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Benthic metabolism and degradation of natural particulate organic matter in carbonate and silicate reef sands of the northern Red Sea

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ABSTRACT: The influence of natural particulate organic matter (POM) input on sedimentary oxygen consumption (SOC) in permeable carbonate and silicate sediments close to a coral reef was investigated in front of the Marine Science Station in Aqaba, Jordan (northern Red Sea). We conducted 7 *in situ* experiments in stirred benthic chambers. Without additional POM input, SOC rates were similar and not significantly different ($p > 0.5$) in carbonate and silicate sands, with average rates of 20 ± 4 (n = 10) and 16 ± 2 (n = 3) mmol O_2 m^{-2} d^{-1}, respectively. Gross photosynthesis in the carbonate and silicate sands accounted for 15 to 23 mmol produced O_2 m^{-2} d^{-1}, characterising both sands as largely independent of allochthonous carbon input. SOC of unamended carbonate sands showed no significant variation in 5 *in situ* experiments conducted within a period of 19 d. Addition of 2 energy-rich sources of naturally occurring POM (coral mucus and clam eggs) resulted in significantly ($p < 0.0001$) increased SOC rates in the carbonate sands, but not in the silicate sands. Addition of a suspension containing high concentrations of zooxanthellae did not result in higher SOC in the carbonate sands, indicating that zooxanthellae cannot easily be degraded in reef sediments. Our results highlight the short cut between coral mucus production and degradation in the adjacent reef sands. Suspended particles are initially trapped by the cohesive mucus on the coral surface, and ensuing mucus strings sink to the seafloor at a short distance from the mucus-producing coral. Carbonate sands as porous filter systems obviously harbour more active heterotrophic microbial communities than silicate sands, and thus may constitute a major site of organic matter degradation in the reef ecosystem.

KEY WORDS: Coral reef · Permeable sediments · Red Sea · Sedimentary metabolism · Organic matter decomposition · Carbonate sands · Coral mucus

INTRODUCTION

Coral reefs sustain their high gross primary production (GPP) by various effective processes for recycling of organic matter, thus retaining essential nutrients within the reef ecosystem (Muscatine & Porter 1977, Crossland & Barnes 1983, Richter et al. 2001, Wild et al. 2004a). The sandy sediments of reef environments have been described as important sites of organic matter degradation (Rasheed et al. 2003b, 2004, Wild et al. 2004b,c). These shallow water sands efficiently couple water column and seafloor processes, since tides, currents and waves filter large volumes of water and dissolved substances through the permeable sediments (Rasheed et al. 2003b, 2004, Wild et al. 2004a,b). Likewise, small suspended particles originating from the

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pelagial are easily transported into the porous sands, which thereby function as a highly effective filter for organic matter. High densities of specialised heterotrophic bacteria attached to the sand grains can rapidly degrade the filtered organic matter (Rusch et al. 2003).

Carbonate sands of biogenic origin are the dominant sediments in reef environments, but terrigenous silicate sands also occur at many sites, especially within fringing reefs located close to the mouth of a river. In the northern Red Sea, rare occurrences of large rain events lead to the deposition of land-derived silicate sands landward of many fringing reef sites. Thus, both kinds of sediments often occur directly next to each other and are exposed to identical environmental conditions.

Carbonates and silicates strongly differ in physicochemical characteristics, e.g. surface structure, dissolution kinetics, transparency to light and heat, and buffering capacity (Schroeder & Purser 1986). These factors may select for different types of microorganisms and may favour different types of metabolic processes. A main factor may be the higher surface area of carbonate grains which, through their porous structure, provides a larger surface area for biofilm formation than silicate grains (Rasheed et al. 2003a). The main objective of this study was to study metabolism and degradation of organic matter in both kinds of sediments.

Natural sources of particulate organic matter in coral reef environments are phyto- and zooplankton, detritus and organic aggregates forming from exudates and colloidal materials. This study investigated the sedimentary decomposition of these 3 sources of particulate organic matter by using zooxanthellae as typical phytoplankton particulate organic matter (POM), eggs of the giant clam *Tridacna squamosa* as zooplankton POM, and coral mucus as organic aggregates. The latter were included because former work and our recent work in the Australian Great Barrier Reef showed that coral mucus is an important carrier of energy and nutrients in the reef ecosystem (Benson & Muscatine 1974, Wild et al. 2004a,b, 2005). In this study, we conducted surveys to assess the potential contribution of coral mucus to the cycling of organic matter in Red Sea fringing reef systems. An indicator for the contribution of coral mucus to the POM pool in the reef system is the formation of visible mucus strings on corals, a process that precedes the release of mucus to the water column. The surveys used the attached mucus strings as indicator and permited a comparison with previously published studies on the Great Barrier Reef.

MATERIALS AND METHODS

Study sites. This study was conducted in the fringing reef near Aqaba, Jordan and Dahab, Egypt, in the northern Gulf of Aqaba. All chamber experiments took place in a marine reserve close to the Marine Science Station (MSS) in Aqaba (latitude 29° 27′, longitude 34° 58′).

