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Degradation and mineralization of coral mucus in reef environments

Christian Wild[1,*], Mohammed Rasheed[2], Ursula Werner[1], Ulrich Franke[1], Ron Johnstone[3], Markus Huettel[1,4]

[1]Max Planck Institute for Marine Microbiology, Celsiusstrasse 1, 28359 Bremen, Germany
[2]Marine Science Station, University of Jordan and Yarmouk University, PO Box 195, Aqaba, Jordan
[3]Centre for Marine Studies, The University of Queensland, Brisbane, Queensland 4072, Australia
[4]Department of Oceanography, Florida State University, Tallahassee, Florida 32306-4320, USA

ABSTRACT: With *in situ* and laboratory chamber incubations we demonstrate that coral mucus, an important component of particulate organic matter in reef ecosystems, is a valuable substrate for microbial communities in the water column and sandy sediments of coral reefs. The addition of coral mucus to the water of benthic chambers placed on lagoon sands in the coral cay Heron Island, Australia, resulted in a rapid and significant increase in both O_2 consumption and DIC production in the chambers. The permeable coral sands permitted the transport of mucus into the sediment with interfacial water flows, resulting in the mucus being mainly (>90%) degraded in the sediment and not in the water column of the chambers. A low ratio of 0.48 (*in situ*) to 0.64 (laboratory) for O_2 consumption/DIC production after the addition of coral mucus, and high sulfate reduction rates (SRR) in natural sediments which were exposed to coral mucus, suggest a large contribution of anaerobic processes to the degradation of coral mucus. Oxygen penetrated less than 5 mm deep into these sediments. The microbial reaction to mucus addition was rapid, with a calculated *in situ* C turnover rate ranging from 7 to 18% h^{-1}. The degradation of coral mucus showed a dependency on the permeability of the carbonate sediments, with faster degradation and remineralization in coarse sands. This indicates the importance of permeable reef sediments for the trapping and degradation of organic matter. We suggest that coral mucus may have a function as a carrier of energy to the benthic microbial consumers.

KEY WORDS: Coral mucus · POM · Degradation · Permeable carbonate sands · O_2 consumption · DIC production · C turnover

INTRODUCTION

Despite the high abundance of coral mucus in the suspended matter of reef waters, its role in the cycling of matter in coral reef environments is unknown. In this study, we present the first experimental results addressing benthic microbial degradation of coral mucus. For these experiments we used stirred benthic chambers that were deployed both in the laboratory and *in situ* at Heron Island, Australia.

Hard and soft corals continuously produce mucus in ectodermal cells and release it as a transparent, moderately viscous, runny liquid (Ducklow & Mitchell 1979b). Coral mucus secretion is a protection mechanism against sedimentation (Hubbard & Pocock 1972, Schuhmacher 1977) or increased particle load in the water (Rublee et al. 1980). It also prevents epiphytic/epizoic or bacterial growth on the coral surface and, thus, acts against fouling (Ducklow & Mitchell 1979a). In addition, mucus is used to capture prey (Lewis & Price 1976, Lewis 1978, Goldberg 2002). Those corals growing very close to the water's surface protect themselves against desiccation during aerial exposure at low tide by mucus secretion (Krupp 1984).

The secreted mucus is transported on the coral surface by ciliary currents, and is subjected to a range of physical and chemical processes that can cause the separation of mucus from the coral surface, leading to

*Email: cwild@mpi-bremen.de

the formation of mucus webs, flocs, threads (Coles & Strathman 1973) or complex organic aggregates (Marshall 1968). These mucus structures are almost neutrally buoyant and, thus, persist in the water column and can dominate the suspended particulate matter in reef waters (Johannes 1967, Marshall 1968).

Coral mucus is primarily a carbohydrate complex (Coffroth 1990), but also contains energy-rich lipid compounds like wax esters (cetyl palmitate), triglycerids, free fatty acids (Benson & Muscatine 1974, Crossland et al. 1980) and proteins or peptides (Krupp 1985, Vacelet & Thomassin 1991). More detailed information about the chemical composition of coral mucus was presented by Richards et al. (1983), who found proteoglycan consisting of D-arabinose, N-acetyl-2-amino-2-deoxy-D-glucose and D-mannose as main component of the mucus released by the staghorn coral *Acropora formosa*. Mucus released from corals has a relatively high nitrogen content (Coles & Strathman 1973), while most other detritus in reef environments is nitrogen-poor (Hickel 1974).

Coral mucus represents a food source for reef zooplankton (Richman et al. 1975, Gottfried 1983, Marsden & Meeuwig 1990), crabs (Rinkevich et al. 1991, Stachowicz & Hay 1999), shrimps (Daumas et al. 1982, Patton 1994), bivalves (Shafir & Loya 1983), fish (Johannes 1967, Benson & Muscatine 1974), Gorgonian soft corals (Coffroth 1984), and even brittle stars (Grange 1991).

Mucus layers on corals and mucus aggregates suspended in the water column are colonised by communities of marine heterotrophic bacteria (Ducklow & Mitchell 1979a). These bacteria may convert mucus compounds into bacterial organic matter, enhancing the nutritional quality (Coles & Strathman 1973), thus making coral mucus more valuable for reef detritus feeders (Ducklow & Mitchell 1979a). Although coral reefs are generally associated with oligotrophic waters, high primary production rates (1500 to 5000 g C m^{-2} yr^{-1}) are reported for these ecosystems (Odum & Odum 1955, Lewis 1977, Kinsey 1983). Many authors explain these findings with a short linked nutrient cycle between autotrophs and heterotrophs. The symbiosis between corals and zooxanthellate dinoflagellates is a well-known example of this nutrient-preserving mechanism. Because of the large number of algal endosymbionts, and the close metabolic dependence on them, hermatypic corals can be seen as functional autotrophic animals (Schlichter et al. 1983). Production, release and consumption of mucus is mentioned as one mechanism for the transfer of energy from corals and their zooxanthellae to other reef organisms (Coles & Strathman 1973, Benson & Muscatine 1974, Ducklow & Mitchell 1979a). Crossland et al. (1980) found that mucus released by the coral *Acropora acumineata* corresponded to approximately 40% of the net carbon fixation by the zooxanthellae. Davies (1984) suggested that a loss of 49% of the fixed energy could be attributed to mucus secretion of *Pocillopora eydouxi*. Similar values were also reported by Herndl & Velimirov (1986), who calculated a 44% respiratory loss due to mucus release in the Mediterranean hermatypic coral *Cladocora cespitosa*, and Johannes (1967), who estimated a mucus release of ca. 40% of coral respiration. Ikeda & Miyachi (1995) even calculated that 98% of the net carbon assimilated by zooxanthellate photosynthesis is released from *Fungia* sp. as exudates, including coral mucus.

Our own observations in the lagoons of Heron and Lizard Island (Great Barrier Reef, Australia) indicated that coral mucus aggregates are an important component of POM (particulate organic matter) in the water column, especially after low tide. We also observed that suspended mucus aggregates gain density due to the attachment of microflora/fauna, resuspended sediment, and eventually sink to the benthos and carbonate sediments.

