Gill 2006). Applied categories were: “non biotic cover”, crustose coralline algae (CCA), non-coralline crusts (NCC; non-coralline red algae, grazed turf algae and crust-like green algae as morphologically hard to distinguish), and filamentous algae. Elemental analyses (organic C (C_{org}; acidified) and N) of tile cover were performed with a EuroVector EURO EA 3000 elemental analyzer.

As cage pictures and tile appearance indicate access of large herbivores to setup, the tile data of algae dry mass, C_{org}, N and functional group assemblage of 1 of 16 frames (No. 4, combined treatment) were removed from the dataset after application of Grubb’s outlier tests.

Water sampling

Directly prior to each tile sampling, ~5 L water samples (n=80; 40 enriched and 40 non-enriched) were taken from the water column directly above each frame setup. For inorganic nutrient measurements ~50 mL of the water were first filtrated on Whatman-GF/F filters, frozen and afterwards analyzed using a continuous flow analyzer (FlowSys Alliance Instruments).

Statistical analysis

Data from nutrient concentrations were analyzed using t-tests. Data of dissolved inorganic nitrogen (DIN) and nitrate were transformed (1/sqrt(x) and 1/x^0.2 respectively) to meet assumptions of normal distribution. For each sampling period (1 week, 2 weeks, 4 weeks, 8 weeks, 16 weeks) a two-factor analysis of variance (ANOVA) was used to test the effect of herbivory exclusion, nutrient enrichment and

their interaction on algae biomass. The data was log-transformed to meet the assumptions of normal distribution and equal variances. However, not all assumptions were met in every case. Accordingly, data of C_{org} and N were analyzed using Kruskal-Wallis tests.

Results

Water parameters

Mean phosphate, ammonium, and nitrite concentration between enriched (fertilizer & combined treatment) and non-enriched (control & cage treatment) differences were significant (t-test, $p<0.05$; Table 1). Nitrate concentrations did not differ significantly (t-test, $p>0.05$), though differences in DIN concentrations of pooled nitrite, nitrate, and ammonium were significant (t-test, $p<0.05$).

Table 1: Inorganic nutrient concentrations (µmol l^{-1}; means ± SE) in the nutrient enrichment treatments (fertilizer & combined) and the non-enriched treatments (control & cage). Asterisks indicate statistical significance: $p<0.05$ of t-test. $N<40$ (8 frames x 5 times) are due to a laboratory mishap. DIN: dissolved inorganic nitrogen.

	N	Non-enriched treatments	N	Enriched treatments
Phosphate	40	0.09 ± <0.01	35	0.15 ± 0.01 *
DIN	26	1.28 ± 0.06	36	1.55 ± 0.06 *
Nitrate	40	0.87 ± 0.05	39	0.94 ± 0.06
Nitrite	40	0.06 ± <0.01	39	0.07 ± <0.01 *
Ammonium	26	0.38 ± 0.02	36	0.53 ± 0.02 *

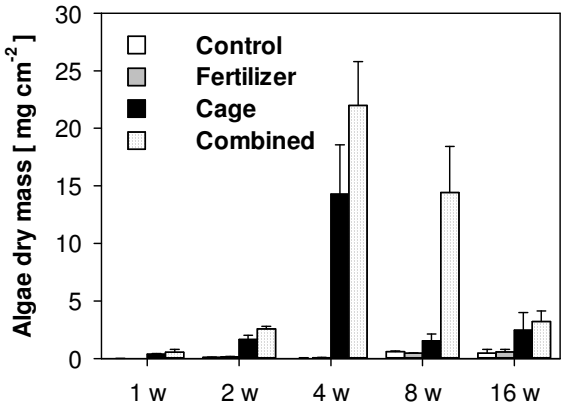

Figure 2: Comparison of algae dry mass [mg / cm²] between the treatments over the 5 sampling time points after 1, 2, 4, 8 and 16 weeks. n = 4 for each treatment (n=3 for combined, see method section).

Tile parameters

Herbivory exclusion led at all sampling times to increased algae dry mass (Fig. 2, Table 2). Nutrient enrichment had no effect on algae dry mass, except for the data of week 8 where they elevated algae growth but only through interaction with the cage treatment (Fig. 2, Table 2).