The chamber incubations were conducted at 2 neighboring backreef sites in front of the MSS, the first site covered by carbonate sands (water depth 2.4 m), and the second by silicate (quartz) sands (water depth 1.8 m) with a $CaCO_3$ content of less than 6% dry mass. Mean grain size of the carbonate and silicate sands were 559 and 229 µm with organic carbon contents of 0.36 and 0.24%, respectively (Rasheed et al. 2003a). Permeability of the sediments, measured with a constant head permeameter (Klute & Dirksen 1986), was $116 \pm 11 \times 10^{-12}$ m^2 for the carbonate sands and $27 \pm 3 \times 10^{-12}$ m^2 for the silicate sands (mean ± SD, n = 3). Porosity, calculated in triplicate from weight loss of wet sediment after drying at 60°C for 24 h, was 44 ± 3 and 35 ± 2 vol/vol for carbonate and silicate sands, respectively. The main identified biogenic components in the carbonate sands were coral skeleton fragments and mollusk shells accounting for more than 50% of the sediment dry mass. The lateral distance between both sites was approximately 200 m, and both sites were located within a radius of 5 m from the adjacent coral reef.

Role of coral mucus in the northern Red Sea. To assess the significance of coral mucus as a source for POM in the study area, 6 surveys at 3 different locations in the northern Red Sea (2 sites near Dahab, Egypt, 1 site near Aqaba, Jordan, with 2 surveys at each location) were conducted to determine the occurrence of mucus strings on the corals. These studies were carried out at comparable water depths (1 to 4 m) and weather conditions (sunny sky, ca. 3 Beaufort wind velocity, no waves). For each survey, between 22 and 115 hard coral colonies were randomly chosen and carefully inspected for strings of coral mucus attached to their surface. In total, 325 colonies were inspected by SCUBA divers. During the 2 surveys in Aqaba, these inspections were carried out for each of 11 dominant hard coral genera as well as for the hydrozoan fire corals *Millepora* spp. In Dahab, parallel to the described surveys, we also quantified the sedimentation behaviour of a number of the observed mucus strings (n = 18) by carefully detaching them from the coral with a weak water flow produced by a plastic pipette. The sinking velocity of the strings was estimated by measuring the height of the strings above the seafloor and the duration required by the detached strings to reach the seafloor. The distance between the coral colony producing the mucus strings and the location of final deposition of the mucus strings on the seafloor was determined with a tape measure.

Collection of natural organic substrates. ***Coral mucus:*** We collected 16 polyps of the hard coral genus *Fungia* spp. (diameter 4 to 29 cm) from water depths of 2 to 4 m from the reef crest in front of the Marine Science Station. Corals were kept in a flow-through aquarium at *in situ* temperature (24°C) and salinity (41) for the study period (May to June 2004). Mucus was collected from the corals by exposing them to air. The polyps immediately started producing and releasing large amounts of mucus. Corals were then turned upside down and the dripping mucus was collected in a clean container. The mucus produced during the first 30 s was discarded, that produced during the following 2 min was collected for subsequent use. The mucus of 5 to 10 polyps was collected during each sampling. Subsequently, the coral mucus was homogenised with a glass tissue grinder and kept at 4°C until further use.

Zooxanthellae: A suspension of freshly released zooxanthellae was collected after exposing 6 *Fungia* spp. polyps to air for 3 h. Upon being covered with water again, the corals immediately started to release large numbers of zooxanthellae. The overlying water containing the zooxanthellae was collected: this suspension was incubated at 4°C, which killed the zooxanthellae.

Tridacna squamosa eggs: During the study period May to June 2004, giant clams of the genus *Tridacna* spp. growing on the attached fringing reef periodically released their gametes into the water. Spawning by these clams usually entails an initial release of sperms, followed by a release of eggs after an interval of minutes to hours to prevent self-fertilisation. We took 3 individuals of *Tridacna squamosa* from the reef (water depth 10 m) and exposed them to air for 1 h. After this stress event they were put in one 1000 l container where they started to release their eggs within 2 h. Egg length was 80 to 90 µm and egg density in the suspension was approximately 16 eggs ml^{-1}. A 2 l subsample of the container water was kept at 4°C until use in the chamber experiments.

Measurement of C and N in substrate samples. Samples of particulate organic carbon (POC) and nitrogen (PON) were prepared by filtering replicate aliquots (n = 3 to 6) of 2.5 to 15.0 ml of the homogenised mucus solutions, 5.0 ml of the *Tridacna squamosa* egg solution and 50.0 ml of the zooxanthellae solution onto precombusted GF/F filters (Whatman) to obtain as much organic material on the filters as possible without clogging them. The filters were rinsed with 1 ml distilled water to remove salts and dried for 48 h at 40°C. Carbon and nitrogen concentrations on the filters were measured using a THERMO NA 2500 elemental analyser with peptone as standard. Standard deviations of replicate standard concentration measurements were <3% of the concentration analysed.

Chamber incubations. Fluxes of O_2 were investigated in 7 independent *in situ* experiments with benthic chambers (n = 4 for each experiment) identical to those described in Huettel & Gust (1992) and Wild et al. (2004b). Cylindrical chambers of transparent acrylic with a height of 30 cm and an inner diameter of 19 cm were used for the incubations. A plastic lid containing a sampling port with syringe holder for water samples and another port to replace the sampled water covered each chamber. The water was circulated by an horizontally rotating disk of 17 cm diameter. The disk, driven by a 12V DC motor, rotated about 8 cm above the sediment at a computer-controlled speed of 20 rpm.