Benthic sediments in reef ecosystems, consisting mainly of carbonates originating from skeletal material of corals and other benthic organisms, are characterised by a high permeability, porosity and specific surface area, and permit water flow through the sediment. Due to their high specific surface area, large numbers of bacteria are able to settle and grow on the carbonate grains. These factors illustrate the biocatalytic potential of permeable reef sands for the filtration and degradation of organic matter. The current knowledge outlined above suggests that coral mucus may play an important role in the cycling of matter in coral reef ecosystems.

In this study we present the first experimental results on the degradation and mineralization of coral mucus in the benthic environments of a reef lagoon. In a set of laboratory and *in situ* chamber experiments, we added mucus to the chamber water and then measured dissolved O_2 as the electron acceptor for aerobic respiration, and dissolved inorganic carbon (DIC) as end product of reduced organic matter mineralization. In order to assess the potential role of carbonate sands for the uptake and degradation of mucus, we also tested the dependence of O_2 consumption and DIC production on sediment permeability. Finally, we also measured sulfate reduction rates (SRR), dissolved O_2 distribution and dissolved O_2 penetration depths in cores from the chamber experiments to assess the contribution of anaerobic processes to the degradation of coral mucus in reef sediments.

We hypothesised that pore-water flows facilitate the transport of coral mucus into the bed, promoting the importance of the carbonate sands for the degradation of this important component of the coral reef POM pool.

Table 1. Physico-chemical properties of, and bacteria counts in, the sediments used for different experiments. TOC: total organic carbon

Sediment	Median grain size (µm)	Permeability (10^{-10} m^2)	Porosity (%)	Surface area (m^2 g^{-1})	TOC (%)	Bacteria count (10^9 cells cm^{-3})
Shark Bay	829	1.22	45.5	0.29	0.24	1.71
Coarse sand	838	3.75	45.0	0.18	0.18	0.85
Medium sand	536	1.17	44.6	0.31	0.21	3.06

MATERIALS AND METHODS

Study site. The experiments were conducted at Heron Island, Australia (23° 27′ S, 151° 55′ E) in February 2001 and January 2002. The island is situated on the Tropic of Capricorn, at the southern boundary of the Great Barrier Reef, 70 km offshore from Gladstone (Fig. 1). Laboratory experiments were carried out in the facilities of the Heron Island Research Station, and field experiments were conducted in Shark Bay, a shallow-water site (at ca. 0.2 to 2.5 m water depth, depending on tide) at the south-eastern end of the island. The sediments used for laboratory experiments were also collected in Shark Bay, and consisted of carbonate sands of biogenic origin (Table 1). During the *in situ* experiments, the weather was calm, wave heights did not exceed 30 cm, and bottom currents (measured 10 cm above the sediment surface) were less than 15 cm s^{-1}. Ripple formation, scouring or re-deposition of sediment was not observed in any of the field experiments. The sediment surface was relatively smooth, with topography not exceeding 1 cm in height.

Sediment analyses. Grain-size distribution was assessed by sieving through a calibrated sieve stack, and sediment permeability was measured in sediment cores using a constant-head permeameter as described by Klute & Dirksen (1986). Porosity was calculated from weight loss of a known volume of wet sediment after drying at 60°C for 24 h. Specific surface areas of the sediments were determined by measuring nitrogen adsorbed to the dry grain surfaces using a Quantachrome Quantasorb instrument. Total organic carbon (TOC) and total nitrogen (TN) content were measured using a Heraeus CHNO rapid elemental analyzer, with sulfanilamide as a calibration standard. The samples were pre-treated with 6 N HCL until gas development ceased, and then washed twice with distilled water and dried at 60°C.

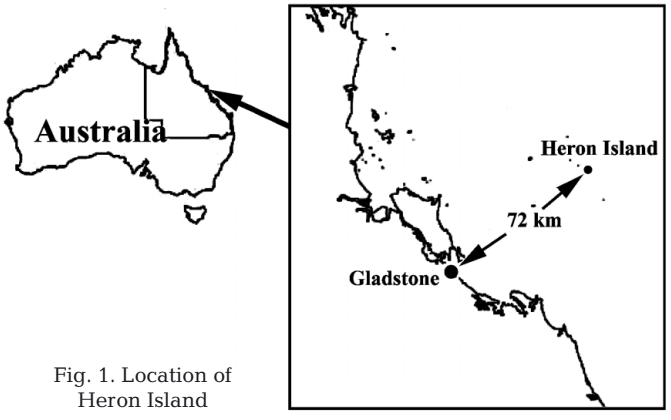

Fig. 1. Location of Heron Island

Bacterial counts in carbonate sediments. For bacterial counts in carbonate sediments, we used the acridin orange direct count (AODC) method (Hobbie et al. 1977) with some modifications. For each sample, 2 ml of formaldehyde (2%) in acetic acid (2%) was added to the sediment (1 cm^3 preserved with formaldehyde at 3% final concentration). The samples then were mixed and subsequently subjected to pulsed ultrasonic treatment (30% for 150 s, Bandelin MD72, vials on ice). The sand grains were allowed to settle for 20 s, and the supernatant was removed. The remaining sediment was washed at least 6 times with the acetic acid solution, and all supernatants were combined. This ultrasonic treatment, with subsequent washing, was repeated 3 more times. Bacteria were counted in subsamples from the combined supernatants. Aggregates were disintegrated by weak ultrasonic treatment (duration: 10 to 30 s) when necessary. Bacteria were counted in natural Shark Bay sediments as well as in both sediment fractions used in the laboratory incubations (Table 1).

Mucus collection. In the reef flats around Heron Island, clusters of branching corals of the genus *Acropora* form scattered patches on the sediment. The lower dead branches anchor the corals in the carbonate sand, and this permits the removal of individual colonies from the sediment without breaking and harming the coral. During low tide, some of these corals are naturally exposed to air. Coral mucus was collected *in situ* by exposing such intact colonies of several *Acropora* species from the reef flat (<2 m water depth) to air. The colonies rapidly released large amounts of mucus, which was immediately collected by inverting the coral over a pre-cleaned container, which caught the dripping mucus material. After this procedure, the corals were re-anchored in the lagoon

sediment. The collected mucus was homogenised and stored refrigerated until use. All samplings and mucus addition experiments were carried out within 24 h of mucus sampling.

Bacterial counts and carbon analysis in coral mucus. Bacteria were counted in triplicate aliquots from the coral mucus that was added to the chambers of the *in situ* incubation Expt 1. As a control, bacteria were also counted in seawater sampled from the reef flat on the day of mucus collection. All counts were performed using the standard AODC method (Hobbie et al. 1977).

