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Influence of coral mucus on nutrient fluxes in carbonate sands

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ABSTRACT: Mucus release by hard corals of the genus *Acropora* under submersed and naturally occurring air exposure was quantified at Heron Island/Great Barrier Reef. These measurements were conducted with beaker and *in situ* container incubation techniques. Mucus release rates for *A. millepora*, normalized to the coral surface area, were 10 ± 5 mg C and 1.3 ± 0.8 mg N m^{-2} h^{-1} for submersed corals, and 117 ± 79 mg C and 13 ± 8 mg N m^{-2} h^{-1} after exposure to air at low tide. This corresponds to increases by factors of 12 for C and 10 for N. The main monosaccharide components of freshly released *Acropora* mucus were arabinose and glucose, accounting for 14 to 63% and 13 to 41% of the carbohydrates. A protein content of 13 to 26 mg l^{-1} caused a low C:N ratio of 8 to 14. The chlorophyll content of 7 to 8 µg l^{-1} in the mucus compared to 0.6 ± 0.004 µg l^{-1} in the surrounding seawater revealed mucus contamination with zooxanthellae. A low pH value of 7.7 compared to 8.3 in the surrounding seawater indicates the existence of acidic components in fresh coral mucus. Concentrations of most measured inorganic nutrients were highly increased in coral mucus, reaching values of 3 to 4 µM for silicate, 19 to 22 µM for phosphate and 20 to 50 µM for ammonium concentration. Phosphate concentrations were 130-fold higher in coral mucus compared to the surrounding seawater, underlining the role of coral mucus as a carrier of nutrients. Addition of coral mucus to stirred benthic chambers resulted in a shift of phosphate, ammonium and nitrate/nitrite fluxes towards the sediments, confirming the transport of nutrients via coral mucus into permeable reef sands.

KEY WORDS: Coral reef · Mucus release · Quantification experiments · Compositional analyses · Nutrient fluxes · Carbonate sands

INTRODUCTION

Coral mucus is continuously released by many species of corals in order to clean their surfaces from sediments (Hubbard & Pocock 1972) and fouling organisms (Ducklow & Mitchell 1979a). Mucus is released into the surrounding water at a magnitude such that it can be a dominant component of suspended matter in the waters above coral reefs (Johannes 1967, Marshall 1968).

Johannes (1967), Coles & Strathman (1973), Benson & Muscatine (1974) and Ducklow & Mitchell (1979a,b) already suggested that coral mucus may provide nutrition or energy to a diverse community of consumers, and also could form the basis of a microbial food chain. However, Krupp (1984), Meikle et al. (1988) and Coffroth (1990) have argued that coral mucus is a material of low nutritional value for reef organisms. Coffroth (1990) concluded, in her pilot study on *Porites* mucus sheets, that their release is not an important nutrient source in coral reefs. In contrast to the *Porites* mucus sheets, it was observed that liquid mucus is continuously produced by many species of hard and soft corals. Liquid mucus may, therefore, quantitatively play a much more important role in coral reef environments than mucus sheets. This is confirmed by low ash contents of 22% in liquid mucus compared to 68% in mucus sheets (Coffroth 1990).

Previously published studies highlighted the importance of liquid coral mucus for energy and nutrient

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supply to lower trophic levels of the food chain in reef environments (Wild et al. 2004a,b). To better understand the significance of this phenomenon, and to be able to calculate fluxes of carbon, nitrogen and phosphorus induced by coral mucus, it is essential to quantify the production and release of coral mucus as well as to identify its main components.

Quantitative analyses

Only a few studies have addressed quantification of coral mucus release in the past. Rublee et al. (1980) and Coffroth (1990) measured mucus production by poritid corals and the soft coral *Briareum asbestinum*, respectively, because of their regular production of easily collectable mucus sheets. Different methods for the quantification of liquid coral mucus release have been used: (1) Johannes (1967) roughly calculated coral mucus release by estimation of aggregate export, mean water depth, current speed and the area of the reef community; (2) Richman et al. (1975) wrapped coral heads *in situ* with plastic bags and measured the particulate matter in the enclosed water after preset time intervals; and (3) Herndl & Velimirov (1986) incubated single colonies of *Cladocora cespitosa* from the Mediterranean in glass beakers in the laboratory and subsequently quantified the released particulate matter by filtering the incubation water.