The total duration of each of the chamber experiments was between 330 and 495 min. At the start of each experiment, chambers were inserted gently into the sediment to a depth of about 12 cm, thus including a water column of approximately 20 cm height, corresponding to a water volume of 5.7 l. Special care was taken to remove any air bubbles enclosed in the chambers. All chambers, except those used to measure gross photosynthesis, were shielded from light by wrapping them with opaque PVC foil. At the end of the experiment, the volume of water in the chambers was determined by measuring the exact chamber water height with a ruler. The sediment enclosed in each chamber was checked for large (>1 cm diameter or length) macrofauna organisms (echinoderms, polychaetes and mollusks) by sifting it manually down to a depth of 5 cm. This revealed that in none of the chambers large macrofauna organisms were present.

Addition of organic matter to chambers: An overview of the chamber experiments and the types of organic matter added to the different chambers is given in Table 1. The 3 organic substrates were injected as suspensions with a known content of

Table 1. Overview of all chamber experiments conducted an hard coral colonies in Aqaba during the field campaign in 2004. DC: dark control; LC: light control; LMA: low mucus addition (40 ml); HMA: high mucus addition (300 ml); EA: egg addition (200 ml); ZA: zooxanthellae addition (300 ml); n: no. of replicates

Date (2004)	Expt	Site	Chamber treatment	n
27 May	A	Carbonate sands	DC	4
31 May	B	Carbonate sands	DC, LMA	2,2
4 Jun	C	Carbonate sands	DC, HMA, EA, ZA	1,1,1,1
5 Jun	D	Carbonate sands	DC, HMA, EA, ZA	1,1,1,1
7 Jun	E	Silicate sands	DC, HMA, EA	1,2,1
9 Jun	F	Silicate sands	DC,LC	2,2
14 Jun	G	Carbonate sands	DC,LC	2,2

POC and PON (see foregoing subsection) through the sampling port at the beginning of each chamber experiment. Natural POM concentrations in reef water samples were 130 ± 9 µg POC l^{-1} and 17 ± 1 µg PON l^{-1} (mean ± SD, n = 6). Coral mucus was added to the chambers in quantities of 60 (Expt B) to 400 (Expts C, D and E) µg POC l^{-1} and 8 to 58 µg PON l^{-1}. Clam eggs were added to the chambers in average quantities of 1500 µg POC l^{-1} and 150 µg PON l^{-1}. Zooxanthellae were added to the chambers in quantities of 95 µg POC l^{-1} and 11 µg PON l^{-1}. The turnover of C in each experiment was calculated by using the POC measurements and the increase in SOC in each chamber with substrate addition relative to the controls, assuming that 1 mol added C is oxidised by 1 mol O_2.

Sample collection and subsequent analyses: Water samples (60 to 100 ml) were taken at pre-set time intervals (30 to 120 min) from the chamber water for later analyses of O_2 concentrations. Fixed samples were measured within 1 h by the Winkler titration method (Winkler 1888). Fluxes of O_2 were evaluated by linear regression of solute concentration over time (at least 4 data points).

RESULTS

Role of coral mucus in the northern Red Sea

A total of 325 hard coral colonies were inspected during 6 surveys in the northern Red Sea. Strings of coral mucus could be detected on roughly half of them (Table 2). In each survey, between 42 and 65% of all corals had mucus strings attached to their surfaces, often located laterally or underneath the coral surface (Fig. 1). The hydrozoan fire corals genus *Millepora* spp. had the highest incidence of mucus strings (72% of all inspected corals), and in most cases more than 1 string could be detected on their surfaces. More than half of all inspected hard corals of the genera *Stylophora* and *Fungia* had mucus strings attached to their

