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Comparative investigation of organic matter release by corals and benthic reef algae – implications for pelagic and benthic microbial metabolism

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Abstract. Global climate change and direct anthropogenic stress factors lead to gradual replacement of hermatypic corals by benthic algae at many reef locations, a process which is commonly referred to as phase shift. Recent research showed that corals via the release of organic matter and concomitant effects on cycles of matter can act as engineers of reef ecosystems. There are strong indications that reef associated benthic algae do also affect reef ecosystem functioning via organic matter release, but relevant information is lacking. To gain a better understanding of the biogeochemical consequences such phase shifts may entail, a series of comparative studies with corals and algae was conducted in reefs of the Northern Red Sea during four seasonal expeditions in 2006-2008. These investigations focused on the quantity and quality of the organic matter released by both groups of organisms involving dissolved organic carbon (DOC), particulate organic carbon (POC) and nitrogen (PN) along with the respective stable isotope signatures. Planktonic and benthic degradation of the released material were investigated using bottle incubation experiments and in-situ stirred benthic chambers. First outcomes show clear differences between organic matter release by corals and algae, thus suggest effects of phase shifts onto reef biogeochemical cycles.

Key words: corals, reef algae, organic matter release, phase shift, community metabolism

Introduction

It is generally assumed, that the global climate change along with direct anthropogenic factors like eutrophication and overfishing lead to phase shifts in coral reefs, i.e. the gradual replacement of reef building corals by benthic algae (Hoegh-Guldberg 1999, Hughes et al. 2003, Pandolfi et al. 2005, Hoegh-Guldberg et al. 2007, Hughes et al. 2007). Recent studies also showed that hermatypic corals can act as engineers of the entire reef ecosystem, particularly by the release of organic matter and associated effects on biogeochemical key processes and element cycles (Wild et al. 2004a, Wild et al. 2005b, Wild et al. 2008). This is a newly discovered aspect of corals as ecosystem engineers besides their long known ability to generate structural frameworks.

Moreover, the work of Smith et al. (2006) indicates that benthic reef algae can also affect processes such as microbial activity in their surroundings via a hypothetical release of organic matter. Reef algae may therefore act as (new) reef ecosystem engineers, but likely in a very different way. This pilot study presents first data based on comparative investigations with the dominant corals and benthic reef algae from four expeditions to the Northern Red Sea comprising the following three interrelated approaches: 1) Quantification of dissolved and particulate organic matter (DOM and POM) release, 2) Determination of POM stable isotope signatures, 3) Planktonic and benthic degradation of released exudates. These data will provide first comparative information on the quantity and quality of benthic algae-derived organic matter and its subsequent degradation in the different compartments of the ecosystem coral reef.

Material and Methods

The work for this study was conducted during four seasonal expeditions (Nov/Dec 2006, Aug/Sep 2007, Feb/Mar 2008, May 2008) to Marine Science Station (MSS), Aqaba, Jordan. Collection of all specimens took place in the MSS fringing reef in water depths of 5 to 7 m. During each of the field trips, 5 replicate fragments (coral branch length: 6 to 10 cm) were broken off in-situ from colonies of the dominant hard corals of the genera *Acropora*, *Pocillopora* and *Stylophora*, which were allowed to heal in a flow-through aquarium for at least 7 d prior to the

subsequent experiments. In addition, 5 replicate small pieces (lengths: 6 to 14 cm) of the 3 most dominant types of benthic algae were collected in-situ: the green algae *Caulerpa* spec., the red algae *Peyssonnelia* spec., and typical filamentous turf algae consortia growing on dead coral skeletons. All algae were left in a flow-through aquarium for at least 12 h prior to the subsequent experiments for cleaning and healing purposes. For the organic matter release quantification the beaker incubation technique described by Herndl and Velimirov (1986) was used. Corals and benthic algae were separately transferred into acetone- and seawater-rinsed 1000 ml glass beakers filled with 800 to l000 ml of untreated seawater freshly pumped from the field. Identical beakers, only filled with seawater, served as controls. Beakers were kept in a flow-through aquarium during day at in-situ temperature of 21 to 29 °C (caused by seasonal differences) as monitored by *Onset HOBO* temperature loggers. Nylon gauze was clamped above the beakers to simulate light intensities very similar to those at 5 m water depth as verified by *Onset Pendant* light loggers. After 6 h incubation duration, corals and algae were removed from the beakers and sub-samples were taken from the incubation water for determination of the following parameters.

