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First evidence of coral bleaching stimulating organic matter release by reef corals

W. Niggl[1,2], M. Glas[1,2], C. Laforsch[2,3], C. Mayr[2], and C. Wild[1,2]

1) Coral Reef Ecology Work Group (CORE), LMU, 80333 München, Germany
2) GeoBio-Center, LMU München, Richard-Wagner-Str. 10, 80333 München, Germany
3) Department Biology II, LMU München, Großhadenerstr. 2, 82152 Martinsried, Germany

Abstract. Corals continuously release mucoid organic exudates in order to clean their surfaces. Additionally, recent research highlighted the fact that this coral-derived organic matter acts as energy carrier and particle trap in the oligotrophic coral reef ecosystem, thus playing an important ecological role for recycling of matter and conservation of nutrients. Environmental stressors such as air exposure, high sediment loads and turbidity are known to increase the release of coral-derived organic matter. However although it is a common statement in the literature, scientific data verifying increased coral-derived organic matter release rates during temperature-induced bleaching events is lacking. This is critical as coral bleaching is the most extensive coral disease world-wide, and bleaching-induced changes in organic matter release potentially have far reaching consequences for reef functioning. In this study, a bleaching event was induced in the laboratory and release of dissolved and particulate organic carbon (DOC and POC) and nitrogen (PN) by the hermatypic coral *Acropora* spec. was quantified. Results show that during a bleaching event coral derived POC and PN release almost doubled compared to unstressed controls. This is the first experimental evidence that coral bleaching affects coral-derived organic matter release and potentially ensuing element cycles in tropical reef ecosystems.

Key Words: organic, matter, release, bleaching, stimulating

Introduction

Mucoid organic exudates continuously released by corals (Meikle et al. 1988) play an important role in heterotrophic feeding (Duerden 1906, Yonge 1930, Lewis and Price 1975, Lewis 1977, Sleigh et al. 1988, Goldberg 2002) as a defence against smothering by sediment (Schumacher 1977), desiccation (Daumas and Thomassin 1977, Krupp 1984), physical (Brown and Bythell 2005) and UVR related (Drollet et al. 1997) damage, pathogens (Ducklow and Mitchell 1979, Rublee et al. 1980, Cooney et al. 2002) or pollutants (Mitchell and Chet 1975, Neff and Anderson 1981, Bastidas and Garcia 2004). However, as mucoid organic exudates can dominate the suspended particulate matter (Johannes 1967, Marshall 1968) in reef waters, they are obviously also major components of the coral reef ecosystem's nutrient cycles. Wild et al. (2004a) suggested that these coral-derived mucoid exudates may function as energy carrier and particle trap, thereby helping to conserve essential nutrients in oligotrophic tropical coral reefs. Astonishingly, although the importance of coral-derived organic matter for reef ecosystem functioning is well documented, studies quantifying release rates in correlation to variations in the key environmental factors are rare.

During the last decades, the phenomenon of coral bleaching, i.e. the whitening of corals due to the loss of their symbiotic algae and/or pigments (Brown 1996), has become more and more evident all over the world. Mass coral bleaching events, triggered mainly by increases in water temperature, have affected the world's coral reefs with increasing frequency and intensity since the late 1970s (Hoegh-Guldberg 2004). It is predicted that due to a continued increase in seawater surface temperature (Bijlsma et al. 1995) from the year 2030 large scale bleaching events will occur annually (Coles and Brown 2003), leaving only a very short recovery period for the affected corals.

Despite the apparent actual threat of coral bleaching for the survival of coral reefs, no data is available concerning the associated release rates of coral-derived organic matter. However, such data is indispensable in order to allow any prediction concerning nutrient and energy budgets for future environmental scenarios in coral reefs. In this laboratory study, release rates of particulate organic carbon (POC), particulate nitrogen (PN) and dissolved organic carbon (DOC) by hermatypic corals of the genus *Acropora* during a temperature induced bleaching event were investigated.