We observed the production of large amounts of coral mucus by many species of corals in response to aerial exposure during low tide at Heron Island, Great Barrier Reef, Australia. Air exposure events have been observed in other reef environments in Australia as well as in New Caledonia, Madagascar, the Red Sea and Hawaii (Daumas et al. 1982, Krupp 1984, Romaine et al. 1997). Exposure of corals to air is, thus, not restricted to the Great Barrier Reef. Corals increase their production of mucus as a general response to stress factors, such as high temperature, salinity change, pollution (Loya & Rinkevich 1980, Kato 1987), high water turbidity (Rublee et al. 1980, Telesnicki & Goldberg 1995) and heavy sedimentation loads (Hubbard & Pocock 1972, Schuhmacher 1977).

This study addresses mucus production under submersed and air exposure conditions, and provides information on the composition of the mucus and its decomposition in permeable reef lagoon sediments.

Qualitative analyses

Several studies, published between 1973 and 1991, have addressed the chemical composition of mucus collected from different coral species (Cnidaria, Anthozoa).

Mucus has been characterized as a primarily carbohydrate complex (Coffroth 1990). Richards et al. (1983) found a proteoglycan consisting of D-arabinose, N-acetyl-2-amino-2-deoxy-D-glucose and D-mannose as the main component of the mucus released by the staghorn coral *Acropora formosa*. Other monosaccharides were also identified as major components in mucus of *Acropora* spp. by Ducklow & Mitchell (1979b).

Benson & Muscatine (1974) and Crossland et al. (1980) detected energy-rich lipid compounds such as waxester (cetyl palmitate), triglycerides and free fatty acids in coral mucus. Means & Sigleo (1986) found palamitic acid and palmitoleic acid to be the main components of colloidal coral mucus from Jamaica. More than a third of coral mucus dry mass can be composed of lipids as reported by Daumas et al. (1982), but in the mucus of some corals, no lipids could be detected (Ducklow & Mitchell 1979b).

Proteins or peptides in coral mucus were found by Krupp (1985) and Vacelet & Thomassin (1991). Daumas et al. (1982) detected abundant dicarboxylic amino acids in the protein fraction of coral mucus, and also found the non-protein fraction accounting for 60 to 70% of total N in mucus of New Caledonian reef corals. This points towards a possible role of dissolved inorganic nitrogen (DIN) of coral mucus in reef nutrient cycles, an aspect not studied in detail before.

Carbohydrates as well as lipids and proteins in coral mucus were found in very different quantities. Coffroth (1990) reviewed the literature and summarized a widely scattered carbohydrate content of 3 to 67% Ash Free Dry Weight (AFDW), a protein content of 2 to 73% AFDW, and lipid contents of 0 to 93% AFDW. These large ranges can be attributed to (1) different definitions of coral mucus, (2) different collection techniques, and (3) different purification methods for coral mucus samples. However, it is generally accepted that coral mucus is enriched in N and contains more organic matter than other particulate material in the surrounding water (Coles & Strathman 1973, Coffroth 1984). In contrast, most other detritus in reef environments was found to be poor in nutrients (Hickel 1974).

Despite the potential role of liquid mucus as a carrier of energy and nutrients, only a few studies have addressed this subject. Hoppe et al. (1988) suggested that coral mucus, with its high content of proteinaceous organic matter, is a major source of nutrients for bacteria in the water column over the reef.

Here, we present results from a study conducted at the Australian Great Barrier Reef focusing on the quantitative and qualitative analyses of coral mucus release, and its influence on nutrient fluxes in the carbonate sands of the reef lagoon. We hypothesize that liquid coral mucus has a function as a carrier of nutrients to microbial communities in the sediment. To this

end, nutrient fluxes into and out of the carbonate sediment with and without the addition of coral mucus were measured using stirred benthic chambers (Huettel & Gust 1992).

