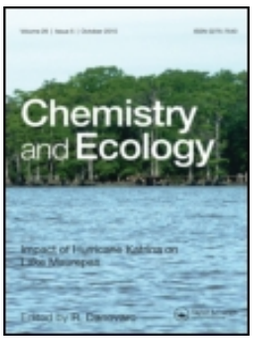

Chemistry and Ecology

ISSN: 0275-7540 (Print) 1029-0370 (Online) Journal homepage: https://www.tandfonline.com/loi/gche20

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To cite this article: Mohammed Rasheed , Christian Wild , Carin Jantzen & Mohammed Badran (2006) Mineralization of particulate organic matter derived from coral-reef organisms in reef sediments of the Gulf of Aqaba, Chemistry and Ecology, 22:1, 13-20, DOI: 10.1080/02757540500456823

To link to this article: https://doi.org/10.1080/02757540500456823

Chemistry and Ecology
Vol. 22, No. 1, February 2006, 13–20

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Mineralization of particulate organic matter derived from coral-reef organisms in reef sediments of the Gulf of Aqaba

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(Received 11 July 2005; in final form 4 November 2005)

In situ and laboratory incubation experiments in a fringing reef in the Gulf of Aqaba were performed to study degradation rates of particulate organic matter in reef sediments. Coral mucus, clam eggs, and zooxanthellae were used as model particulate organic compounds for these experiments. Aerobic and anaerobic mineralization rates were calculated by dissolved inorganic carbon (DIC) and O_2 fluxes from the sediments under different particulate organic matter additions. Fast enhancement (approximately twofold) of O_2 and DIC fluxes were found with the addition of coral mucus and clam eggs compared with control incubations without addition. Most of the degradation is believed to have occurred anaerobically rather than aerobically (DIC:O_2 ratios were 4.3–28.1). Higher degradation rates of coral mucus and clam eggs were estimated in carbonate sediment than in silicate sediment (1.2–1.6-fold), which was attributed to the different physical and chemical properties of both sediments. Our study shows the significance of the reef sediment as a suitable site for microbial degradation of particulate organic material excreted from different reef community organisms. This may increase the regeneration of nutrients in the reef environment necessary to sustain high biological productivity.

Keywords: Coral reef; Nutrient; Sediment; Particulate organic matter; Mineralization

1. Introduction

Particulate organic matter released from different benthic organisms in the reef environment represents a key source of energy in the nutrient-poor reef environments [1–5]. Degradation of these matters in the reef environment leads to release of inorganic nutrients like ammonium and phosphate, which support autotrophic growth in the reef [3, 6–7]. Particulate organic

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Chemistry and Ecology
ISSN 0275-7540 print/ISSN 1029-0370 online © 2006 Taylor & Francis
http://www.tandf.co.uk/journals
DOI: 10.1080/02757540500456823

matter may be mineralized in reef sediment [6, 7], in the reef community [8–10], or in reef biota such as reef-dwelling organisms [10–14].

Carbonate sands, the dominating fraction in reef environment, are usually porous and permeable, exhibiting a large surface area. They thus have many suitable sites for bacterial growth [6–7, 15]. In this type of sediment, as a result of interaction between bottom current and permeable carbonate sands, particulate organic matters may be filtered and mineralized through the benthic microbial food chain [1, 10, 16]. Sandy sediments in reef environments cover roughly half of the surface area [10]; therefore, degradation of particulate organic matter in the reef sediment may be considered as the most important process in sustaining primary productivity in these environments.

In this study, we investigated the degradation of coral mucus, clam eggs, and zooxanthellae in carbonate and silicate sediments located in a coral reef environment. Degradation rates have been previously assessed from fluxes of dissolved inorganic carbon (DIC) and oxygen, which can be calculated by laboratory or *in situ* chamber incubation of sediment with measurements of the temporal variation of DIC and O_2 in the water enclosed in the chamber [15, 17–19]. *In situ* incubations do produce more realistic results than the laboratory incubations which suffer from artefacts caused by the removal of the sediment core from its particulate environment and the transport to the laboratory, which may seriously disturb the sediment core. However, in the laboratory, the conditions of the experiment can be controlled exactly. For this reason, we conducted both laboratory and *in situ* experiments with stirred benthic chambers.