Dissolved Organic Carbon (DOC): Circa 10 ml of the incubation water were filtered through 0.2 µm sterile syringe filters (polyethersulfone membrane). The first 4 ml of the filtrate were discarded, but the following 6 ml were collected in pre-combusted brown glass bottles or ampoules, which were instantly frozen at -20 °C and kept frozen until analysis. DOC concentrations were determined by high temperature catalytic oxidation (HTCO) using a Rosemount Dohrmann DC-190 total organic carbon (TOC) analyser. After defrosting, each sample was treated by adding 100 µl of 20 % phosphoric acid and purging for 5 min in order to remove dissolved inorganic carbon. DOC concentration of each sample was measured five times. An outlier test was conducted and the DOC concentrations of the remaining samples were averaged. Potassium hydrogenphtalate was used as standard for calibrating the DC-190 TOC analyser.

Particulate Organic Carbon (POC) and Nitrogen (PN): Between 400 and 940 ml of the incubation water were filtered onto pre-combusted GF/F filters (Whatman, 25 mm diameter), which were dried for at least 48 h at 40 °C and kept dry until analysis. POC and PN concentration measurements and respective stable isotope analyses were performed with a Carlo Erba NC 2500 elemental analyzer, coupled with a THERMO/Finnigan Conflo II- interface to a THERMO/Finnigan MAT Delta plus isotope ratio mass spectrometer. Elemental concentrations were calculated from certified elemental standards (Atropine, Cyclohexanone-2,4-dinitrophenylhydrazone; Thermo Quest, Italy) and typically showed standard deviations < 3 %. Stable isotope ratios are given in the conventional delta notation ($\delta\ ^{13}C$, $\delta\ ^{15}N$) relative to Vienna PeeDee Belemnite (VPDB) standard (Craig 1957, Coplen 1995) and atmospheric nitrogen (Mariotti 1984), respectively. Standard deviations for repeated stable isotope measurements of lab standard (Peptone) were better than 0.15 ‰ for nitrogen and carbon, respectively. Respective surface areas of all coral fragments and algae pieces were measured as reference parameter using geometric approximations (all corals and turf algae growing on dead coral fragments, see Naumann et al. (2009) or the image analysis software *Image J* to analyze digital photographs of the predominantly 2-dimensionally growing macro algae *Caulerpa* spec. and *Peyssonnelia* spec..

Planktonic microbial degradation: Circa 140 ml of the incubation water from each beaker was used to fill two 60 ml gas-proof glass bottles. Oxygen concentration in one of the bottles was measured immediately and in the second bottle after incubation of the enclosed water for at least 16 h in the dark and at in-situ temperature using Winkler titration (Winkler 1888) or a *Hach HQ 10* optode. Microbial activity in the incubation water was determined by subtracting final from start oxygen concentration. Planktonic microbial degradation of the added TOC was calculated by using the respective POC + DOC amounts and the increase in O_2 consumption in the bottles relative to the controls assuming that 1 mol added organic material is oxidized by 1 mol O_2.

Benthic degradation: Degradation of algae and coral exudates was studied in-situ by addition of algae- and coral derived organic material to stirred benthic chambers identical to those described by Huettel and Gust (1992). These in-situ experiments were conducted at a reef site with carbonate sands (2.5 m water depth) described in (Wild et al. 2005a). The duration of the individual chamber experiments ranged between 5 to 8 h. Prior to each experiment, chambers were gently inserted into the loose calcareous sands to a depth of about 12 cm, thus including a water column of approximately 20 cm height and 5.7 l volume. At the beginning of the first experiment, 81 µmol coral- and 310 µmol algae-derived organic matters were added to two chambers each. In a second independent experiment, 91 µmol coral- and 186 µmol algae-derived organic matters were again added to two chambers each, but only one of these two replicate chambers was stirred (advection