In contrast to the methods of previous studies that have investigated release rates of organic matter in

relation to varying environmental factors excluding coral bleaching (Crossland 1987, Riegl and Branch 1995, Wild et al. 2005a), this study distinguished released coral-derived organic matter (mucoid exudates and host cells) from algal (zooxanthellae)-derived organic matter.

Material and Methods

Experimental description

All experiments were conducted in August and September 2007 in the aquarium facilities of the Department Biology II of LMU München, Germany. One coral colony of the genus *Acropora* was fragmented three weeks prior to the subsequent experiment in order to allow healing and regeneration. After the fragmentation, 10 coral fragments (surface Area: 72.4 - 126.2 cm²) were fixed on ceramic tiles (4.6 x 4.6 cm) using conventional coral glue. The experimental set-up consisted of two aquaria, the resident aquarium (215 L control aquarium), in which the fragments were maintained at non-heat-stress conditions, and a 30 L aquarium (bleaching aquarium), in which the temperature could be adjusted using a thermostat (HAAKE E52, Germany). The temperature in the resident aquarium was monitored by an ONSET underwater temperature logger revealing a temperature range between 25.6 °C and 29.3 °C in diurnal cycles. At the beginning of the incubation experiments, the coral fragments were placed in ten 1000 ml beakers filled with ca. 900 ml of filtered seawater (0.2 µm pore size) from the control aquarium. Manual transference into the beakers resulted in an expose to air of less than two seconds. Five beakers, each with one submersed colony (C1-C5), were placed in the control aquarium, thereby being exposed to the same temperature conditions as prior to the start of the experiment. The submersed fragments in the remaining five beakers were placed in the bleaching aquarium and acted as bleaching samples (B1-B5).

Initial water temperature for the bleaching samples was adjusted to 27 °C and kept at that temperature for 24 h, which complied with two incubation periods (one incubation period = 12 h). Introduction of compressed air ensured sufficient air supply and water circulation. After 12 h incubation, all coral colonies (B1-B5, C1-C5) were transferred to additional 1000 ml beakers filled with ca. 900 ml of freshly filtered seawater (0.2 µm). The incubation water of the precedent incubation period (IP) was kept for further processing as described below. This procedure was repeated every 12 h. After 24 h at 27 °C (IP 1 and 2), the temperature of the bleaching aquarium was raised every 12 h to a maximum of 32 °C at IP 7. Temperature was decreased to 29 °C and 27 °C for IP 8 and IP 9, respectively.

The occurrence of bleaching was defined as the point in time when zooxanthellae release rates of the bleaching samples were significantly higher than the release rates of the control samples. The surface areas of all coral fragments were measured as a reference parameter using the advanced geometry method described in Naumann et al. (submitted) and based on computer tomography reference as described by Laforsch et al. (2008).

Incubation water processing

The exact volume of the incubation water from all beakers was determined using a graduate 1000 ml glass cylinder with an accuracy of ± 20 ml. The incubation water was then stirred using a glass pipette and sub-samples (n = 1 for each parameter) were taken in order to determine the following parameters.

For subsequent **DOC measurements,** 5 ml of the incubation water were filtered through 0.2 µm syringe filters (FP 30/0.2 CA, Schleicher and Schell). The first 2 ml of the filtrate were discarded, but the following 3 ml were collected in precombusted brown glass bottles, which were instantly shock-frozen at -80 °C and kept frozen until analysis. For **POM quantification** (particulate organic matter), 50 ml of the incubation water were extracted and filtered by a vacuum filtration unit onto precombusted GF/F filters (Whatman, 25 mm diameter). Filters were dried for at least 48 h at 40 °C and kept dry until analysis. Another 50 ml were fixed with 2-3 drops of Lugol's solution and stored at room temperature for subsequent **enumeration of zooxanthellae** using counting towers and backlight microscopy at 400-times magnification (Axioplan, Zeiss Germany).