2. Materials and methods

2.1 *Study site*

The study was carried out in a fringing reef of the northern Gulf of Aqaba at about 3 m water depth. The *in situ* chamber experiments took place in a marine reserve close to the Marine Science Station (MSS) in Aqaba (latitude: 29° 27′, longitude: 34° 58′). The incubations were conducted at two sediment sites in front of the MSS, the first site covered by carbonate sands (water depth ∼2.5 m), and the second site covered by silicate sands (water depth ∼2 m). The distance between the two sites was approximately 200 m, and both sites were located within a radius of 5 m adjacent to coral reef. The mean grain size of both sediments was 229 and 559 μm, the organic carbon content was 0.24 and 0.36%, and the permeability was $27 \pm 11 \times 10^{-12}$ m^2 and $116 \pm 3 \times 10^{-12}$ m^2 for the silicate and carbonate sands, respectively [6, 20].

2.2 *In situ and laboratory incubations*

Seven *in situ* experiments and one laboratory incubation experiment were performed in order to estimate the degradation rate of different particulate matter in two different types of reef sediments. Fluxes of DIC and O_2 from the sediments were calculated under different organic matter additions and different light conditions (table 1), and used to calculate the mineralization rate of these organic substances. The particulate organic materials were collected as described by Wild *et al.* [20]. A description of the *in situ* incubation chambers can be found in Huettel and Gust [21]. These were transparent cylindrical acrylic containers 19 cm diameter and 30 cm height. Flat plastic lids covered the chambers and were fixed by four stainless steel clips. The lid contained a sampling port with a syringe holder for water samples and another port to replace the sampled water. The water inside the chambers was stirred at 20 rpm by a

Table 1. Summary of *in situ* and laboratory experiments performed for this study.

Experiment	Sediment used	Light condition	Process	No. of incubated cores and types of organic matter added
In situ A	Carbonate	Dark	Control	4 control
In situ B	Carbonate	Dark	Control and spiked	2 control 2 with 40 ml of coral mucus
In situ C	Carbonate	Dark	Control and spiked	1 control 1 with 300 ml of coral mucus 1 with 300 ml of zooxanthellae 1 with 200 ml of clam egg
In situ D	Carbonate	Dark	Control and spiked	1 control 1 with 300 ml of coral mucus 1 with 300 ml of zooxanthellae 1 with 200 ml of clam egg
In situ E	Carbonate	Dark	Control and spiked	1 control 2 with 300 ml of coral mucus 1 with 200 ml of clam egg
In situ F	Silicate	Dark and light	Control	4 control
In situ G	Carbonate	Dark and light	Control and spiked	3 control 1 with 300 ml of coral mucus
Laboratory A	Carbonate	Dark	Control and spiked	3 control 3 with 100 ml of coral mucus
Laboratory B	Silicate	Dark	Control and spiked	3 control 3 with 100 ml of coral mucus

15 cm-diameter flat rotating disk, connected to a DC motor with a gear box. The chambers were inserted gently into the sediments to a depth of about 10 cm and thus included a water column of approximately 20 cm height, corresponding to a water volume of 5.7 l. The lids were then fitted to the chambers and fixed by the clips. Chambers used for dark incubations were covered with tough opaque black plastic foils secured with rubber bands at the top and the bottom. At defined time intervals (figures 1 and 2), 100 ml of water was removed for DIC, and O_2 determination and replaced by ambient sea water. The total duration of the incubations was around 400 min. The sea water volume in the chambers was determined after removing the lid by measurement of the sea water height at four different points in the chamber. For the laboratory incubation, the same chambers were employed under identical conditions as described by Rasheed *et al.* [6, 15]. These were cylindrical acrylic chambers with an inner diameter of 9.5 cm and a height of 40 cm. The lengths of sediment cores were about 20 cm, and the depth of the water column above the sediments was approximately 20 cm. The sediments used for the laboratory experiments were collected from the two sites by diving to the appropriate location, and upon return to the laboratory the sediments were washed with distilled water and dried in an oven at 60 °C. Fluxes of solutes in both the laboratory and *in situ* incubations were evaluated from linear regressions of solute concentrations over time.

2.3 *Analytical procedure*

Oxygen concentrations in the sea water were analysed using the Winkler titration method [22]. Dissolved inorganic carbon (DIC) concentrations in the water samples were measured using a flow-injection system [23]. Calibration standards were always freshly prepared from $NaHCO_3$.