While the algae dry mass in the non-caged treatments did not change over the 5 sampling times, we could observe a gradual increase from the first week to the 4th week for the cage treatments. This was followed by a drop off to significant lower values in week 8 and week 16 (both MW-U test, $p<0.05$). The decrease of dry mass in the cage treatment occurred rapidly down to week 2 levels (11 to 17 % of peak values of week 4), unlike the combined treatment, where the decline was delayed and after 8 weeks algae dry mass still remained at 66 % of the peak values (Fig. 2).

Correspondingly, the algae nitrogen and organic carbon contents were affected. No differences occurred between the non-caged control and the fertilizer treatment. N content on the tiles significantly increased 8- and 11-fold over the entire time between the non-caged treatments (4.7 ± 0.5 µg cm^{-2}, mean ± SE) on the one hand and both cage (36.7 ± 8.8 µg cm^{-2}), and combined treatment (55.0 ± 13.0 µg cm^{-2}) on the other hand. Organic carbon content on the tiles increased 7- and 9-fold between non-caged treatments (0.12 ± 0.01 mg cm^{-2}), cage (0.83 ± 0.21 mg cm^{-2}) and combined treatment (1.08 ± 0.23 mg cm^{-2}), respectively.

The comparison of functional groups on the settling tiles revealed that the control and fertilized treatment and the cage and combined treatment exhibited similar patterns (Fig. 3). While algae cover on the control and fertilized tiles was only composed of patchy NCC, filamentous algae were the major algae group on the tiles in the cage and combined treatments. They made up almost 100 % after 4 weeks before declining in both treatments, but less pronounced in the combined treatment. Rather than filamentous algae, NCC and areas of "no biotic cover" were counted in the cage treatment, while NCC were rarely found in the combined treatment. CCA were only observed after 8 weeks in small amounts in the control (6 %) and fertilized treatment

Table 2: Results from 2 factorial ANOVAs for all five sampling times comparing the effect of herbivory, nutrient enrichment and their interaction on algae biomass. Significant effects ($p < 0.05$) are highlighted in bold. No results were obtained for week 1 because the dataset contained too many zeros.

Effects	df	1 week		2 weeks		4 weeks		8 weeks		16 weeks	
		F	p	F	p	F	p	F	p	F	p
Herbivory (H)	1	-	-	0,000	**0,000**	379,2	**0,000**	36,15	**0,000**	5,964	**0,045**
Enrichment (E)	1	-	-	0,146	0,146	1,7	0,222	11,54	**0,006**	0,060	0,813
H x E	1	-	-	0,767	0,767	0,2	0,657	16,73	**0,002**	0,191	0,675

(2 %) with one exception of 0.5 % after 4 weeks in the fertilizer treatment.

Discussion

Our study was able to show that the top-down factor herbivory had a stronger effect on algae parameters than the bottom-up factor nutrient availability, whose potential effects could only be seen in the combined treatment. Interestingly, data of algae biomass showed strong successional effects and peaked at week 4.

Herbivore exclusion had the strongest single impact on quantitative and qualitative algae development, while the nutrient treatment increased algae development only in interaction with the cages. This highlights the potential effect of elevated nutrient concentrations in the study area. We were not able to detect an effect from the fertilizer with herbivore access, however it is likely to have caused algal growth, but compensatory feeding by herbivores may have masked this effect (cf. Burkepile & Hay 2009). However, since the deployment of the fertilizer only led to a moderate albeit significant increase of nutrients, we cannot exclude that algae were still nutrient limited and may not have reached their full growth potential. Nutrient concentrations from the fertilizer may have been underestimated due to possible dilution effects caused by large sampling volumes.

Absolute values of C_{org} and N increased parallel to algae biomass in both caged treatments, whereas relative values did not change, giving no indication for nitrogen accumulation in the tissue.

The similar algae communities in both non-caged and both caged treatments (Fig. 3) indicate that functional algae group composition is mainly controlled by herbivores. The treatments excluding herbivores featured dense filamentous algae lawns instead of patches of non-coralline crusts.