chamber) , whereas the other one was left without stirring (diffusive chamber). All 8 chambers of both experiments were incubated for 8 h in the dark. Water samples were regularly (at least every 2 h) collected from all chambers through a sampling port using plastic syringes, whereby the water from the diffusive chambers was thoroughly mixed before sampling in order to avoid O_2 concentration gradients. Oxygen concentrations were measured in the chamber waters using Winkler titration and benthic TOC degradation of the added algae or coral exudates were calculated as described above.

Results

All investigated benthic reef algae released both DOM and POM in measurable quantities. Data from the first two seasonal expeditions showed that organic matter release by corals and benthic algae was very different. In particular, DOC fluxes were one order of magnitude higher during autumn 2006 compared to summer 2007 (Table 1). There was no correlation between organic matter release and water temperature. All investigated benthic reef algae during both seasons showed DOC release, whereas DOC release by the corals was highly variable (as indicated by the large error bars) with often negative values, i.e. DOC uptake (Table 1). POC release could be detected for all investigated specimens, but showed no seasonal differences with similar release rates in autumn and summer. However, corals generally released significantly more POC than algae (U-test after Wilcoxon, Mann and Whitney, $p < 0.05$). The C:N ratios and nitrogen stable isotope signatures of algae and coral-derived particulate organic matter (POM) were not significantly different, but carbon stable isotope signatures of algae-derived POM ($\delta\ ^{13}C$: -10.1 ± 1.4 ‰) were significantly more positive ($p < 0.05$) than those of coral-derived POM ($\delta\ ^{13}C$: -18.3 ± 0.3 ‰). POM C stable isotope signatures were very similar to that of sterile coral mucus ($\delta\ ^{13}C$: -18.2 ± 1.2 ‰; Naumann et al. unpublished data), thereby demonstrating the apparent dominance of this material in the coral beakers. The respirometric experiments from all 4 seasons revealed that microbial activity measured as O_2 consumption was only significantly higher in the algae incubation water compared to that of the corals in autumn, but not during the other three seasons. Resulting microbial Total Organic Carbon (TOC = POC + DOC) degradation rates in autumn were 0.57 ± 0.38 and 0.18 ± 0.02 % h^{-1} for the algae- and coral-derived exudates, respectively. Benthic degradation of both organic matter sources showed an opposite trend with twice as high TOC degradation rates for the added coral exudates (23.7 ± 4.8 % h^{-1}) than those for the algae exudates (12.1 ± 3.9 % h^{-1}) under advective conditions. Advective transport of matter induced by the stirred benthic chambers increased benthic C degradation by a factor of 8 for the coral exudates, but only doubled for the algae exudates.

Discussion

This study confirms that benthic reef algae similar to hermatypic corals release organic matter in dissolved and particulate form to their surrounding. The assumed differences in organic matter release between benthic reef algae and corals (please see introduction) are verified by the tendency that corals release more POC and algae more DOC as well as by the differences in carbon stable isotope signatures. The latter finding may be caused by a more pronounced photosynthetic C assimilation of the benthic reef algae (Fry 2006), but may also indicate different chemical composition of algae compared to coral exudates. This aspect needs further detailed chemical analyses, but the differences in natural C stable isotope signatures suggest the suitability of this material for natural tracer studies.