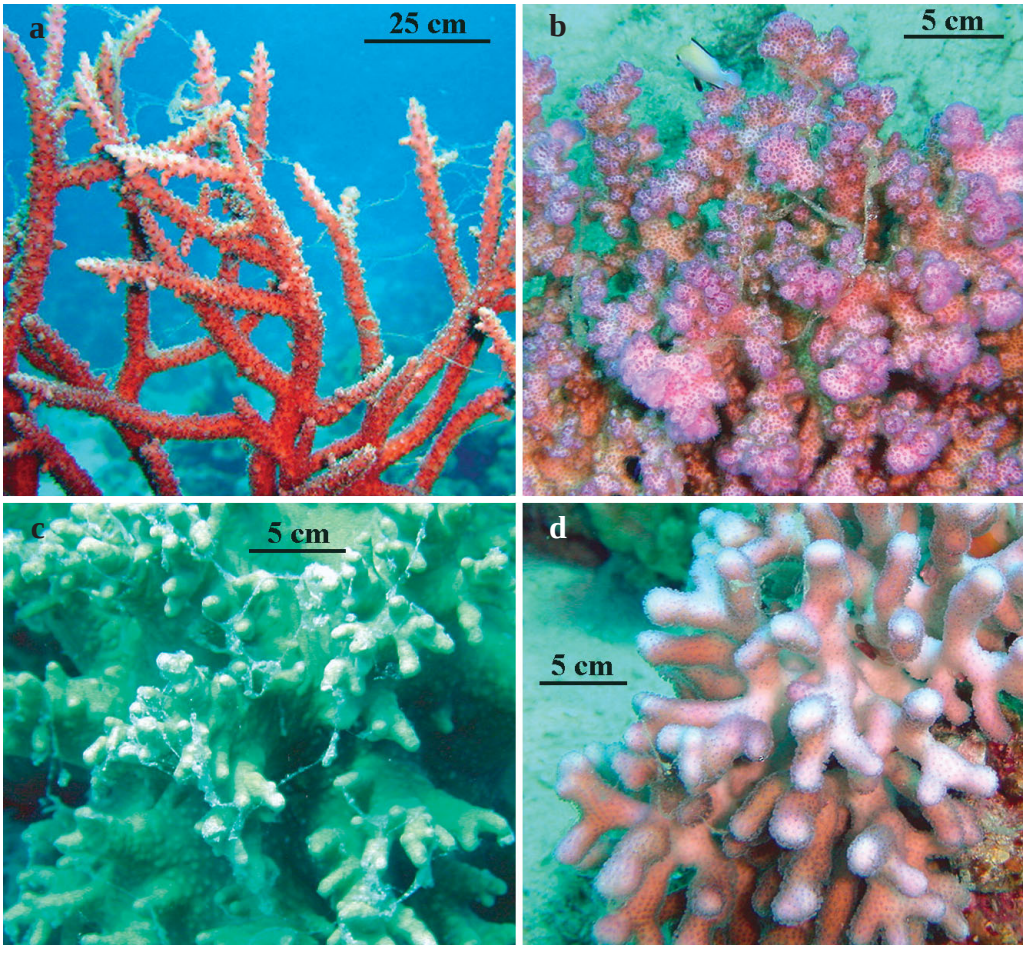

Fig. 1. Strings of mucus observed on different corals in the northern Red Sea. (a) *Acropora* spp., (b) *Pocillopora* spp., (c) soft coral *Lobophyton* spp., (d) *Stylophora* spp.

Table 2. Coral mucus strings observed on various hard coral colonies during 6 surveys in the northern Red Sea. MSS: Marine Science Station

Date (2004)	Location	No. of coral colonies Inspected	With mucus strings	(%)
12 May	Dahab, Three Pools	22	12	55
12 May	Dahab, Three Pools	27	12	44
18 May	Dahab, Lagoon	23	15	65
18 May	Dahab, Lagoon	49	21	43
1 Jun	Aqaba, MSS reef	89	37	42
1 Jun	Aqaba, MSS reef	115	57	50
Total		325	154	47

surfaces. No strings could be detected on the massive corals *Galaxea* spp. and *Favia* spp. (data not shown).

Microscopic observation of a number of freshly collected mucus strings showed an intense contamination with phyto- and zooplankton organisms as well as unidentifiable detritus and small carbonate grains (Fig. 2). Consequently, all 18 tested mucus strings showed negative buoyancy and started to sink if detached from the coral. Resulting sedimentation velocities were between 0.3 and 2.5 cm s^{-1}. The place of sedimentation on the seafloor was located within a distance of 0 to 125 cm relative to the place at which the string had been attached to the producing colony.

Chamber experiments

Sedimentary O_2 consumption and gross photosynthesis

The O_2 concentration decreased in all 4 chambers during Chamber Expt A. The resulting sedimentary O_2 consumption rates ranged from 13 to 25 mmol m^{-2} d^{-1} (20 ± 5 mmol O_2 m^{-2} d^{-1}, mean ± SD). The addition of small coral mucus volumes (40 ml, equivalent to an input of 30.1 µmol C and 3.5 µmol N) during Chamber Expt B did not produce a detectable increase in O_2 consumption compared to the control chambers. Sedimentary O_2 consumption was 22 ± 6 mmol m^{-2} d^{-1} (n = 4), and thus not significantly different (2-tailed *t*-test, $p > 0.05$) from the 4 untreated dark chambers of Expt A used as control.