Herbivory exclusion and nutrient enrichment were only interacting at week 8 in the combined treatment, i.e. the nutrients could only significantly enhance algae biomass inside the cage treatment. The enrichment buffered the decline of algae biomass and of filamentous groups that started after week 4 and was still visible in the combined treatment but not as distinct as in the cage treatment. We suspect that the decline of filamentous algae together with algae biomass was possibly triggered by elevated temperatures or salinity, as other factors did not show seasonal variations over the study period (nutrient concentrations, turbidity, oxygen saturation and chlorophyll along the transect) (data not shown). Similar factors may have been responsible for the observation that macroalgae were absent from the tiles. In another exclusion experiment in the Red Sea (Jessen & Wild unpublished), macroalgae were already observed after four weeks on settling tiles. Seasonal mixing patterns in the Red Sea can trigger macroalgae growth (Benayahu & Loya 1977) so that certain species (e.g. *Turbinaria*, *Stypopodium*, *Liagora*, *Halimeda*, *Cystoseira*) occur in the reefs from winter to summer. However, since our tiles were not deployed until June, the actual spawning and dispersion point could have been exceeded and

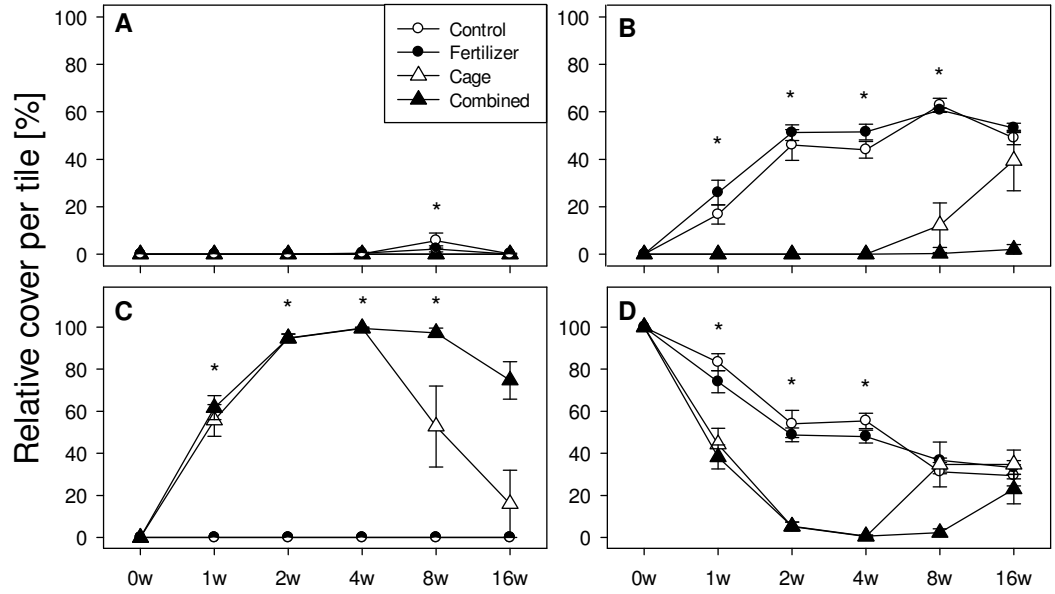

Figure 3: Relative cover of functional algae groups on settling tiles. Panels A-D show the proportional cover (± SE) of the functional algae groups on the settling tiles over all sampling times and for all treatments. Panel A depicts crustose coralline algae (CCA), B Non-coralline crusts (NCC), C Filamentous algae, and D No biotic cover. Asterisks indicate statistical significance between caged (cage & combined treatment) and non-caged treatments (control & fertilizer) (Mann-Whitney U test: $p<0.05$). No significant differences between other treatments.

therefore would explain the lack of macroalgae.

The exclusion of herbivores and the concomitant growth of filamentous algae also prevented CCA from growing on the tiles. Nonetheless, the treatments with herbivore access could not generate strong growth of CCA and were subject to variations. Smith et al. (2010) reported similar variations in CCA coverage in the first months after the deployment of tiles and did not observe considerable increments before six months. The same study detected the first appearance of CCA on settling tiles after 4 weeks and Belliveau & Paul (2002) found CCA 8 weeks after the start of the experiments, indicating that settling and growth of CCA on the tiles was inhibited in this study. However our study did not reveal parameters that could explain the lack of this important settling substrate for coral recruits (Arnold 2010).