Samples for particulate organic carbon (POC) were prepared by filtering triplicate aliquots of 5 to 10 ml of coral mucus on precombusted GF/F filters (Whatman) using a low vacuum of 150 mm Hg pressure. The filters were dried for 24 h at 40°C and wrapped in precombusted aluminium foil. Small carbonate grains in the mucus were removed by exposing the filters to a fuming HCl atmosphere for 24 h. Carbon values were measured using an elemental analyser (Fisons AT1500) with sulfanilamide (HEKAtech) as standard.

Mucus respiration. In order to measure the O_2 consumption of coral mucus in the water column, we incubated freshly collected undiluted *Acropora* mucus, and as reference (control) local seawater, in 30 ml Winkler bottles under dark conditions and at *in situ* temperature (26 to 29°C). The O_2 concentrations in both treatments were measured in parallel time series using the Winkler titration method.

This mucus respiration measurement was performed for 5 different mucus samplings, including material from 3 mucus samples that were also sub-sampled and used for subsequent incubation in benthic chambers. For each bottle incubation experiment, O_2 consumption rates were calculated in µM d^{-1} using linear regression with at least 4 data points.

Chamber incubation experiments. The benthic degradation and mineralization of coral mucus was investigated in 2 laboratory and 4 *in situ* chamber incubation experiments (Table 2). The *in situ* incubations were undertaken in Shark Bay, while sieved sediment fractions characterised by different permeabilities were used as the sedimentary medium incubated in the laboratory experiments. The *in situ* incubations started 2 h after low tide and ended 2 to 7 h later. The laboratory incubations ran for 6 h. During all incubations, water samples (30 to 100 ml) were taken at preset time intervals (30 to 60 min) from the chamber water for later analyses of O_2 and DIC. In one experiment, additional water samples were taken for the analysis of Br^-, a solute tracer added to the chamber water (see below and Table 2). Fluxes of solutes were evaluated by linear regression of solute concentrations over time. After termination of one *in situ* chamber experiment, sediment cores (1 core per chamber) were collected for the analysis of SRR.

Chamber design: We used cylindrical chambers made of acrylic with a height of 30 cm and an inner diameter of 19 cm. Plastic lids covered the chambers and were fixed by 4 stainless-steel clips. Each lid contained a sampling port with syringe holder for water samples, and another port to replace the sampled water with seawater. A third opening in the lids contained a fibre-optic oxygen microsensor. A horizontally rotating disk of 15 cm diameter agitated the water in the chambers. The disks, driven by 12 V DC motors, rotated at ca. 8 cm above the sediment at an electronically controlled speed of 20 rpm. The ensuing water column rotation generates a pressure gradient at the sediment surface of 1.2 Pa between the centre and the chamber wall. Pressure gradients at this order of magnitude develop when sediment topography and boundary flows found at the study site interact (Huettel & Gust 1992, Glud et al. 1996a, Huettel & Rusch 2000).

In situ incubations: The chambers were inserted gently into the sediments to a depth of ca. 8 cm, marked by a ring of tape on the chamber wall, and thus included a water column of approximately 22 cm height. The chambers were then closed and sealed from light by wrapping with opaque black PVC foil. Recordings of light intensity and temperature at 2 min intervals underneath the PVC foil and in the surrounding areas, using Onset™ HOBO light loggers made

Table 2. Overview of all mucus chamber incubations carried out at Heron Island. DIC: dissolved inorganic carbon; SRR: sulfate reduction rate

Date (dd/mm/yy)	Expt	Mucus (control) chambers	Water temperature/ salinity (°C/PSU)	Parameters measured in chamber water (-sediment)
04/02/2001	*In situ* 1	3 (4)	28.2/34.0	O_2, DIC, NaBr
07/02/2001	Laboratory 1 (coarse)	3 (3)	27.2/34.5	O_2, DIC
08/02/2001	Laboratory 2 (fine)	3 (3)	27.4/34.0	O_2, DIC
15/01/2002	*In situ* 2	2 (2)	26.2/34.5	O_2, (SRR)
21/01/2002	*In situ* 3	2 (2)	27.2/34.0	O_2
25/01/2002	*In situ* 4	2 (2)	28.3/35.5	O_2

waterproof by shrink-wrapping them in transparent, non-light-absorbing clingwrap, and Tidbit temperature loggers, revealed that no light intrusion or heating occurred in the chambers. Finally, the chambers were secured with lead weights to prevent any movement due to bottom currents or waves.

For each experiment, 4 or 6 of the described benthic chambers were used (Table 2).

At the start of each experiment, 150 to 280 ml *Acropora* mucus (characteristics listed in Table 3) was added to half of the deployed chambers via one of the syringe ports. In one experiment, the tracer NaBr (1.5 mM final concentration) was added to all chambers to assess advective interfacial solute exchange. At the end of each experiment, the volume of water in each chamber was determined after removing the lid of the chambers by measurement of water height with a ruler at 4 different positions (N, E, S, W) close to the chamber wall.

Laboratory chamber incubations: In order to assess the effect of sediment permeability on the degradation of coral mucus, 2 laboratory chamber incubations were conducted using sediments of different grain size. Sediment was collected from Shark Bay (6 February 2001) and separated with a sieve (500 µm) into a coarse and medium grain-size fraction (829 and 536 µm median grain size, respectively; see Table 1). The experiments were conducted in a similar manner as the *in situ* experiments. Six benthic chambers, identical to those described above except that they were sealed at the bottom with lids, were placed in a large container flushed by natural seawater, which kept the temperature of incubation at *in situ* temperature (26 to 28°C). The chambers were filled with 4.5 dm^3 of either the coarse (7 February) or the medium (8 February) sediment fraction. The overlying unfiltered seawater had a volume of 4 l. After closing the lids, volumes of 200 ml of *Acropora* mucus were added to 3 of the chambers of each set. During the 6 h of incubation, the chambers were kept in the dark. At pre-set time intervals, dissolved O_2 was measured and water samples were withdrawn for DIC analysis.

Measurements and analyses: Dissolved O_2 concentrations in the chambers were continuously measured in the stirred chambers throughout the incubations by fibre-optic oxygen microsensors (PreSens; Sensor type A, tip diameter <50 µm. For the measuring principle see Klimant et al. 1995) mounted in the lids of the chambers or by the Winkler titration method. The microsensors were connected to a Microx-TX fiber-optic oxygenmeter (PreSens). Sensors were calibrated before and after the experiments using a 2-point calibration in oxygen-free (addition of sodium dithionite) and air-saturated seawater.

DIC concentrations in the water samples were determined using a flow injection system (Hall & Aller 1992). Calibration standards were prepared freshly from $NaHCO_3$. The detection limit of the method was 0.1 mM.

Bromide concentrations were determined by ion chromatography using NaBr as the standard for calibration.

In order to assess whether anaerobic decomposition contributed to the degradation processes associated with addition of coral mucus, SRR were measured within 12 h of sediment cores being taken (1 core from each chamber) at the end of *in situ* Expt 2.