	Autumn 2006	
	DOC net release	POC net release
Turf	66.0 ± 23.0	2.7 ± 1.3
Caulerpa	10.0 ± 8.0	0.8 ± 0.2
Peyssonnelia	22.0 ± 18.0	2.2 ± 0.3
Acropora	105.0 ± 193.0	2.5 ± 0.6
Stylophora	-75.0 ± 45.0	7.8 ± 1.5
Pocillopora	-435.0 ± 30.0	2.8 ± 0.8
	Summer 2007	
	DOC net release	POC net release
Turf	1.46 ± 1.50	1.34 ± 0.34
Caulerpa	1.63 ± 0.81	0.48 ± 0.34
Peyssonnelia	1.57 ± 1.15	n.m.
Acropora	4.00 ± 0.70	2.24 ± 0.41
Stylophora	-3.81 ± 11.06	5.04 ± 1.77
Pocillopora	-6.75 ± 3.52	3.88 ± 0.58

Table 1: Organic matter release by the dominant benthic algae (Turf algae, green algae *Caulerpa*, red algae *Peyssonnelia*) and hermatypic corals (*Acropora*, *Stylophora*, *Pocillopora*) in the study area during the first two expeditions to the Northern Red Sea (means ± SE given as mg C m^{-2} coral or algae surface area h^{-1}; n.m = not measured; data from other expeditions not measured yet).

The comparably high DOC release by benthic reef algae in combination with the observed stimulation of planktonic microbial activity supports previously postulated statements (Kline et al. 2006, Smith et al. 2006, Dinsdale et al. 2008), which suggested that DOM released by benthic algae could stimulate microbial O_2 consumption with subsequent damage of corals in direct vicinity via hypoxia or anoxia.

Generally, algae-derived organic matter is obviously rapidly degraded in the water column, whereas this applies for coral-derived organic matter in the reef sands. Reasons for that may be that a high proportion of the algae-derived organic matter enters the DOM pool and can be taken up by planktonic microbes via the microbial loop. Kuntz et al. (2005) could demonstrate that because of this interrelationship DOM is more deleterious for corals than inorganic nutrients in reef waters.

Figure 1: Coral (upper panel) versus benthic algae dominated (lower panel) fringing reef areas in front of MSS, Aqaba, Jordan, photographed during spring expedition 2008.

Coral-derived organic matter in contrast contains more POM, which is often dominated by mucus. This material can be degraded by (specialized) microbes inhabiting the calcareous coral reef sands in high abundances (Wild et al. 2004b, Wild et al. 2005b, Wild et al. 2006), thus providing an explanation for the comparably high benthic degradation rates observed in the present study. Coral mucus in addition, because of its gel-like structure, can easily be transported via advection into the highly permeable reef sands, which act as biocatalytical particle filter systems. Such transport may not be possible to that extent for the particulate fraction of algae-derived organic matter, which can explain the pronounced advective stimulation of benthic coral-derived organic matter degradation. Algae-derived POM may in addition have a distinctive refractory character (Buchsbaum et al. 1991, Kristensen 1994), which prevents rapid degradation and leads to deposition and ultimately blockage of the reef sands. This may compromise the important function of reef sands for the recycling of organic matter and thus has potential implications for reef management.

The observed strong seasonal differences concerning algae- and coral derived organic matter release in the study area between autumn and summer were probably caused by higher availabilities of inorganic nutrients in autumn due to colder temperatures and the beginning of deep water mixing typical for the Northern Red Sea (Rasheed et al. 2002). A higher availability of inorganic matter may have resulted in increased algae growth rates and associated high synthetisation of DOM. Monitoring of benthic reef algae coverage also showed strong seasonal differences (Haas et al. unpublished data) with temporal overgrowth of reef corals by algae during late winter and early spring (see Fig. 1). However, algae blooms collapsed soon after due to depletion of inorganic nutrients in late spring. Permanent phase shifts will thus likely not appear in the study area if inorganic nutrient input from land or mariculture facilities and direct reef damage are avoided.

In summary, both investigated groups of organisms can obviously act as reef ecosystem engineers via organic matter release. However, the hard corals as “old” engineers (i.e. before phase shift) contribute differently to reef processes than benthic algae as the “new” engineers after phase shift. Element cycles via coral-derived organic matter as described by Wild et al. (2004a) contributing to the conservation of essential nutrients in the reef ecosystem will likely not take place in an algae dominated post phase shift reef, as algae-derived organic matter can apparently not substitute the important particle trapping function of coral mucus. This pilot study therefore suggests that phase shifts from coral to benthic algae may have far reaching consequences for biogeochemical processes and general reef functioning.

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