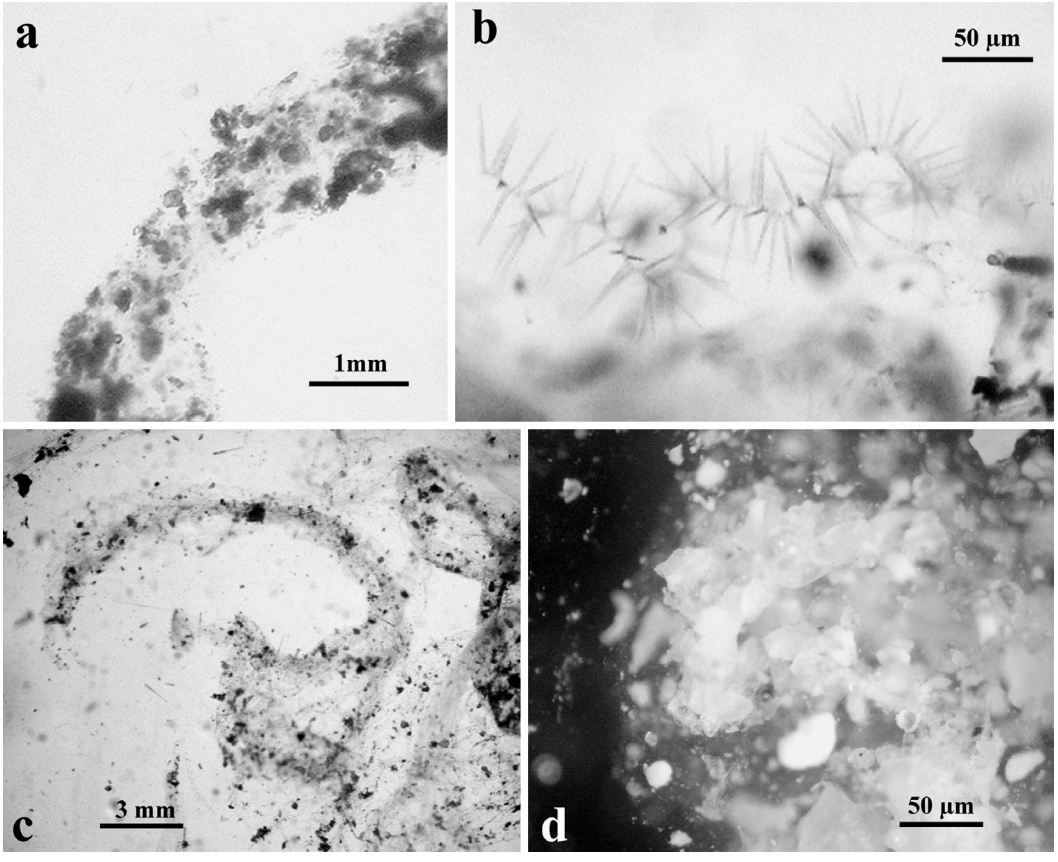

Fig. 2. *Acropora* spp. Microscopic observation of mucus strings freshly collected from several colonies. (a) Heavy contamination of the initially transparent mucus. Among several other unidentifiable contaminants, (b) diatom chains, (c) diatom frustules, and (d) carbonate grains were observed on the mucus strings

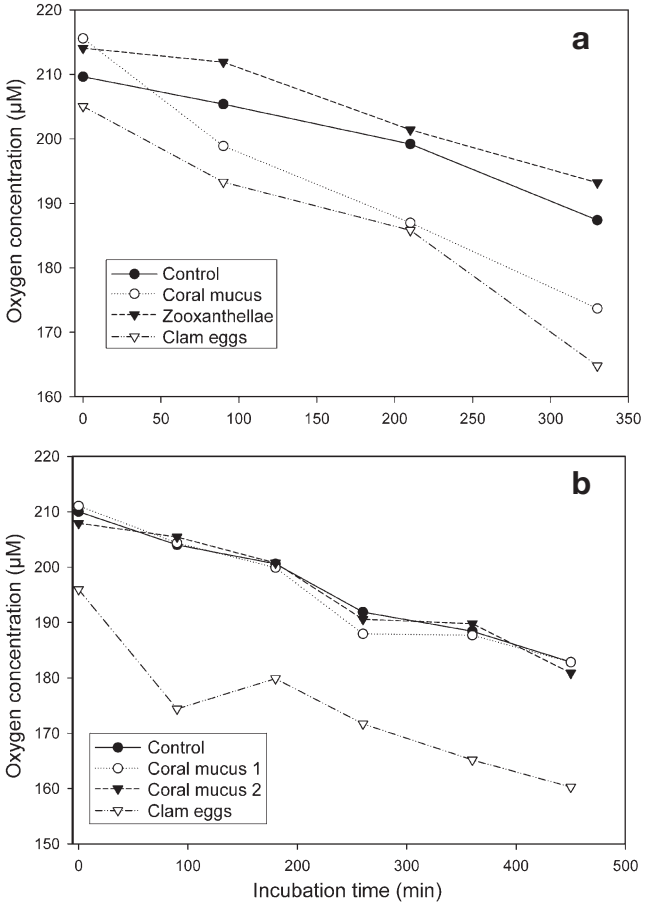

Fig. 3. (a) *In situ* Chamber Expt C, and (b) *in situ* Chamber Expt E showing O_2 concentration in 4 light protected benthic chambers that were simultaneously deployed on (a) carbonate sands and (b) silicate sand, to measure sedimentary degradation of different sources of added particulate organic matter

Fig. 3a shows that decreases in O_2 concentration in the control chamber and in the chamber with zooxanthellae addition in Expt C on carbonate sands were very similar, with SOC rates of 18.9 and 19.2 mmol m^{-2} d^{-1}, respectively. However, O_2 consumption was significantly higher (2-tailed *t*-test, $p < 0.0001$) in the chamber with the addition of large coral mucus volumes (300 ml; 230 µmol C and 28 µmol N) and clam eggs (200 ml; 900 µmol C and 72 µmol N) (Fig. 3a), with corresponding SOC rates of 37 and 33 mmol m^{-2} d^{-1}, respectively (Table 3). The results of the replicate experiment D with an identical experimental design and substrate addition confirm the findings of Expt C (data not shown in figure). Hence, O_2 consumption in the chambers with mucus and egg addition were 33 and 34 mmol m^{-2} d^{-1}, respectively, compared to 22 and 13 mmol m^{-2} d^{-1} in the control chamber and the chamber with addition of zooxanthellae, respectively.

In contrast, the addition of coral mucus and coral eggs to chambers deployed on silicate sands in Expt E resulted in only minor differences in O_2 concentration decrease compared to the control chamber (Fig. 3b). Absolute O_2 concentration was lower in the chamber with added clam eggs, but the concentration decrease was very similar to that in the other 3 chambers. The resulting SOC rates were very similar and ranged between 17 and 20 mmol O_2 m^{-2} d^{-1} (Table 3).

Expts G (carbonate sands) and F (silicate sands) were carried out to compare gross photosynthesis rates in the light to oxygen consumption in the dark (Fig. 4). The resulting mean rates of gross photosynthesis were 19 ± 6 mmol O_2 m^{-2} d^{-1} for the carbonate sands and 15 ± 0.2 mmol O_2 m^{-2} d^{-1} for the silicate sands. Mean sedimentary oxygen consumption was 20 ± 3 and 15 ± 1 mmol O_2 m^{-2} d^{-1} for the carbonate and silicate sands, respectively (ranges of all gross photosynthesis SOC and GP rates are shown in Table 3). Photosynthetic O_2 production equalled SOC in both sediments over the experimental period. SOC in carbonate sands showed no significant variation during the study period of 4 wk in May and June.