SRR were measured in the sediment cores by adding a radiolabelled solution of $^{35}SO_4^{2-}$ (Amersham; specific activity of added solution: 340 MBq per mol SO_4^{2-}) to the overlying water of each core. By using a peristaltic pump, the overlying water was transported into the permeable core sediment and equally distributed. The cores were then incubated in the dark for 6 h at ambient temperatures (Expt 1: 33°C; Expt 2: 28°C). The sediment was subsequently sliced into 1 cm thick sections and fixed in 20% ZnAc. Samples were processed using a cold chromium distillation procedure (Kallmeyer et al. unpubl.), with the slight modification that HCl was added until all carbonates were dis-

Table 3. Carbon content and bacterial abundance in coral mucus (*Acropora* spp.) used for the chamber incubations. Values are means ± SE (n in replicates, nd = no data available). SW: seawater; nd: no data

Sampling date (dd/mm/yy)	Used for:	C (mg l^{-1})	Bacterial count (10^5 cells ml^{-1})
03/02/2001	*In situ* 1	36.8 ± 7.2 (3)	295 ± 149 (3)
03/02/2001	SW control	nd	3.0 ± 1.7 (3)
06/02/2001	Laboratory experiments	51.6 ± 7.7 (3)	292 ± 31 (3)
14/01/2002	*In situ* 2	30.9 ± 0.4 (3)	nd
14/01/2002	SW control	1.8 ± 0.1 (3)	nd
20/01/2002	*In situ* 3	12.1 (1)	nd
22/01/2002	SW control	0.3 ± 0.1 (3)	nd
25/01/2002	*In situ* 4	10.8 ± 0.8 (3)	nd
25/01/2002	SW control	0.43 ± 0.03 (3)	nd

solved. The activity of $^{35}SO_4^{2-}$ and TRIS (total reduced inorganic sulfur) were determined using a liquid scintillation counter (Packard 2500 TR); the scintillation cocktail used was Lumasafe Plus® (Lumac BV, Holland). Sulfate concentrations were determined by non-suppressed ion-chromatography with conductivity detection. SRR were calculated according to:

$$SRR = a_{TRIS} \times SA^{-1} \times \alpha \times t^{-1} \text{ (nmol cm}^{-3} \text{ d}^{-1}\text{)}$$

where SRR are sulfate reduction rates (nmol cm^{-3} d^{-1}); a_{TRIS} is activity (counts per min; CPM) in TRIS cm^{-3}; α is correction factor for the expected isotopic fractionation (1.06); SA is specific activity of sulfate, SA = $CPM_{sulfate} \cdot nmol_{sulfate}^{-1} \cdot l^{-1}$ (CPM $nmol^{-1}$); t is time (d).

Oxygen profiles within the stirred chambers: The 2D oxygen distribution and penetration depths in the stirred chambers were measured using semi-transparent planar O_2 optodes (Glud et al. 1996b, 1998). The optical measuring principle of O_2 planar optodes is based on dynamic quenching of the luminescence light of an indicator dye by oxygen (Kautsky 1939). In this study, the sensing layer of the optode consisted of Platinum (II) meso-tetra pentafluorophenyl-porphyrin (Pt-PFP) embedded in a Poly-styrol-co-acrylacidnitril matrix. Detailed description of the planar O_2 optode used, acquisition and processing of the images, design of the modified stirring chambers and treatment of the sampled sediment can be requested form U. Franke (ufranke@mpi.bremen.de).

Sediment cores (length 15 cm) from Shark Bay were transferred to chambers similar to those used in the laboratory incubations. The overlaying water in the chambers was stirred with a rotating disc at 40 rpm, 2-fold the stirring speed used in the incubation experiments, to get information about the maximum O_2 penetration into the sediment. Oxygen penetration depths for 3 sediment cores were determined by extracting 5 oxygen profiles out of a smoothed (box-car filter, smoothing value: 8) 2D O_2 image for each sediment sample. This was done when the overlying enclosed chamber water was still saturated with O_2. All profiles were extracted at the same relative positions of the O_2 images. With the help of black and white digital images taken just before the O_2 measurements, the sediment surface was detected and the O_2 profiles were normalised to the sediment surface. These digital images covered an area of 24 × 19 mm and the spatial resolution was 40 × 40 µm $pixel^{-1}$.

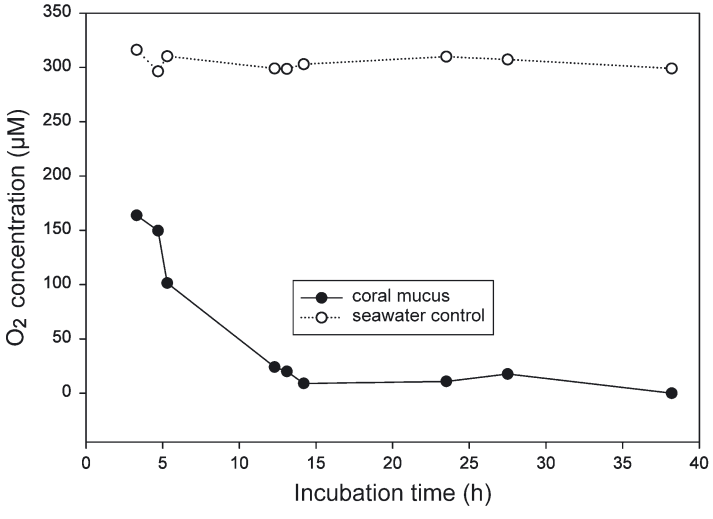

Fig. 2. Oxygen concentrations in bottles filled with natural *Acropora* mucus or seawater over time. Bottles were incubated at 28°C for 38 h

RESULTS

Bottle incubations

In the bottle incubations, coral mucus consumed more O_2 than equivalent volumes of seawater, indicating aerobic degradation of the mucus. This result was supported by the bacterial counts, which revealed a ca. 100-fold increase in bacterial numbers in coral mucus compared to the surrounding seawater. Further characteristics of the mucus are listed in Table 3. From the onset of the bottle experiment throughout the entire incubation period, O_2 concentrations in the mucus bottles were always significantly lower, and decreased faster, than in the control bottles filled with seawater (Fig. 2). A conservative linear regression analysis (period of 3 to 14 h) results in O_2 consumption rates of 334 µM d^{-1} for coral mucus and 21 µM d^{-1} for the ambient seawater, corresponding to a >15-fold increase in O_2 consumption in coral mucus. This result was confirmed by the other 4 mucus incubation experiments, which showed O_2 consumption rates to range from 130 to 445 and 5 to 41 µM O_2 d^{-1} for mucus and seawater incubations, respectively.

Chamber incubation experiments

The coarse Shark Bay sediment was highly permeable (permeability k in the range of 10^{-10} m^2), and permitted advective pore-water exchange as reflected by our tracer measurements. The average flux of NaBr into Shark Bay sediments was 54.0 ± 6.8 mmol m^{-2} d^{-1}, which corresponds to a flushing rate of 26 l m^{-2} d^{-1} at the stirring speed of 20 rpm.