The remaining incubation water was fixed with formaldehyde (1 % formaldehyde end concentration) and stored in the dark at 4 °C until further treatment.

Organic matter analysis

POM analyses were conducted using an Elemental Analyzer NC 2500 for C- and N determinations (Carlo Erba, Italy). For calibration of the elemental content of the samples, two standards, Atropine ($C_{17}H_{23}NO_3$) and Cyclohexanone-2,4-dinitrophenylhydrazone ($C_{12}H_{14}N_4O_4$) were used. Obtained POC and PN values equal the total amount of released particulate organic matter (POMt). In order to obtain the released amounts of coral-derived particulate organic matter (POMc) the amount of released algal-derived organic matter (POMa) was subtracted from POMt**.** Consequently coral-derived organic matter is defined as any organic matter (mucoid exudates, host cells) released by the corals except algal cells.

For calculating the amount of released POMa, the POC and PN contents of a distinct number of

zooxanthellae was determined. Therefore a zooxanthellae suspension was produced by centrifugation (6000 g) of 400 ml incubation water from B2 after IP8. The pellet was resuspended in filtered seawater and the zooxanthellae concentration (9330 cells ml^{-1}) was determined (methodology see above). Dilution series of 0.1, 1.0, 10.0 and 50.0 ml of this solution were subsequently filtered in triplicates onto precombusted GF/F filters (Whatman). The filters were dried at 40 °C for at least 48 h before POM analysis as described above.

The released amounts of algal derived particulate organic matter (POMa) was determined by multiplying released numbers of zooxanthellae by the respective calculated carbon and nitrogen contents of a single *Symbiodinium* cell.

Bacteria abundances for 2 bleaching and 2 control samples were determined using standard DAPI coloration and fluorescence microscopy. Assuming a carbon content of 20 fg C per cell (Lee and Fuhrmann 1987), bacteria in the bleaching samples would account for 3.1 to 5.2 % of the total recorded C content. In the control samples, bacteria would account for 4.0 to 6.0 % respectively. In the light of these calculations microbial contribution was considered minor.

Unfortunately, bleaching samples B1, B4 and B5 showed necrosis after IP 7 (12 h at 32 °C). The incubation water of these fragments was therefore excluded from all further analyses unless otherwise stated.

DOC concentrations were determined by high temperature catalytic combustion (HTCO) using a Rosemount Dohrmann DC-190 total organic carbon (TOC) analyser and Potassium hydrogenphtalat as standard solution. Each sample was acidified by adding 100 µl of 20 % phosphoric acid and purged for 5 min in order to remove inorganic carbon. The DOC concentrations of each sample were measured five times. An outlier test was conducted, and the DOC concentrations of the remaining sub-samples were averaged.

Results

Induction of a bleaching event

A bleaching event was induced in the laboratory by exposing the investigated coral fragments to temperatures increased by 3 to 5 °C (Fig. 1a). Zooxanthellae enumeration revealed that from the IP 5 (30 °C) to the IP 9 (27 °C) significantly more (Table 1) zooxanthellae were released by the coral fragments incubated under elevated temperature compared to the controls (Fig. 1a).