Carbon turnover

Table 4 presents an overview of the calculated carbon turnover in all chambers with substrate addition, except for the 2 mucus chambers with low mucus addition from Expt B, which did not show any increased SOC rate compared to the control chambers. The highest C turnover was observed in the 2 mucus chambers deployed on carbonate sands during Expts C and D. Between 5 and 9% of the added C as coral mucus was respired h^{-1}, highlighting the high degradability of this substrate for heterotrophic bacteria in carbonate sands. In contrast, the same substrate quantity and quality was degraded in the silicate sands at very low rates of <0.3% C turnover h^{-1}. Clam eggs were degraded in the carbonate sands at C turnover rates that were more than 2 times lower than those of coral mucus, whereas they were degraded in the silicate

Table 3. Values of sedimentary oxygen consumption (SOC) and gross photosynthesis rates (mmol O_2 consumed or released m^{-2} d^{-1}) measured in all chamber experiments. nd: no data

Parameter	Carbonate sands	Silicate sands
SOC control	13–25 (n = 10)	14–20 (n = 3)
Gross photosynthesis	15,23 (n = 2)	15,16 (n = 2)
SOC with addition of coral mucus	33,37 (n = 2)	17,18 (n = 2)
SOC with addition of clam eggs	33,34 (n = 2)	20 (n = 1)
SOC with addition of zooxanthellae	13,19 (n = 2)	nd

sands at very low C turnover rates of 0.3 % h^{-1} (Table 4). Zooxanthellae, added to the chambers with carbonate sands, were barely degraded. Only 1 of 2 experimental chambers showed a low C turnover of 0.7 % h^{-1}.

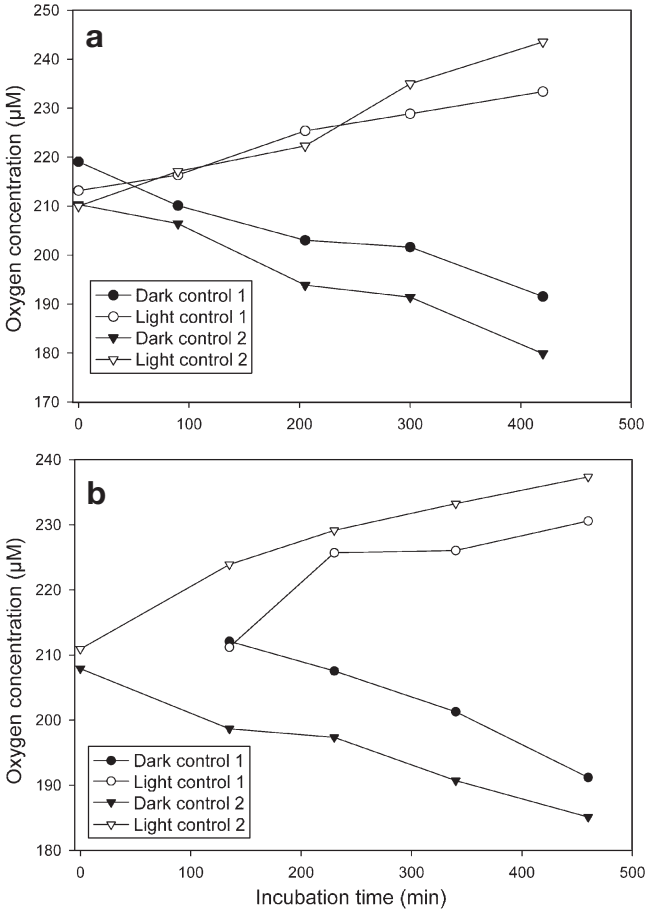

Fig. 4. (a) *In situ* Chamber Expt G and (b) *in situ* Expt F, showing O_2 concentration in 4 benthic chambers (2 light-protected, 2 transparent) simultaneously deployed on (a) carbonate sands and (b) silicate sands to compare gross photosynthesis and sedimentary O_2 consumption

DISCUSSION

Coral mucus release in the northern Red Sea

The surveys revealed that corals mucus strings occur on many different genera of hard and hydrozoan fire corals of the study area in the northern Red Sea. We also observed these strings on several soft corals. Because of a lack of strong tidal currents, mucus stays longer on the coral surface in this area than (for instance) in the Heron Island reef system of the Great Barrier Reef that we investigated in previous studies (Wild et al. 2004a,b). Thus, trapping of numerous particles by the adhesive mucus matrix already occurred while it was still attached to the coral. This mechanism is different from the trapping of particles by drifting coral mucus aggregates in a reef system with enclosed lagoon and strong tidal currents as described by Wild et al. (2004a). However, our results confirm the suggestion of Pascal & Vacelet (1981) that coral mucus from the reefs of Aqaba seems to be a major trap for suspended detritus and phytoplankton.

The composition of particulate material attached to the mucus strings (larger phyto- and zooplankton detritus, many carbonate grains) was very similar to that of POM trapped by the mucus floats described by Wild et al. (2004a). These mucus floats are the last stage in the ageing process of coral mucus aggregates during their drift through the lagoon water column, and display a sedimentation behaviour with sinking rates of 4 to 8 cm s^{-1}, which is a somewhat higher rate than those measured in the present study (0.3 to 2.5 cm s^{-1}).