Despite its large median grain size, the Shark Bay sediment contained 1.71 ± 0.57 × 10^9 bacteria cm^{-3} (Table 1).

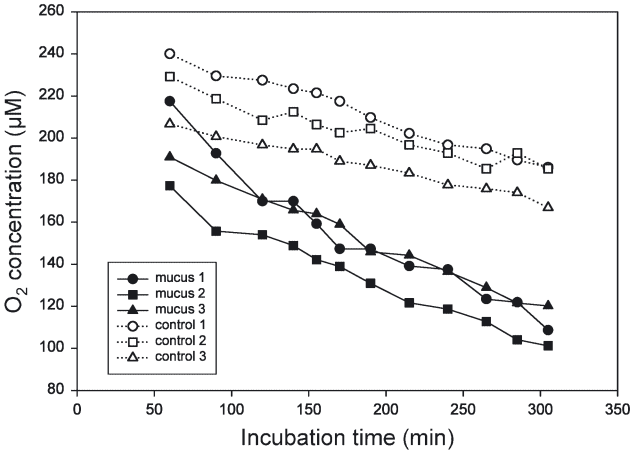

Fig. 3. O_2 concentration in 6 benthic chambers during *in situ* Expt 1. Coral mucus (*Acropora* spp.) was added to the 3 chambers represented by black symbols. Control chamber values are shown using open symbols

In situ chamber incubations

In the *in situ* experiments, the addition of coral mucus (for characteristics see Table 3) caused a 1.2- to 1.7-fold increase in the O_2 consumption rate of the amended chambers relative to the control chambers without mucus (Fig. 3). In Expt 2, much higher sulfate reduction rates (up to 1200 nmol cm^{-3} d^{-1}) were recorded in one of the mucus chambers compared to the control chambers. Integration of sulfate reduction over the first 5 cm showed sulfate reduction rates of 22.7 to 56.9 mmol m^{-2} d^{-1} in the mucus chambers, compared to between 12.0 and 19.3 mmol m^{-2} d^{-1} in the control chambers. Maximum O_2 penetration depths in 14 of 15 profiles (5 measured in each of 3 cores from Shark Bay) were 2.0 to 2.5 mm; only 1 profile showed an O_2 penetration <4.8 mm into the sediment (Fig. 4). This locally enhanced O_2 penetration was caused by bioturbation, as indicated by the shape of the profile.

Higher O_2 consumption in the chambers with mucus was accompanied by higher DIC production. In the chambers with mucus, DIC concentrations increased 1.3-fold faster than in the control chambers (Fig. 5).

Laboratory chamber incubations

Addition of mucus to the laboratory chambers caused a faster O_2 decrease relative to the control chambers (Fig. 6) and, thus, supported the results of the bottle and *in situ* incubations. The effect was more pronounced than in the *in situ* incubations, and so strong that in the chambers with mucus, anoxia was reached after 200 to 280 min (coarse sand) and 300 to 360 min (medium sand). This result was unexpected, because the bacterial abundance in the medium sand fraction was 3 times higher than that recorded for the coarse sand fraction (Table 1).

As in the *in situ* incubation, the DIC increase in the laboratory incubation chambers reflected the higher decomposition activity in the chambers with mucus. Here, the DIC production increased 2.6- (coarse fraction) and 3.2- (fine fraction) fold faster than in the control chambers (Fig. 7).

The amount of organic carbon added as mucus to the chambers ranged from 240 to 870 µmol (corresponding to 40 to 220 µmol POC l^{-1}) in all experiments (Table 4). In the laboratory experiments, the mucus concentrations in the chambers were highest (214 to 220 µmol POC l^{-1}) due to the smaller chamber-water volumes. During the *in situ* experiments, POC concentrations in the chambers were between 40 and 124 µmol l^{-1}. Natural POC water-column concentrations on the Heron Island reef flat ranged between 14 and 41 µmol l^{-1} (n = 56).

The fluxes of O_2 and DIC calculated from all chamber experiments are summarised in Fig. 8. In the 4

Table 4. Degradation of reduced carbon derived from coral mucus (*Acropora* spp.). Amounts of carbon added to the chambers were calculated from carbon analysis in coral mucus (Table 3). Rates for dissolved inorganic carbon (DIC) production and O_2 consumption are calculated from the rates measured in the mucus chambers reduced by the rates measured in the control chambers. Carbon turnover represents the ratio between addition of reduced carbon and the increased release of oxidized carbon as DIC, or the increased consumption of O_2 under the assumption that 1 mol of O_2 mineralizes 1 mol of reduced C; nd: no data

Expt	C addition (µmol)	Release of oxidized carbon		Oxygen consumption	
		DIC produced (µmol h^{-1})	C turnover (% h^{-1})	O_2 consumed (µmol h^{-1})	C turnover (% h^{-1})
In situ 1	857.9	125.3	14.6	60.3	7.0
In situ 2	360.2	nd	nd	23.2	6.5
In situ 3	302.2	nd	nd	20.1	6.7
In situ 4	242.8	nd	nd	44.2	18.2
Laboratory (coarse sand)	859.2	352.0	41.0	224.9	26.2
Laboratory (medium sand)	872.5	208.0	23.8	113.6	13.0