MATERIALS AND METHODS

Study site

Coral mucus sampling and all experiments took place during February 2001, November 2001 and January 2002 at Heron Island, Australia (23° 27′ S, 151° 55′ E). The island lies on the Tropic of Capricorn, at the southern end of the Great Barrier Reef, 70 km off the coast of Gladstone (Fig. 1), and is part of an elongated platform reef with a pseudo-lagoon. The reef belt consists of many different living coral species, which are partly exposed to air at most low tides, and all spring low tides.

Field experiments were conducted in the Heron Island lagoon at Shark Bay, a shallow water site (at ca. 0.2 to 2.5 m water depth depending on the tide), which is located at the south eastern end of the island (Fig. 1). The sediments used for laboratory experiments were also collected in Shark Bay. All laboratory experiments were performed using the facilities of the Heron Island Research Station.

Quantitative studies

***In situ* mucus release quantification.** These experiments were conducted to quantify mucus release during and after naturally occurring exposure of corals to air at low tide on the reef flat. Three independent experiments were conducted over 3 d with very similar weather conditions (water temperature: 25 to 28°C, salinity: 35 to 36 PSU, sunny, few clouds, weak wind velocities). For each of these experiments, 3 similar-sized colonies of *Acropora millepora* (average size L × W × H: 16 × 12 × 9 cm) were collected from the reef flat and transferred into three 10 l containers (lidless cylindrical polypropylene buckets) without exposing the coral colonies to air. These corals were individual colonies that grew on the reef sediments anchored with their lowest branches in the carbonate sands. Corals were, thus, not broken off a larger coral colony, and transferred to their original location on the reef flat after the experiment. Each container had a circular opening (∅ 5 cm) in the sidewall approximately 2 cm above the bottom. A rubber stopper (hereafter referred to as the 'large stopper') sealed this opening. The stopper itself had a gauze-covered hole (2 cm, 125 µm mesh gauze) that was closed by a second smaller stopper (hereafter referred to as the 'small stopper').

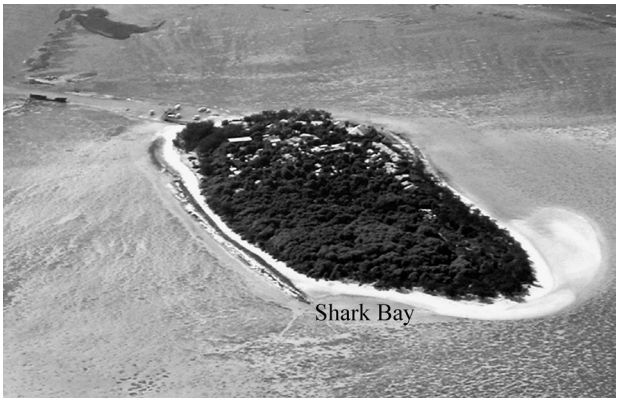

Fig. 1. Location of the study site Heron Island in the Capricorn Bunker Group, Central Section, Great Barrier Reef Marine Park

The containers with the corals and 3 other control containers without corals were stabilized with 3 kg weights and placed either directly on the reef flat or on the beach if wind and wave conditions did not allow a stable positioning of the containers on the reef flat. To simulate tidal water level changes, the large stopper was removed during ebb tide resulting in a slow decrease of the water level in the container similar to that in the reef flat. The corals then were left exposed to air for 15 to 105 min, equalling the exposure duration of the ambient corals. When the water started to rise again, the large stoppers were mounted into the openings of the containers, permitting local water to enter the containers through the gauze-covered hole in the stoppers, filling up the containers at the rate of the rising tide. When the corals in the containers were fully submerged again, the gauze-covered openings were sealed with the small stoppers and the water level in the containers was measured for later calculation of the enclosed water volume. Then, a submergible electrical pump (12V DC) was run for exactly 3 min in each container to create a water current similar in strength to ambient currents. This water current caused the detachment of mucus from the corals. After this procedure, the corals were removed from the containers. The spatial dimensions of the colony, the number of branches and the length of 10 randomly-chosen branches were noted, and then the corals were re-anchored in the reef flat. The water level in the containers was measured again to assess the volume of the coral colony. To homogenize the water with the mucus, it was stirred again for exactly 3 min using the submergible pump before triplicate aliquots (50 to 150 ml) were sampled and filtered onto pre-combusted GF/F filters (Whatman) for carbon and nitrogen measurements. The filters were dried for 24 h at 40°C, wrapped in pre-combusted aluminium foil and stored at –20°C until further analysis.