In the prevailing slow water currents of the Red Sea reefs, detached mucus aggregates sink to the reef sands very close (< 2 m) to the producing colony. Our chamber experiments revealed that coral mucus can be degraded rapidly in the adjacent carbonate reef sands. This may lead to a release of nutrients with direct benefit to the corals. The cycling of elements via coral mucus in the Red Sea consequently may even be

Table 4. Turnover of C added as natural organic substrates during the different chamber experiments. Vol. substr. add.: volume of substrate added; C substr. cont.: C substrate content; O_2 cons. – Contr.: consumption minus that in relative control chamber

Sediment	Substrate	Vol. substr. add. (ml)	C substr. cont. (mg l^{-1})	C added (µmol)	O_2 cons. – Contr. (µmol $chamber^{-1}$ h^{-1})	C turnover (% h^{-1})
Carbonate	Clam eggs	200	54	897	12.9	1.4
Carbonate	Clam eggs	200	54	897	17.1	1.9
Carbonate	Coral mucus	300	9	231	11.1	4.8
Carbonate	Coral mucus	300	9	231	20.4	8.8
Carbonate	Zooxanthellae	300	2	54	0.0	0.0
Carbonate	Zooxanthellae	300	2	54	0.4	0.7
Silicate	Clam eggs	200	54	897	2.5	0.3
Silicate	Coral mucus	300	9	231	0.6	0.3
Silicate	Coral mucus	300	9	231	0.1	0.04

shorter than that described by Wild et al. (2004a) for Heron Island, Australia. Through this mechanism, essential nutrients can be retained and recycled within the reef ecosystem. Thus, coral mucus also seems to have an important function in the recycling of nutrients in Red Sea fringing reefs with open lagoons.

Metabolism of carbonate and silicate sands

Both investigated sediments, carbonate and silicate sands, come from the same ecosystem and receive the same amount of organic matter supply. Photosynthetic O_2 production and SOC in both sediments were similar: approximately 20 mmol O_2 m^{-2} d^{-1} during our experiments. In the laboratory, Rasheed et al. (2003a) found lower rates of 5 to 6 mmol m^{-2} d^{-1} for carbonate and silicate sands from the same study site, but their results confirm the SOC similarity in both sediment types. The quantitative difference may be attributable to laboratory artifacts such as sieving of the sediment, but not to different incubation temperatures (24 to 25°C in both studies). SOC measured *in situ* with identical chamber experiments in carbonate sands of Heron Island, Australia, were approximately 50 mmol m^{-2} d^{-1} (Wild et al. 2004a,b). This higher rates may be attributable to a larger grain size (829 vs. 559 µm) and hence higher permeability and filtration rates, as well as higher water temperatures (28 vs. 24°C) at Heron Island than at Aqaba. Clavero et al. (2000) demonstrated that fluxes of solutes increase with increasing temperatures, facilitating biological activity. SOC rates at Aqaba were also similar to those measured at a variety of different field sites, e.g. 13 to 38 mmol m^{-2} d^{-1} in Hiroshima Bay (Seiki et al. 1989, 1994) and 35 mmol m^{-2} d^{-1} in a coastal lagoon in the South Atlantic Bight (Marinelli et al. 1998).

The similarity of gross photosynthesis and SOC characterises both sands as largely independent of allochthonous carbon input. Net photosynthesis was only 0.8 mmol m^{-2} d^{-1} in the silicate sands, whereas in the carbonate sands photosynthetic O_2 production did not compensate for respiration in the dark (net photosynthesis was −0.9 mmol m^{-2} d^{-1}). Green mats of filamentous algae covering ca. 30% of the silicate sediment surface during May and June 2004 suggest the possible net-autotrophic character of these sands, whereas carbonate sands in the Red Sea may be more net-heterotrophic because of their higher organic matter degradation rate at the same photosynthesis rates. The comparative pigment profiles of carbonate and silicate sands measured in March 2002 (Rasheed et al. 2003a) and September 2004 (Rasheed & Wild unpubl. data) showed no higher chlorophyll *a* concentrations in the surface layer (0 to 10 cm sediment depth) of silicate sands. At Heron Island, Australia, it was found that gross photosynthesis of carbonate reef sands was 163 mmol O_2 m^{-2} d^{-1}, much higher than the SOC rates in the same sediments of 65 mmol O_2 m^{-2} d^{-1} (Rasheed et al. 2004).