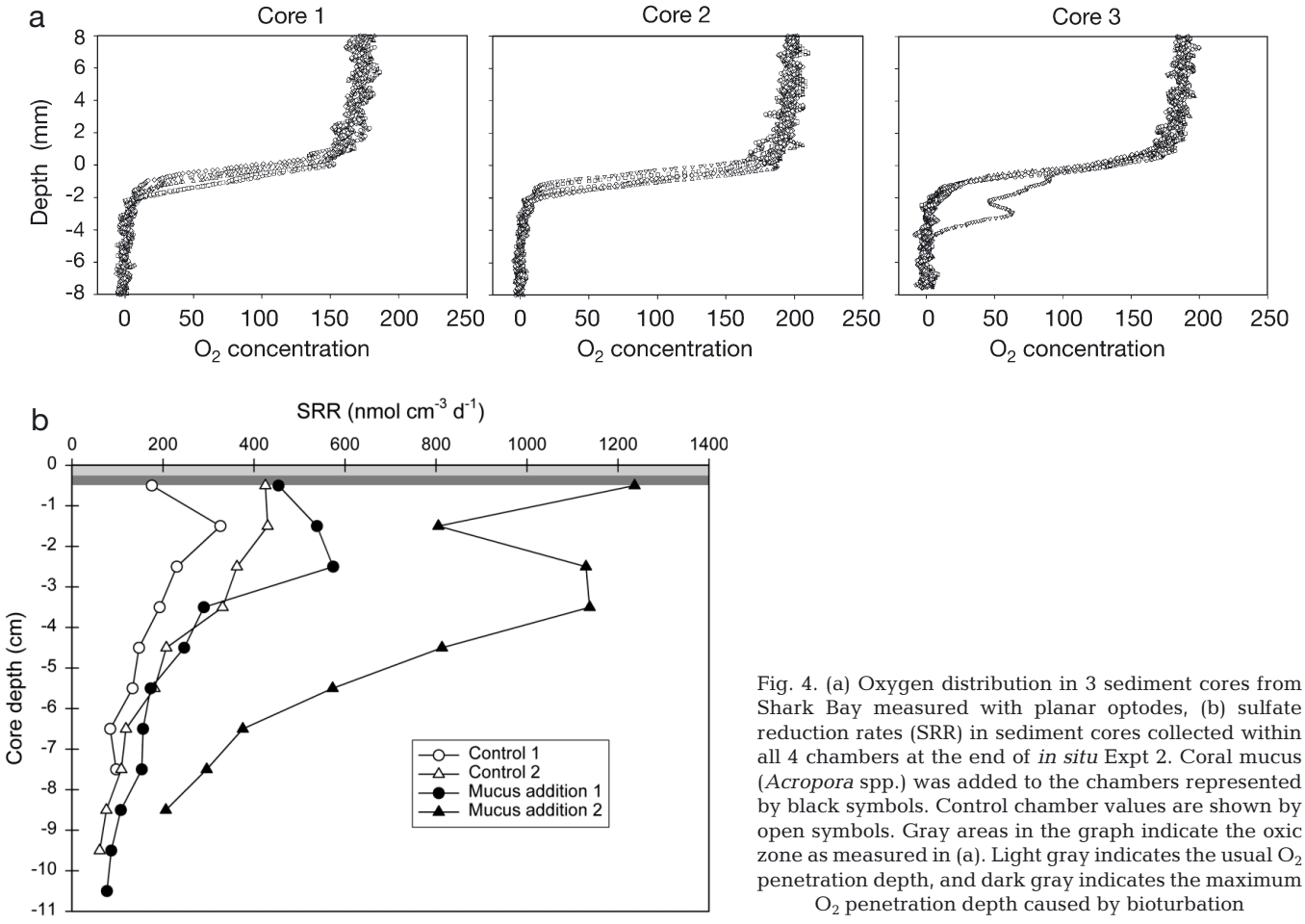

Fig. 4. (a) Oxygen distribution in 3 sediment cores from Shark Bay measured with planar optodes, (b) sulfate reduction rates (SRR) in sediment cores collected within all 4 chambers at the end of *in situ* Expt 2. Coral mucus (*Acropora* spp.) was added to the chambers represented by black symbols. Control chamber values are shown by open symbols. Gray areas in the graph indicate the oxic zone as measured in (a). Light gray indicates the usual O_2 penetration depth, and dark gray indicates the maximum O_2 penetration depth caused by bioturbation

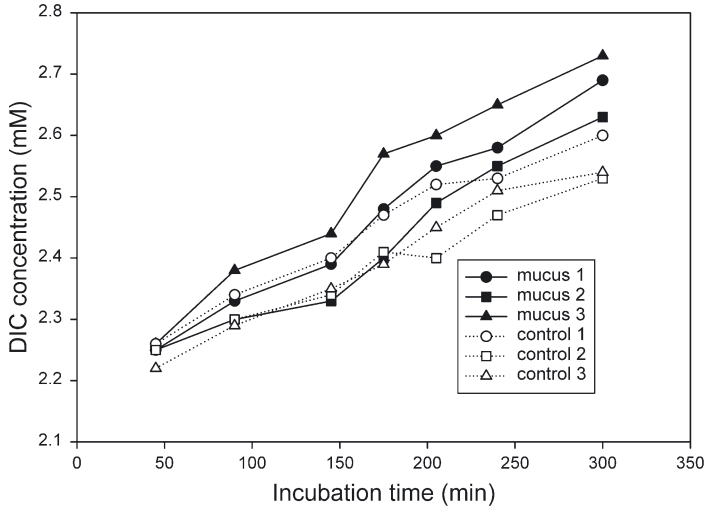

Fig. 5. Dissolved inorganic carbon (DIC) concentration in 6 benthic chambers during *in situ* Expt 1. Coral mucus (*Acropora* spp.) was added to the 3 chambers labeled with black symbols. Control chamber values are shown using open symbols

in situ experiments, we found in the chambers with mucus addition an increase in O_2 consumption of 17 to 46 mmol m^{-2} d^{-1} relative to the controls, while in the 2 laboratory experiments, increases of 109 to 199 mmol m^{-2} d^{-1} were reached. A 2-sided *U*-test after Wilcoxon, Mann and Whitney showed significant differences (α = 0.002) in sedimentary oxygen consumption between the control and mucus incubation chambers used *in situ*.

Consumption of O_2 was lowest in the controls of laboratory Expt 1 (coarse fraction) and highest in the mucus addition chambers of the same experiment.

Acropora mucus caused an increase in DIC concentration in the overlying water of all 9 experimental chambers where DIC was measured (3 *in situ* chambers, 6 laboratory chambers). This increase varied between the experiments, with a more pronounced response (higher DIC production) in the addition of coral mucus in the laboratory experiments (176 to 298 mmol m^{-2} d^{-1} compared to 141 mmol m^{-2} d^{-1} for the *in situ* Expt 1).

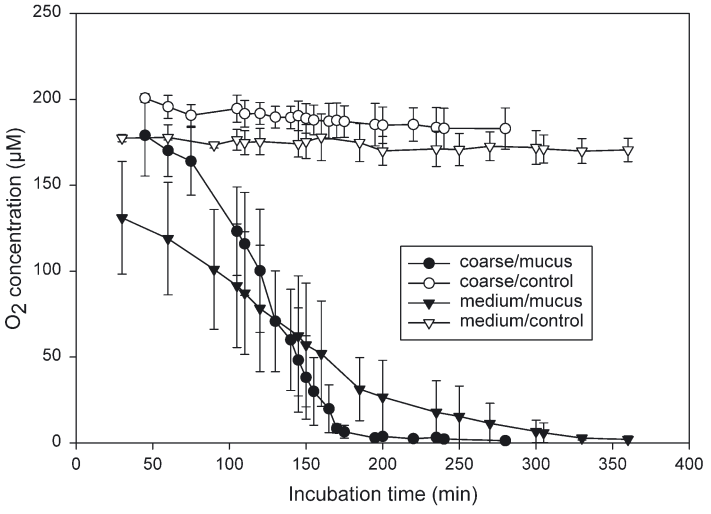

Fig. 6. Mean O_2 concentrations in the incubation chambers during both laboratory experiments. Coral mucus (*Acropora* spp.) was added to the chambers represented by black symbols. Control chamber values are shown by open symbols. Carbonate sediment with either medium (triangles) or coarse grain size (circles) was used. Error bars indicate the SDs of 3 replicate chambers