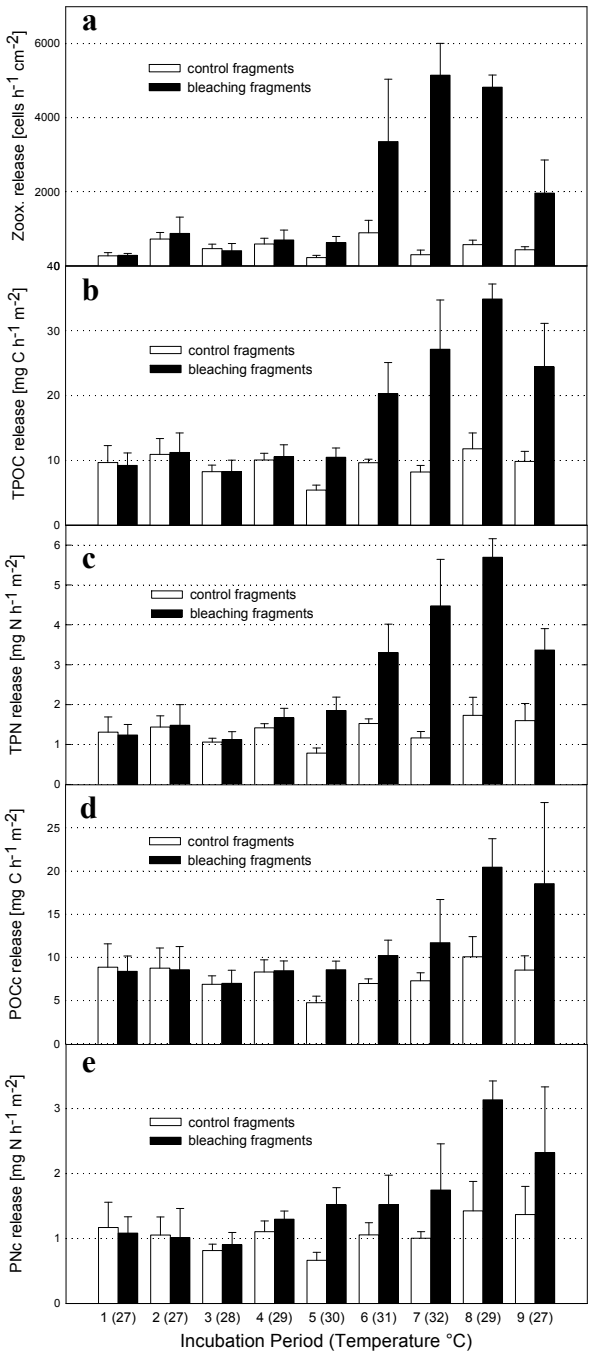

Figure 1: Summary of organic matter release rates during artificial bleaching experiment a) zooxanthellae release b) total POC release c) total PN release d) coral-derived POC release e) coral derived PN release.

Release of POCt and PNt

Throughout non-bleaching conditions there was no significant difference between the controls and the bleaching samples (Fig. 1b,c). Under bleaching conditions, from IP 5 (30 °C) until IP 9 (27 °C),

bleaching samples showed significantly (Table 1) higher POCt and PNt release rates. During IP 8 (29 °C), bleaching samples exhibited highest POCt and PNt release rates.

Regarding all bleaching samples (B1-B5), including those partially necrotic, POCt release rates were also highest during IP 8 (29 ° C) with release rates of 114 ± 75 mg C h^{-1} m^{-2} (mean ± SD, n = 5) and 14.0 ± 7.6 mg N h^{-1} m^{-2} (mean ± SD, n = 5).

Table 1: Summary of statistical analysis (independent samples t-test): given are p values for hypothesis for no differences between control fragments and bleaching fragments. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Temp	Zoox.	TPOC	TPN	POCa	PNa	POCc	PNc
30 °C	***	***	***	***	***	***	***
31 °C	*	**	***	*	*	**	0.065
32 °C	***	**	***	***	***	0.079	*
29 °C	***	***	***	***	***	**	**
27 °C	**	**	**	**	**	*	0.115

Release of POMa and POMc

The released amounts of algal derived particulate organic matter (POMa) directly correlated with the zooxanthellae release rates, as POMa release was calculated by multiplying the released numbers of zooxanthellae with obtained POC and PN content of 0.3 and 0.05 ng $cell^{-1}$, respectively (linear regression of zooxanthellae numbers against respective POC content, $R^2 = 0.999$). Consequently, POCa and PNa release of the bleaching samples was significantly higher than that of the control samples whenever bleaching, as defined above, occurred (Table 1).

Algal-derived POC and PN release of the bleaching samples was lowest at IP 1 (27 °C) and highest during IP 7 (32 °C). The highest increase of algae-derived POC/PN release was found during IP 8 (32 °C), when bleaching samples released 11 to 35 times more algae-derived POC and PN than the control samples.