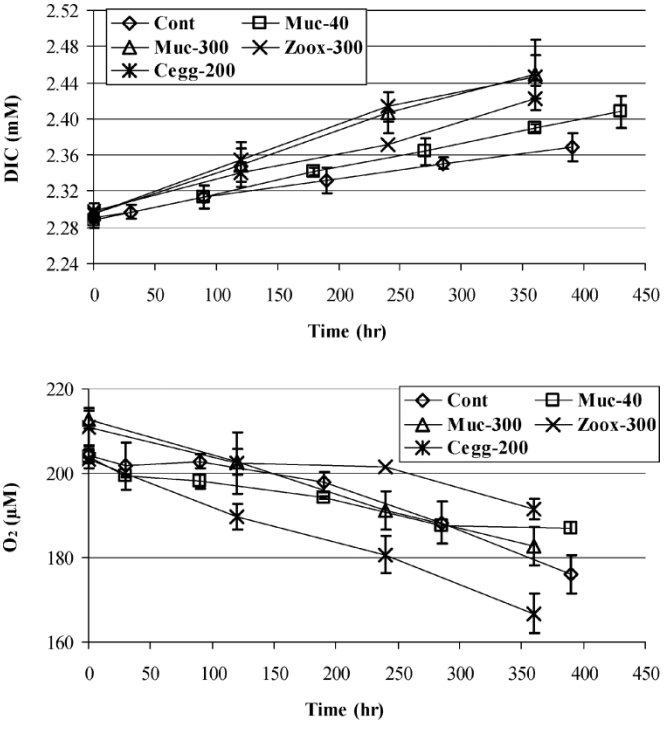

Figure 1. Time course of oxygen (µM) and DIC (mM) during different *in situ* incubations (table 1) for the control chambers and spiked chambers. C: control, Muc-300: with 300 ml of mucus added; Muc-40: with 40 ml of mucus added; Cegg: with 200 ml of clam eggs, Zoox: with 300 ml of zooxanthella. The error bars represent the standard deviation of the results from the *in situ* experiments A–E.

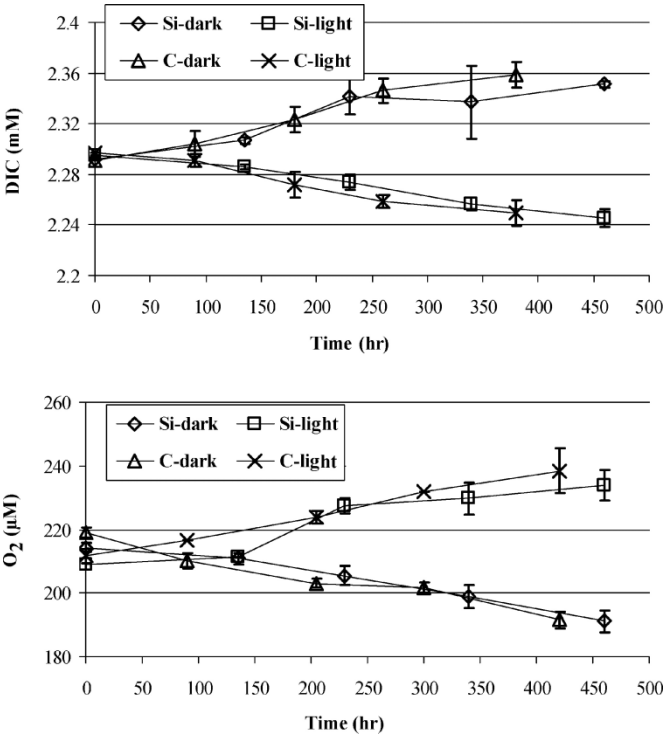

Figure 2. Time course of oxygen (µM) and DIC (mM) during different *in situ* incubations (experiments *in situ* F and *in situ* G) of control chambers in silicate and carbonate sediments. C: carbonate chambers; Si: silicate chambers.

3. Results

3.1 *Degradation of coral mucus in carbonate sediments*

Concentrations of dissolved inorganic carbon, as the end product of organic matter re-mineralization, and dissolved oxygen, as the terminal electron acceptor of the aerobic metabolism, were measured in the reef sands. In dark control chambers as well as in spiked chambers, the DIC concentration increased gradually over time (figure 1), whereas O_2 concentrations decreased gradually in all chambers. The DIC release and oxygen consumption were always higher in the chambers with coral mucus than in the control chambers. Also, the changes in the chambers with high amounts of mucus (300 ml) were greater than those in the chambers with a low amount (40 ml). However, the differences between different chambers were more pronounced in DIC than in O_2. Flux calculations showed that positive DIC fluxes were always higher than the negative O_2 fluxes (table 2).