Laboratory mucus release quantification. In order to quantify mucus production of corals under submerged conditions, a method similar to that described by Herndl & Velimirov (1986) was applied. Two colonies (*Acropora millepora* and *A. aspera*) were collected from the Heron Island reef flat. Each colony was split into 8 similar-sized fragments. These coral fragments were kept in a 60 l aquarium (seawater exchange rate: 3 l min^{-1}) 2 wk prior to experimentation to permit healing and acclimatization. The colony surfaces were cleaned of organic and inorganic material by a gentle jet of seawater. The corals were then transferred without exposure to air into seawater-filled glass beakers (500 to 2000 ml) and incubated for 4 to 6 h (experiments with *A. millepora* and *A. aspera*, respectively) at *in situ* temperature in a water bath outside, which was protected by a small roof against rain and direct sun exposure. Three additional beakers with unfiltered seawater were left as controls without coral. The water temperature (26.6 to 27.7°C) was kept at *in situ* levels by keeping the beakers in a flow-through tank flushed with local seawater. The corals in the beakers experienced slightly decreased light intensities compared to the field due to shading by the roof. At the end of the incubation time, corals were removed from the glass beakers, and the volume of the remaining water noted and then thoroughly mixed. Homogenized water samples from each of the 11 beakers were taken for carbon and nitrogen determination as described above.

Quantification of particulate C and N. The GF/F filters were incubated for 12 h in an atmosphere of fuming HCl in order to remove calcium carbonate particles from the filters. Carbon and nitrogen values on these filters were measured using an elemental analyser (Fisons AT1500) with a sulphanilamide (HEKAtech) standard.

Coral surface determination. All measured parameters were related to the surface area of the respective scleractinian corals. For coral surface determination, we used all 16 fragments from the beaker experiments and several *Acropora* skeletons of similar size collected from the reef flat. The surface area of the fragments was determined using liquid paraffin wax (melting point 51°C, adjusted temperature 55°C) as surfactant. The coral fragments were cleaned, dried and then submersed for 2 s into the wax to fill all pores. The wax cover was allowed to solidify for 5 min before weighing and again submersing the coral into the wax. After a second weighing, the weight increase caused by the second wax coating was calculated. This weight increase was correlated to the surface area by using wax coating weights of chalk pieces with known surface area as reference values.

For the large coral colonies used during the *in situ* quantification experiments, we did not apply this method for reef conservation reasons. Instead, we calculated the surface area of the large colonies by relating their branch length to the surface area ratio of the small fragments by using the number of branches times the average branch length of the large colonies. The surface areas of the large colonies used in the *in situ* experiments were, thus, calculated from the number and mean length of their branches.

Qualitative studies

Coral mucus collection. Clusters of branching corals of the genus *Acropora* form scattered patches on the sediment on the reef flat of Heron Island. During low tide, some of these corals are naturally exposed to air. These individual colonies can be removed from and replanted in the sediment without breaking or harming the coral. Coral mucus was collected *in situ* by exposing such intact colonies of *Acropora* from the reef flat (<2 m water depth) to air. These colonies immediately began to produce and release large amounts of mucus. The corals were then turned upside-down and the dripping mucus was collected in a clean container for 2 min after discarding the initial 30 s of dripping. Each individual colony (maximum diameter 30 cm) released between 0.1 and 0.3 l of liquid mucus. The mucus of between 5 and 10 colonies was collected during each sampling. The collected mucus did not show any signs of macroscopical contamination. The mucus was homogenized with a glass tissue grinder, and all further characterizations were performed with this emulsion.