POMc was calculated subtracting POMa from POMt. Throughout non-bleaching conditions there was no significant difference between the treatments concerning POCc and PNc release (Fig. 1d,e). Coral-derived POC release accounted for 76 to 91 % of the total released POC and coral-derived PN for 68 to 88 % of total released PN under non-bleached conditions. Bleaching samples during IP 5 (30 °C) released significantly (Table 1) more POCc and PNc compared to the controls. During bleaching, coral derived POC release accounted for 42 to 82 % of released POCt and coral-derived PN accounted for 38 to 82 % of total released PN. Maximum POCc and PNc release could be detected during IP 8 (29 °C).

Release of DOC

No significant differences between bleaching and control samples concerning DOC concentrations could be found after any incubation period and treatment.

Discussion

Coral bleaching and organic matter release

Coral bleaching was induced at elevated temperatures (30 °C – 32 °C), but also occurred when temperature was decreased to 29 °C and 27 °C at the end of the experiment. This temporal delay may be explained by the effect of heat stress, which can lead to the breakdown of enzymatic pathways in plants and animals, resulting in metabolic or biochemical dysfunction (Cossins and Bowler 1987). Reinstalling these enzymatic pathways may take a few hours to days, depending on the damage evoked by heat stress. Thus, although temperatures were adjusted to non-bleaching conditions, the release rates were still elevated in the bleaching samples.

Besides the total release of POM, the exclusive release of particulate coral-derived organic matter was increased. This may be attributed to either increased release of mucoid exudates or increased release of coral cellular material as a consequence of the bleaching mechanism (e.g. host cell detachment). If the mechanism of bleaching, i.e. the release of zooxanthellae, was solely responsible for increased coral-derived organic matter release, the release of coral-derived organic matter should be highest when zooxanthellae release during bleaching was highest. However, coral-derived organic matter release was highest at 29 °C when zooxanthellae release had already decreased (Fig. 1a,d,e). Consequently, the mechanism of bleaching was very likely not the only factor responsible for increased coral-derived organic matter release. Therefore, increased release of mucoid exudates apparently co-occurred during bleaching.

The measured total organic matter release rates of the non-stressed control fragments are in the same range as release rates described in previous field studies (Table 2). Including coral fragments with partial necrosis, release rates were similar to those measured during air exposure (Table 2). As necrosis is one of five possible mechanisms resulting in expulsion of zooxanthellae (Gates et al. 1992), and commonly occurs during bleaching (Glynn et al. 1985), these findings underline the relevance of bleaching events for energy and nutrient cycles in the reef ecosystem. This is confirmed by the study of Wild et al. (2004b), who found that coral-derived organic matter is rapidly degraded by reef microbes, in contrast to zooxanthellae-derived organic matter, which may rather represent a loss of energy and nutrients for the reef ecosystem (Wild et al. 2005b).

Table 2: Summary of studies examining organic matter release rates by corals of the genus *Acropora*. In the present study 45 replicates are displayed, because 5 coral fragments were incubated at 9 different periods. (Note: Previous studies used old definition of mucus and did not distinguish between coral- and algal-derived organic matter).