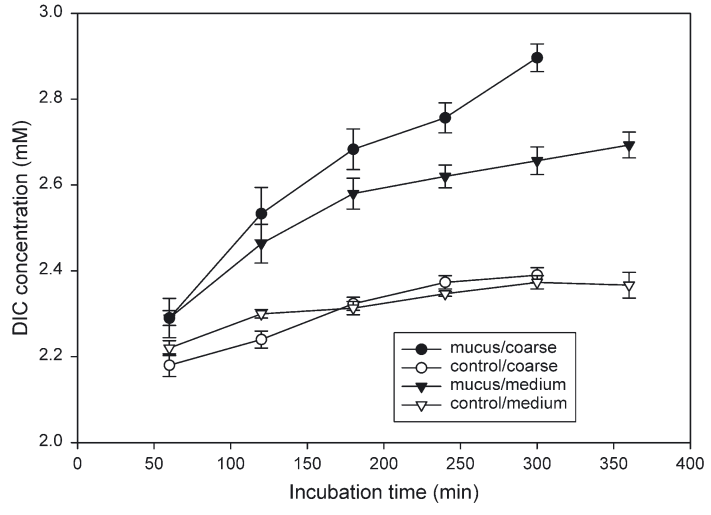

Fig. 7. Mean dissolved inorganic carbon (DIC) concentrations in the incubation chambers during both laboratory experiments. Coral mucus (*Acropora* spp.) was added to the chambers represented by black symbols. Control chamber values are shown by open symbols. Medium (triangles) or coarse grain size (circles) was used. Error bars indicate the SDs of 3 replicate chambers

The ratio between O_2 consumption and DIC production was always below 1, with the lowest value of 0.48 in the field Expt 1, and values of 0.64 and 0.55 in the laboratory experiments with the coarse and medium sand fraction, respectively.

Carbon degradation and mineralization

Carbon turnover rates, calculated from both the O_2 consumption and DIC production rates, revealed C turnover rates ranging from 7 to 18% h^{-1} during the *in situ* experiments, and rates from 13 to 24 and 26 to 41% h^{-1} in the laboratory experiments with the medium and coarse sand, respectively (Table 4). *In situ* C turnover rates and rates derived from the experiments with the medium sand fraction were similar, which can be caused by very similar permeabilities of both sediments (see Table 1).

The molar equivalent of increased inorganic C release to added organic C was reached *in situ* after between 5.5 and 15.5 h, indicating that coral mucus can cause a rapid microbial response in the sediment and water column of reef environments, and that the added material was mineralised within less than a day.

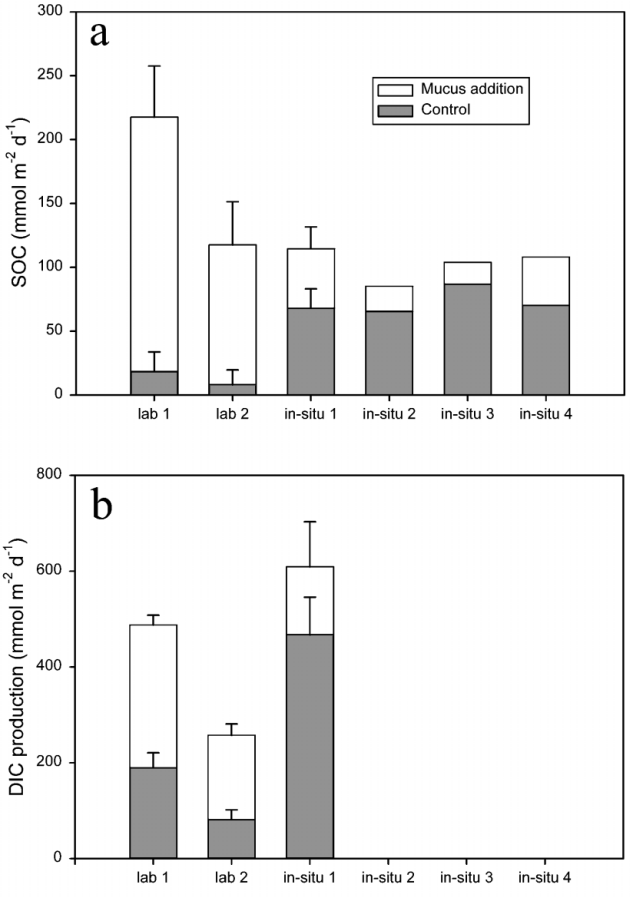

Fig. 8. Sedimentary O_2 consumption (SOC); (a) and dissolved inorganic carbon (DIC) release (b) as calculated from all chamber incubation experiments. Open bars indicate mean chamber values with mucus (*Acropora* spp.) addition; gray bars show the control values. Error bars indicate the SDs of all experiments (n = 3)

DISCUSSION

Degradation of coral mucus in the water column

The observed bacterial numbers on coral mucus were on average 100-fold higher than in the surrounding seawater (Table 3), and confirm the observation of Ducklow & Mitchell (1979a) who reported an increased abundance of bacteria on coral mucus. These findings can explain the higher O_2 consumption rates of mucus relative to seawater, and reveal that bacteria aerobically degrade coral mucus. Ferrier-Pages et al. (2000) showed that even small amounts of coral exudates can significantly stimulate microbial growth. *Escherichia coli* can survive in marine waters with coral mucus as the sole energy and nutrient source (Griffin 1999), and a significant number of mucus-colonising bacteria are able to grow on coral mucus as the sole source of carbon (Pascal & Vacelet 1981). In addition, in incubation experiments with and without mucus from *Acropora* and *Porites*, Moriarty et al. (1985) found that the bacterial production in mucus-enriched seawater was significantly greater than in untreated seawater. These observations indicate that coral mucus is an attractive substrate for water column bacteria.

Nonetheless, Vacelet & Thomassin (1991) characterised coral mucus as a poor, even inhibiting, medium for bacterial degraders in the water column, because they found (1) higher bacteria numbers in diluted than in pure mucus; (2) a lower percentage of dividing cells in coral mucus than in local seawater; and (3) higher bacterial production rates in cultures on peptone. The mucus webs they used in their long-term incubation experiments were not completely degraded, even after 21 d of incubation. Vacelet & Thomassin (1991) surmised that water column bacteria utilise only certain components of the mucus, primarily the energy- and nutrient-rich components such as proteins, triglycerides and wax ester.

Notably, however, all authors agree that mucus is degraded partly in the water column. No inhibiting effect of coral mucus on bacterial growth and activity was observed, as reflected by our Winkler incubations showing an O_2 consumption of coral mucus ranging from 130 to 445 µM d^{-1}, which is much higher than the O_2 consumption in the surrounding water. However, it is noted that other suspended aggregates can have much higher O_2 consumption rates, as reported for diatom aggregates (2400 µM d^{-1}) (Ploug & Grossart 2000).

Where is coral mucus degraded?