3.2 *Degradation of zooxanthellae and clam eggs in carbonate sediments*

The DIC concentration increase and O_2 concentration decrease in the chambers with zooxanthellae addition were very low compared with the control (figure 1). This may indicate low degradation rates of zooxanthellae in carbonate sediments compared with the other organic substances. In the chambers with clam eggs, DIC concentrations increased steadily, and dissolved oxygen concentration decreased (figure 1). The flux results (table 2) were similar compared with coral mucus incubations, with DIC production being higher than oxygen consumption in most chambers.

Table 2. Fluxes of coral mucus and clam eggs (mg C ml^{-1} substrate m^{-2} d^{-1}) inferred from DIC and O_2 fluxes of different *in situ* and laboratory experiments.

	Sediment	Addition	No. of replicate	DIC flux (mmol m^{-2} d^{-1})	O_2 flux (mmol m^{-2} d^{-1})
In situ A	Carbonate	Control	4	58.3 ± 2.9	−20.4 ± 6.2
In situ B	Carbonate	Control	2	45.6 ± 7.2	−27.1 ± 4.3
	Carbonate	Mucus	2	91.3 ± 0.1	−12.5 ± 0.9
In situ C	Carbonate	Control	1	45.6	−22.5
	Carbonate	Mucus	1	172.4	−30.0
	Carbonate	Zooxanthellae	1	86.2	−13.6
	Carbonate	Clam eggs	1	121.7	−33.5
In situ D	Carbonate	Control	1	45.6	−19.8
	Carbonate	Mucus	1	157.2	−37.0
	Carbonate	Zooxanthellae	1	106.5	−20.1
	Carbonate	Clam eggs	1	142.0	−34.9
In situ E	Silicate	Control	1	30.4	−18.3
	Silicate	Mucus	2	103.9 ± 10.8	−25.5 ± 10.1
	Silicate	Clam eggs	1	116.6	−20.6
In situ F	Silicate	Dark	2	38.0 ± 3.6	−15.2 ± 1.0
	Silicate	Light	2	−35.5 ± 7.2	15.6 ± 0.7
In situ G	Carbonate	Dark	2	88.7 ± 46.6	−20.1 ± 2.6
	Carbonate	Light	2	−38.0 ± 3.6	19.5 ± 6.9
Laboratory A	Carbonate	Control	3	29.0 ± 1.5	−7.6 ± 1.6
	Carbonate	Mucus	3	48.0 ± 1.9	−13.14 ± 2.1
Laboratory B	Silicate	Control	3	23.9 ± 2.8	−6.6 ± 1.5
	Silicate	Mucus	3	42.8 ± 3.7	−11.2 ± 1.7

3.3 *Benthic metabolism in carbonate and silicate sediments under light and dark conditions*

Degradation of organic matter found naturally in carbonate and silicate sediments has been investigated to study the different rates with different sediment types. *In situ* and laboratory incubations were performed for this purpose. The *in situ* incubation (figure 2) shows that DIC was produced in the dark chambers and consumed in the light chambers, whereas the opposite was found for O_2 (figure 2). Laboratory incubations (not shown) showed the same trend as during the *in situ* incubation. Flux calculations for both *in situ* and laboratory incubations also showed similar trends, as positive values were obtained for DIC in dark chambers and negative values in light chambers (table 2). Here, also, apart from one exception (light silicate chamber), flux calculations showed that DIC fluxes were always higher than O_2 fluxes irrespective of the direction of the flux. As for the sediment type used in the *in situ* and laboratory incubations, generally higher fluxes were obtained for carbonate sediments compared with silicate sediments (figure 2 and table 2).