Analysis of coral mucus composition. *Carbohydrate composition.* Coral mucus for carbohydrate composition analyses was purified after the method introduced by Ducklow & Mitchell (1979b). Mucus was desalted via dialysis through a membrane (10 000 Da limit) in triplicate aliquots of 20 to 30 ml (3 × 30 min against distilled water). Desalted mucus solutions were combined, lyophilized and sent to the Complex Carbohydrate Research Centre (CCRC) at the University of Georgia, USA. There, the sample extracts were hydrolyzed using freshly prepared 1 M methanolic HCl for 16 h at 80°C. The released sugars were derivatized with Tri-Sil and the samples then were measured on a GC using a Supelco column. Myo-inositol (10 µg) was added as an internal standard.

For the following analyses, freshly collected, non-dialyzed, but homogenized coral mucus was used. As controls, all listed parameters were also measured for ambient seawater samples collected parallel to the mucus.

Dry mass. Triplicate coral mucus aliquots of 10 to 30 ml were filtered on pre-weighed polycarbonate filters (0.4 µm, Millipore) and dried at 60°C for 24 h prior to weight determination.

Protein. Coomassie Brilliant Blue was added to triplicate aliquots of coral mucus. Protein contents were measured with bovine gamma globulin (both purchased from Biorad Laboratories) as standard according to the method proposed by Bradford (1976).

Carbon and nitrogen. Samples for particulate organic carbon (POC) and nitrogen (PON) were prepared by filtering triplicate aliquots of 5 to 10 ml homogenized mucus on precombusted GF/F filters (Whatman). The filters were exposed to HCl fumes for 12 h to remove carbonate particles, then dried for 24 h at 40°C and finally wrapped in precombusted aluminium foil. Carbon and nitrogen contents of the filters were measured as described above.

Chlorophyll a and phaeophytin. Coral mucus in triplicates was filtered and dried as described above for the C and N measurements (except acid treatment). Chlorophyll and phaeophytin concentrations were determined fluorometrically using standard procedures described in Strickland & Parsons (1972).

Inorganic nutrients. Mucus was sampled in triplicate aliquots of 15 ml and preserved with 0.1 ml of saturated $HgCl_2$ for later inorganic nutrient analysis according to Strickland & Parson (1972).

Chamber incubations. The effect of mucus on sediment-water nutrient fluxes was investigated in 1 *in situ* and 2 laboratory chamber experiments. The *in situ* chamber incubation was conducted in Shark Bay on the natural sediments, while sieved sediment fractions were incubated in the laboratory experiments. The *in situ* incubation started 2 h after low tide and ended 5 h later; the laboratory incubations ran for 6 h. During all incubations, 15 ml samples were taken at the start and end of the experiments from the water of all chambers (n = 6 each) and preserved with 0.1 ml of saturated $HgCl_2$ for later analyses of the inorganic nutrients: NO_3^-, NO_2^-, NH_4^+, PO_4^{2-}, $Si(OH)_4$ according to Strickland & Parson (1972). Fluxes of nutrients were calculated from nutrient concentration changes in the chambers over experimental time.

Chamber design: Cylindrical chambers of transparent acrylic with a height of 30 cm and an inner diameter of 19 cm were used (Fig. 2). A plastic lid, fixed by 4 stainless steel clips, covered each chamber. The lid contained a sampling port with syringe holder for water samples and another port to replace the sampled water (Fig. 2). In each chamber, the water was agitated by a 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.

In situ chamber incubations: The chambers were inserted gently into the sediment to a depth of about 10 cm and, thus, included a water column of approximately 22 cm height. The lids then were fitted to the chambers and fixed by the clips. Finally, the chambers were secured with weight belts to prevent movement caused by wind and waves.