Study site	Stress	Mucus C release (mg h^{-1} m^{-2})		Mucus N release (mg h^{-1} m^{-2})		N	Method	Reference
Heron Island	Air expos.	117 ± 79		13 ± 8		8	Container	Wild et al. 2005
Heron Island	No	10 ± 5		1.3 ± 0.8		8	Beaker	Wild et al. 2005
Heron Island	No	7 ± 3		0.8 ± 0.4		8	Beaker	Wild et al. 2005
Eilat	No	1.4 - 4.2					Perspex Chamber	Crossland 1987
Aqaba	No	1.0 - 3.0		0.1 - 0.4		5	Beaker	Naumann unpubl.
		coral-derived	algal-derived	coral-derived	algal-derived			
Laboratory	No	7.8 ± 2.1	1.5 ± 0.8	1.1 ± 0.3	0.3 ± 0.1	*45*	Beaker	This study
Laboratory	Bleach. 30°	8.6 ± 1.0	1.9 ± 0.5	1.5 ± 0.3	0.3 ± 0.1	5	Beaker	This study
Laboratory	Bleach. 31°	10.2 ± 1.8	10.1 ± 5.0	1.5 ± 0.5	1.8 ± 0.9	5	Beaker	This study
Laboratory	Bleach. 32°	11.7 ± 5.0	15.4 ± 2.6	1.7 ± 0.7	2.7 ± 0.5	2	Beaker	This study
Laboratory	Bleach. 29°	20.4 ± 3.3	14.5 ± 1.0	3.1 ± 0.3	2.6 ± 0.2	2	Beaker	This study
Laboratory	Bleach. 27°	18.5 ± 9.4	5.9 ± 2.7	2.3 ± 1.0	1.0 ± 0.5	2	Beaker	This study

This study also showed that DOC release was not influenced by coral bleaching. This is surprising as Wild et al. (2004a) demonstrated that between 56 and 80 % of coral mucus can dissolve in the surrounding seawater. However, it is very likely that a high proportion of the released DOC was re-consumed by the coral and associated bacteria (Sorokin 1973, Al-Moghrabi et al. 1993). This explanation is supported by the studies of Ferrier-Pages et al. (1998) and Naumann et al. (unpublished data), who found that it is generally difficult to detect any DOC release by corals in a closed system such as a beaker.

Furthermore, DOM polymers can spontaneously assemble to form polymer gels, thus entering the POM pool (Chin et al. 1998), which could have lead to a removal of surplus DOC from the incubation water.

Ecological implications

Increased coral-derived POM release during bleaching can probably be attributed to increased release of cellular matter and/or to increased release of mucoid exudates. Increased release of cellular matter during bleaching can be explained by the mechanism of bleaching, which may lead to loss of parts of or entire coral cells. However, the reason for increased release of mucoid exudates is harder to surmise. Up to 45 % of carbon fixed daily by the zooxanthellae can be released as organic matter by the host coral (Davies 1984, Crossland 1987, Bythell 1988, Edmunds and Davies 1989). A bleached coral is in a state of energy shortage as the algal symbionts, which are capable of providing the coral host with up to 100 % of its daily metabolic energy requirements (Muscatine et al. 1981), are lost. Thus, it is not surprising that coral bleaching can affect the release rates of organic matter.

However, there are some ecological advantages and disadvantages of up-regulation of mucoid organic matter release during coral bleaching. On one hand, energy loss via mucoid organic matter release may further reduce the ability of corals to cope with bleaching, whereas on the other hand mucoid exudates release may function for heterotrophic feeding (reviewed by Brown and Bythell 2005), which could partly compensate the missing autotrophic contribution to the coral's energy demand during bleaching. Further, increased mucoid exudates release during bleaching may also help to protect the coral against high UV radiation often associated with coral bleaching (e. g. Jokiel 1980, Fisk and Done 1985, Gleason and Wellington 1993) as UV-absorbing substances such as mycosporine-like amino acids (MAAs) have been detected in coral mucus (reviewed by Dunlap and Shick 1998).

Coral mucus may play an important role in providing various defence capabilities against pathogenic organisms (reviewed by Brown and Bythell 2005). During bleaching, corals are in a state of stress owing to energy shortage and damaged epithelia, and thus are more vulnerable to pathogens which may occur with increased abundances at elevated temperatures. Increased mucus release may be a response to decrease vulnerability and support defence against pathogens.

Recent research revealed that azoxanthellate cold water corals release POM in comparable quantities to zooxanthellate warm water corals (Wild et al. in press). This indicates that the release of mucoid exudates by corals is largely decoupled from the presence of zooxanthellae and thus represents a general response to any kind of environmental stress, including bleaching.

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