4. Discussion

The degradation rate of different substrates in sediment can be inferred either from DIC production or from O_2 consumption. When the degradation of organic matter exclusively occurs aerobically, the ratio between DIC production and O_2 consumption should be 1 [24]. Herein (table 3, figure 3), the mineralization rates of coral mucus and clam eggs illustrate that the ratios between the rates inferred from DIC production and from O_2 consumption are always more than 1 (3.43–28.11). This indicates that the mineralization of the substrates used occurs partially anaerobically in addition to aerobic degradation. When the oxygen concentration is very low, DIC can be produced anaerobically using different electron acceptors such as SO_4^{2-} and NO_3^- [25–26]. This was confirmed by several authors; Canfield *et al.* [27] estimated a minor contribution of oxygen in organic-matter degradation (4–17%), and Rasheed *et al.* [15] found DIC:O_2 flux rates of 5–33. Also, Wild *et al.* studied the degradation rate of mucus in permeable sediments and found DIC production to be twice as high as O_2 consumption. However, DIC production might also be enhanced by the precipitation and dissolution of carbonate sediments used in the incubation experiments of this type of study [28–30].

Table 3. Mineralization rates of coral mucus and clam eggs (mg C ml^{-1} substrate m^{-2} d^{-1}) inferred from DIC and O_2 fluxes of different *in situ* and laboratory experiments.

Experiment	Addition	DIC	O_2	Ratio
In situ B	Mucus	13.71	−4.38	
In situ C	Mucus	5.07	0.4	12.78
	Clam eggs	4.56	0.88	5.21
In situ D	Mucus	4.46	0.92	4.85
	Clam eggs	5.78	1.21	4.78
In situ E	Mucus	2.94	0.38	7.66
	Clam eggs	5.17	0.18	28.11
Laboratory A	Mucus	2.28	1.11	3.43
Laboratory B	Mucus	2.27	0.92	4.11

Note: The calculations were performed by subtracting the control flux (table 2) from the average flux values of each substrate and then multiplying by the atomic weight of carbon or oxygen and dividing by the volume of each substrate in ml. The negative value indicates a higher chamber O_2 control consumption than the chamber with substrate.

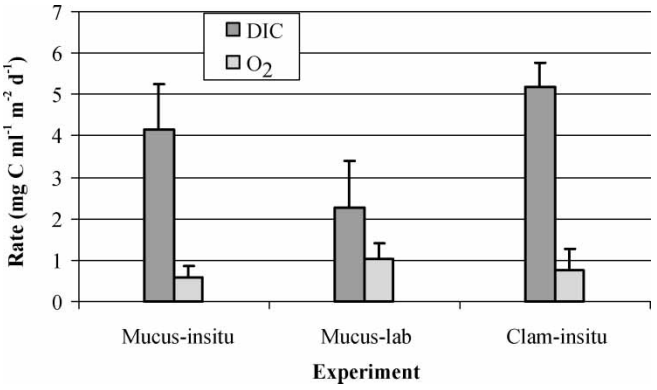

Figure 3. Mineralization rates of coral mucus and clam eggs (mg C ml^{-1} substrate m^{-2} d^{-1}) inferred from DIC and O_2 fluxes of different *in situ* and laboratory experiments. Error bars represent the standard deviation of the *in situ* experiments C, D, E and the laboratory experiments A and B.

Minor differences existed between the mineralization rate of coral mucus estimated in the laboratory experiments and the *in situ* experiments (table 3, figure 3). These can be attributed to differences in the experimental conditions [6]. However, mineralization rates of coral mucus and eggs estimated from *in situ* or laboratory experiments in carbonate sediments were always higher than those in silicate sediments (∼1.2–1.6-fold). This was also reported by Rasheed *et al.* [6], who found a 1.5–3.8-fold higher degradation rate for *Spirulina* in carbonate sediments than in silicate sediments. The authors attributed this to the different mineralogical structure, larger carbonate surface area, higher permeability, and porosity of carbonate sand. In addition, higher numbers of fauna and flora live in the carbonate sands compared with the silicate sediments [7]. Besides high bacteria found in carbonate sand; cell number: 10^9-10^{10} cm^{-3} as compared with silicate sediments [5] may also facilitate degradation processes aerobically and anaerobically.

This investigation clearly shows the importance of sediment as a major incubator of organic-matter degradation. These particulate organic materials are produced by different organisms living in the coral-reef community. A significant fraction of these organic products is reworked by the coral reef itself [3]. The fraction that reaches the sediment does not stay there inert [4–5, 31] but becomes partially mineralized to inorganic nutrients such as ammonium and phosphate, which support a high level of biological productivity in the nutrient-deficient coral-reef environment.

Acknowledgements

Thanks are due to Marine Science Station staff in Aqaba-Jordan for their help in the laboratory and in the field. This work has been funded by the Deanship of Academic Research in Yarmouk University, Higher Council of Science and Technology, Jordan and Max Planck Society, Germany.

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