Organic matter degradation in carbonate and silicate sands

Carbonate sands showed a fast reaction to the addition of energy-rich POM (mucus + eggs), while silicate sands did not show this response. The 2-fold larger grain size of the carbonate compared to the silicate sands may affect the permeability and porosity of the respective sediments. Rasheed et al. (2003a) found a stronger reaction to the addition of the cyanobacterium *Spirulina* sp. in carbonate sands than in silicate sands, and attributed this difference to the higher permeability of carbonate sands leading to a more intense transport of organic matter into the sands via advection. This is confirmed by the measurements in this study and in other studies of Rasheed et al. (2003a,b), who found a 4- to 8-fold higher permeability and fluid exchange in carbonate sands than in silicate sands from the same study site. In addition, the porous surface structure of carbonate sands may be more effective in retaining POM than the relatively smooth surfaces of silicate sands. It was found that carbonate sands may exhibit a 50% larger specific surface area (Rasheed et al. 2003a) and 30% higher porosity (present study) than silicate sands of a similar grain size; this is critical for microbial colonisation. Wild et al. (2004b, and unpubl. data) found high bacteria densities in carbonate sands from Australia, the Red Sea and Hawaii, with cell numbers of 10^9 to 10^{10} cm^{-3}, resulting from the large specific surface area available as settling substrate for microorganisms, and the fact that bacteria exist also within the matrix of carbonate grains. Bacteria abundance is about 1 order of magnitude higher than bacteria counts in silicate sands of the same grain size (Rusch et al. in press) and may partly explain the 50-fold and 6-fold stronger response of carbonate sands to the addition of coral mucus and clam eggs. It is also possible that different properties (e.g. buffering and heat capacity, transparency) of both sediments caused the differences in organic matter degradation rates. Another reason could be that bacteria communities in carbonate sands differ from those in silicate sands. Specific bacteria living in and on the carbonate grains may be differently adapted to the rapid degradation of organic matter transported into the sandy sediments via advective processes. This aspect needs further study with molecular tools that allow identification of the phylogeny and function of microbial popula-

tions (Llobet-Brossa et al. 2002). Irrespective of the exact mechanisms, the rapid response of carbonate sediments to organic matter input suggests that much of the organic matter produced within the coral reef ecosystem will also be degraded on site, rather than being exported to adjacent ocean waters. This is in agreement with the observations of Duarte & Cebrian (1996), who reported that 76% of primary production by reef algae was degraded within the coral reef ecosystem, the highest value amongst the 8 ecosystem types covered by their study.

Carbon turnover in the chambers with mucus addition was 5 to 8% h^{-1}. This is very similar to the rates of C turnover (at least 7% C h^{-1}) derived from chamber experiments with coral mucus addition at Heron Island, Australia (Wild et al. 2004b). The addition of zooxanthellae did not cause increased SOC rates, not even in the carbonate sands. This may be due to the quality and reactivity of the added organic matter, which affects microbial remineralization, and depend on its molecular as well as its biochemical composition (Westrich & Berner 1984, Dauwe et al. 1999). Like other symbiotic dinoflagellates, zooxanthellae possess a stable shell composed of cellulose (Markell et al. 1992), a polysaccharide that can only be degraded by a few specialized microorganisms (Hedges & Oades 1997, Pareek et al. 2000). In contrast, coral mucus contains a variety of monosaccharides, free amino acids, proteins and lipids (Benson & Muscatine 1974, Ducklow & Mitchell 1979, Krupp 1981, Pascal & Vacelet 1981, Meikle et al. 1988, Wahbeh & Mahasneh 1989, Wild et al. 2005), characterizing this substrate as an energy and nutrient source for microbes. We can also assume that *Tridacna squamosa* eggs are mainly composed of proteins and lipids, as found by Sedano et al. (1995) for another bivalve, *Mytilus galloprovincialis*. A higher C:N ratio (16 to 21) was found for coral eggs (Wild et al. 2004c) than for coral mucus (5 to 14) (Wild et al. 2004a). This and the higher C turnover of coral mucus (5 to 9% C h^{-1}) compared to clam eggs (1 to 2% C h^{-1}) indicate a higher reactivity of coral mucus.

In conclusion, our research demonstrated that permeable carbonate reef sands are sites of efficient organic matter degradation, with decomposition rates exceeding those of silicate sands of similar grain size exposed to the same environmental conditions. The higher specific surface area and associated higher densities of bacterial colonisation may be the leading causes for the higher decomposition rates in the carbonate, but also the higher sediment permeability due to the porosity and surface roughness of the grains may enhance organic matter uptake and degradation in the carbonate sands. Because these carbonate sands cover the reef around the corals, they are the primary recipients of sinking organic material produced and released from living corals, i.e. particle-enriched mucus. Corals invest a large amount of the energy harvested by their symbiotic zooxanthellae in mucus (approximately 50%; Crossland et al. 1980, Davies 1984); thus, recovering some of the nutrients released with the mucus should provide a significant ecological advantage. The rapid decomposition of the mucus and trapped particles in the sediment in close vicinity to the corals permits this efficient recycling, and in a fringing reef may fulfil the same role as the decomposition of mucus in the lagoon sediments of circular reef plateaus or atolls, as reported earlier by Crossland et al. (1980), Davies (1984), and Wild et al. (2004a,b). Our present study expands this coral–permeable sediment–recycling hypothesis to other important particulate organic matter species in the reef environment, namely spawning products and zooxanthellae. Large amounts of spawning products reach the reef sediments after mass spawning events of reef organisms (e.g. Wild et al. 2004c), underlining the importance of permeable reef sands for the recycling of the nutrients contained in these products. Coral bleaching events, which have recently became more frequent (possibly due to temperature increases in the marine environment) (Hoegh-Guldberg 1999), represent mass releases of zooxanthellae to reef waters. Our study has shown that despite a probable substantial filtration of these algae from the water column by the permeable reef sands (Huettel & Rusch 2000), a rapid degradation of this rich particulate organic matter in the sands may be not possible. Our study suggests that bleaching events may not result in an immediate return of nutrients (as seen for *Tridacna squamosa* eggs) and, if water currents are present, may instead result in a relatively larger loss of nutrients from the reef system in comparison to rapidly degrading POM as spawning products and coral mucus.

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