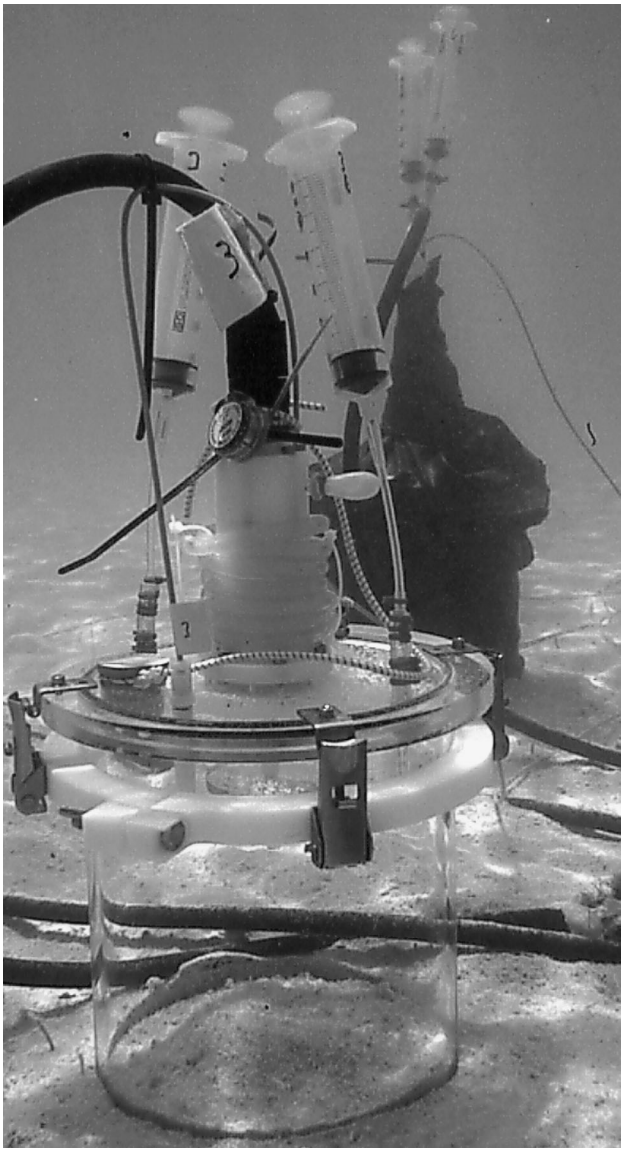

Fig. 2. *In situ* deployment of stirred benthic chambers in Shark Bay. Coral mucus was injected with a syringe port visible in the foreground. Light was excluded from all chambers used for the experiments presented in this study by wrapping them with PVC foil (background)

For the *in situ* experiment, 6 of these benthic chambers were deployed. At the start of the experiment, 280 ml of *Acropora* mucus (sampled the same day and kept at 4°C until the start of the experiment) was added to 3 of the chambers. The mucus-containing chambers and the control chambers were sealed from light by wrapping them with black PVC foil. Recording of light intensity and temperature underneath the PVC foil and in the surrounding seawater at 2 min intervals, using Onset HOBO and

Tidbit dataloggers, revealed that no light intrusion and heating occurred in the chambers. At the end of the experiment, the volume of water in the chambers was determined by measuring the water height with a ruler at 4 different positions in the chamber.

Laboratory chamber incubations: Two laboratory chamber incubations were conducted using coral sands of different grain sizes, to assess degradation of coral mucus in sediments of different permeability. Sediment was collected from Shark Bay (6 February 2001) and separated with a sieve (500 µm) into a coarse and a medium sand fraction (grain sizes 829 and 536 µm median, respectively). The lab experiments were conducted in a very similar manner to the *in situ* experiment. Six benthic chambers, identical to those described above, were placed into a big trough flushed by natural seawater, which kept the temperature of the incubation at *in situ* temperature (26 to 28°C). Approximately 4.5 dm^3 of either the coarse (7 February) or the medium (8 February) sediment fraction was filled in the chambers. The overlying unfiltered seawater had a volume of 4 l. After closing the lids, volumes of 200 ml of *Acropora* mucus (sampled the same day or the day before and kept at 4°C) were added to 3 of the chambers. During the 6 h incubations, chambers were kept in the dark.