Higher O_2 consumption rates in the benthic chambers with mucus, relative to the consumption rates measured in seawater with mucus, demonstrated that coral mucus is a degradable substrate for microbial communities in the sandy sediments of coral reef ecosystems. In the mucus used for *in situ* Expt 1, we measured an O_2 consumption of 334 µM d^{-1}. According to this rate, an addition of 280 ml of this mucus to chambers with an average volume of 6.9 l (as done during *in situ* Expt 1) would lead to a calculated increase in O_2 consumption of approximately 14 µM d^{-1}. This consumption rate is ca. 5% of the oxygen consumption in the control chambers (284 ± 60 µM d^{-1}). However, we measured an average O_2 consumption of 473 ± 86 µM d^{-1} in the 3 mucus chambers. After subtraction of the consumption in the control chambers, this results in an increase in O_2 consumption by 189 µM d^{-1} caused by the addition of coral mucus, a much higher increase than expected from the respiration measurements in the bottle incubations. According to this calculation, water column O_2 consumption may only be responsible for less than 8% of the observed increase after the addition of coral mucus.

These findings lead to the conclusion that coral mucus added to the benthic chambers was primarily degraded in the carbonate sediment. High permeability of the carbonate sands permitted the transport of coral mucus into the permeable sands via interfacial water flows, where it was trapped by the rough surfaces of the carbonate grains. Due to this filtration process, the mucus became available to the sedimentary bacteria in the upper centimeters of the sands. Here, the number of bacteria per unit volume was 4 orders of magnitude higher than in the water column, causing the degradation rates of coral mucus in the sediment to exceed that in the water column by up to a factor of 12. In addition, the biomass of bacteria in a coral reef was reported to be 100 to 200 times greater in the sediment compared to the entire water column (Wilkinson 1987). Moriarty et al. (1985) reported a 10-fold higher bacterial productivity in reef sediments compared to the water column.

We could not directly measure the trapping of coral mucus by the chamber sediments. Flow-through column experiments with the same sediments as those used in the chamber experiments showed that suspended mucus can easily be transported into the carbonate sands, with water flows percolating the sediment (C.W. & M.H. unpubl. data). This may be an explanation as to why the results of this study initially contradicted the findings of Vacelet & Thomassin (1991). It is likely that a highly diverse and dense sedimentary bacterial population, adapted to the decomposition of more refractory material, can decompose mucus more effectively than the bacterial community in the water column.

Degradation of coral mucus in the sediment

In the laboratory chamber experiments, O_2 consumption and DIC production after mucus addition were more pronounced than in the *in situ* experiments. This was caused by the higher flushing rates through the sieved sediments. Sieving removed the fine fraction from the coarse sand, resulting in more permeable sediments than the natural Shark Bay sediments (see Table 1). O_2 penetration depth increases with increasing permeability due to faster transport of O_2 into the sediment (Ziebis et al. 1996, Huettel & Rusch 2000). More water and O_2 could be carried into the sieved sediments per unit time, resulting in the higher O_2 consumption rates we recorded in the coarse and medium sands. This flushing effect exceeded the effect of bacterial abundance that was 3-fold higher in the medium sand. These explanations are supported by findings of Forster et al. (1996), Marinelli et al. (1998), Huettel & Rusch (2000) and Dauwe et al. (2001), who also reported increased O_2 consumption rates with increased sediment permeability. The lower O_2 consumption rates in the laboratory control cores relative to the *in situ* controls may be caused by the removal of the fine fraction, containing the majority of the organic matter, during the sieving procedure.

Utilisation and degradation of coral mucus in the laboratory experiments with highly permeable sediment was most likely dominated by O_2 respiration. This is supported by the calculated ratios of increased O_2 consumption/DIC production after the addition of coral mucus. We found values of 0.64 (coarse sand) and 0.55 (medium sand) for the 2 laboratory experiments, but only 0.48 for the field experiment. These values show an imbalance between O_2 consumption and DIC production in all experiments. The low value for the field experiment suggests a relatively large contribution of anaerobic processes, with SO_4^{2-} or NO_3^- as electron acceptors (Jørgensen 1977, Thamdrup & Canfield 1996) during utilisation and decomposition of coral mucus. Theoretically, the value between O_2 consumption and DIC production should be 1 (Kristensen 2000), because of biological or chemical re-oxidation of reduced inorganic compounds. However, the short duration of our chamber experiments did not allow for complete oxidation of all reduced compounds.

Wilkinson (1987) reviewed that approximately 20% of the organic matter in coral reefs are degraded anaerobically by sedimentary bacteria. Our SRR measurements hint to SO_4^{2-} reduction as an important process for the degradation of organic matter in permeable reef sediments. The SRR of <1200 nmol cm^{-3} d^{-1} in a core taken from one of the mucus chambers at the end of *in situ* Expt 2 are twice as high as in the control cores. In other experiments with natural sediments at this site in January 2002, SRR never exceeded values of 660 nmol cm^{-3} d^{-1} (U.W. unpubl. data).

Our finding that O_2 can only penetrate 2 to 5 mm deep in these sediments supports the hypothesis that anaerobic processes are important for the degradation of organic matter in carbonate sands. The measured O_2 penetration depths can be regarded as maximum values because of the 2-fold increase in stirring speeds in the chambers for O_2 measurements with planar optodes compared to the stirring speed used for the *in situ* and laboratory incubations. We can therefore state that the oxic surface layer of reef sands may be even thinner than the 1 cm estimated by Skyring (1985).

Rasheed et al. (2003) suggested that high permeability, porous grains, and the mineralogy of carbonate sands are important factors making these sands sites for efficient organic matter degradation. Our results support this hypothesis and show that carbonate sands are able to act as biocatalytical filters that effectively degrade trapped coral mucus. Despite the complex carbohydrate matrix of coral mucus, this material was metabolised rapidly.

Fate and importance of coral mucus

Our observations in the Great Barrier Reef showed that coral mucus is not only produced in response to aerial exposure, but is continuously exuded by submerged hard, soft and fire coral, visible as strings that are released from the coral. These strings are only clearly visible if they are contaminated with material like detritus or fine carbonate grains.

The residence time of coral mucus in the water column depends on its consistency (dissolved or particulate) and the degree of contamination. The attachment of material can increase the density of mucus, leading to sinking and deposition. The degree of contamination itself is dependent on the amount of particles in the water column and, thus, also on weather conditions influencing the resuspension of benthic material into the water of shallow reef environments.

At Heron Island we observed that under the influence of tidal currents, mucus is washed from the coral heads and reacts with (re-)suspended material leading to a deposition of particle-loaded mucus aggregates onto the lagoon sediment surface within a few hours of release. Especially during extreme low tides, this process takes place twice a day. Nevertheless, we could not find any mucus accumulations in calm areas of the reef lagoon, which also indicates that mucus is rapidly degraded after reaching the sediment. This is also demonstrated by our chamber experiments, and shows that the permeable lagoon sediments of atolls, fringing and platform reefs function as biocatalytical filters.

We conclude that coral mucus, a product from excess carbohydrate production by zooxanthellate photosynthesis, can act as a carrier for energy from the corals to the food chains of the reef (see also Wild et al. 2004). This mechanism is another example of the short-linked nutrient cycle between autotrophs and heterotrophs in coral reefs, which may contribute to the explanation for the high productivity of this ecosystem.

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