The finding that the top-down factor herbivory clearly controls development of reef algae development more than the bottom-up factor nutrient availability has also been reported from other reefs around the globe (e.g. Belliveau & Paul 2002, Burkepile & Hay 2009). In contrast, other studies by Littler et al. (2006) and Smith et al. (2010) also reported an important role for nutrient concentrations. These results do not have to necessarily exclude each other, since most support for the thesis that herbivores are more important was obtained from small-scale enrichment experiments. Burkepile & Hay (2009) proposed that small-scale nutrient enrichment studies may be biased because they do not consider that herbivorous fish may not be capable of controlling all algae when nutrients are elevated over a broad spatial scale. Smith et al. (2010) raised another important point by demonstrating that the effect of fertilization lagged a few months behind the effects of herbivore exclusion and proposed that this may be a reason why other, shorter studies could not find strong nutrient enrichment effects.

Conclusions

Our study showed that reduced herbivory as a distinct factor has a more pronounced impact than nutrient enrichment over the study period. However, herbivores may have prevented a stronger response from the fertilizer, as indicated by the combined treatment that added up on the effects. Both factors were favoring algal growth and altered their composition, which can indirectly threaten the calcareous frame builders of the reef. A comprehensive management of the studied region needs to target eutrophication and overfishing in order to enhance coral reefs resilience against increasing global warming and ocean acidification.

Acknowledgement

Many thanks for support goes to the CMOR team at KAUST, L. Smith, F. Mallon, E. Aravantinos and the boat crew Khaled, Esam, and Ghazi. We also would like to acknowledge the field and laboratory assistance of T. Bayer, A. Roik, C. Arif, T. Brown, M. Kruse, C. Jhen and V. Gregoire. For invaluable advice and support in the laboratory, we thank the KAUST ACL lab team N. Fayad and M. Masry, as well as ZMT lab team D. Dassbach and M. Birkicht. Comments from S. Connolly, D. Burkepile and one anonymous reviewer greatly improved the manuscript.

References

Arnold SN, Steneck RS, Mumby PJ (2010) Running the gauntlet: inhibitory effects of algal turfs on the process of coral recruitment. Mar Ecol Prog Ser 414:91-105

Belliveau S, Paul V (2002) Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. Mar Ecol Prog Ser 232:105-114

Benayahu Y, Loya Y (1977) Seasonal occurrence of benthic-algae communities and grazing regulation by sea urchins at the coral reefs of Eilat, Red Sea. Proc 3rd Int Coral Reef Sym 2:383-389

Burke LM, Reytar K, Spalding M, Perry A (2011) Reefs at Risk Revisited. In. World Resources Institute, Washington, DC

Burkepile DE, Hay ME (2009) Nutrient versus herbivore control of macroalgal community development and coral growth on a Caribbean reef. Mar Ecol Prog Ser 389:71-84

Done T (1992) Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247:121-132

Harrington L, Fabricius K, De'ath G, Negri A (2004) Recognition and selection of settlement substrata determine post-settlement survival in corals. Ecology 85:3428-3437

Hixon MA, Brostoff WN (1996) Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. Ecol Monogr 66:67-90

Hoey AS, Bellwood DR (2011) Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? Ecol Lett 14:267-273

Hughes T, Rodrigues M, Bellwood D, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett M, Steneck R, Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr Biol 17:360-365

Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Comput Geosci 32:1259-1269

Lapointe B (1997) Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnol Oceanogr 42:1119-1131

Littler MM, Littler DS, Brooks BL (2006) Harmful algae on tropical coral reefs: bottom-up eutrophication and top-down herbivory. Harmful Algae 5:565-585

Lough JM, Cooper TF (2011) New insights from coral growth band studies in an era of rapid environmental change. Earth-Sci Rev 108:170-184

Mumby P, Hastings A, Edwards H (2007) Thresholds and the resilience of Caribbean coral reefs. Nature 450:98-101

Mumby PJ, Steneck RS (2011) The resilience of coral reefs and its implications for reef management. In: Dubinsky Z, Stambler N (eds) Coral Reefs: An ecosystem in transition. Springer, Amsterdam, pp 509-519

Schaffelke B, Mellors J, Duke NC (2005) Water quality in the Great Barrier Reef region: responses of mangrove, seagrass and macroalgal communities. Mar Pollut Bull 51:279-296

Smith J, Hunter C, Smith C (2010) The effects of top-down versus bottom-up control on benthic coral reef community structure. Oecologia 163:497–507

Wild C, Hoegh-Guldberg O, Naumann MS et al. (2011) Climate change impedes scleractinian corals as primary reef ecosystem engineers. Mar Freshw Res 62:205-215