RESULTS

Quantitative analyses

All studied corals of the genus *Acropora* released liquid mucus, which for the first time could be quantified with the container incubation technique under *in situ* conditions and naturally-occurring air exposure. The results of the *in situ* experiments and laboratory incubation experiments are summarized in Table 1. Mucus production under submersed conditions ranged from 7 to 10 mg C m^{-2} coral surface h^{-1} and 0.8 to 1.3 mg N m^{-2} coral surface h^{-1}. Under conditions of natural air exposure, corals started to produce significantly more mucus (non-parametric 1-sided *U*-test after Wilcoxon, Mann and Whitney, $\alpha = 0.001$), enhancing the release rate by 1 order of magnitude.

Table 1. *Acropora* spp. Release of particulate organic C and N as coral mucus, quantified with container (natural air exposure) and beaker (submersed conditions) incubations and related to the coral surface. Values are means of replicate measurements ± SD

Species	Mucus C release (mg m^{-2} h^{-1})	Mucus N release (mg m^{-2} h^{-1})	N	Method
A. millepora	117 ± 79	13 ± 8	8	Container
A. millepora	10 ± 5	1.3 ± 0.8	5	Beaker
A. aspera	7 ± 3	0.8 ± 0.4	8	Beaker

Qualitative analyses

All *Acropora* samples contained arabinose, glucose, mannose, galactose and N-acetyl glucosamine (GlcNAc) as the main carbohydrate components (Table 2). In *A. millepora* and *A. aspera*, arabinose accounted for more than 50% of all carbohydrates. Linkage analyses showed the occurrence of 3,4-arabinose and 2,5-arabinose, and 4-linked glucose. Galactose was also detected in all samples, but in low quantities of 3 to 6 mole percent. The monosaccharides rhamnose, fucose and xylose were only detected in some of the samples, and in quantities of less than 10 mole percent. In addition, the fatty acid β-OHC 6:0 was observed in all samples. The carbon content of *Acropora* mucus varied between 9 and 52 mg l^{-1} (Table 3), depending on the dilution of the mucus with seawater during the sampling procedure, but was at least 3 times higher than in the surrounding seawater. Particulate organic nitrogen concentrations in *Acropora* mucus ranged from 0.7 to 5 mg l^{-1}, and were 2- to 17-fold higher than in the ambient seawater. A non-parametric 2-sided *U*-test showed significantly higher values for POC and PON ($\alpha = 0.002$) in coral mucus compared to the surrounding water.

There were no significant differences between the C:N ratios of coral mucus and those of POM in the surrounding seawater (2-sided *U*-test).

Proteins were not detectable in seawater samples with our measuring method, but were found in coral mucus in quantities of 17 to 26 mg l^{-1}. The chlorophyll *a* content of coral mucus was at least 12 times higher than in the seawater (Table 3).

Inorganic nutrients in coral mucus

All measured inorganic nutrients showed, on average, higher concentrations per volume in coral mucus compared to the ambient seawater (Table 4). Concentrations of silicate, phosphate and ammonium were significantly higher (2-sided *U*-test, $\alpha = 0.1$) in coral mucus compared to the surrounding seawater, whereas nitrate and nitrite concentrations were not significantly increased (2-sided *U*-test). Silicate showed 3-fold higher values in coral mucus relative to the surrounding seawater. Coral mucus was also rich in ammonium, but concentrations showed large variations. Ammonium could only be detected in 1 of 4 seawater controls, and here the concentration was 20-fold lower than the average mucus ammonium concentration. We also measured remarkably high concentrations of

Table 2. *Acropora* spp. Carbohydrate composition (in mole percentage of all detected carbohydrates) of mucus from hard corals of the genus *Acropora* (nd = not detected). Carbohydrate composition analyses were carried out by the Center of Complex Carbohydrate Research of the University of Georgia in Athens, USA

Carbohydrate composition	*A. aspera*	*A. digitera*	cf. *A. formosa*	*A. millepora*	*A. nobilis*	*A. pulchra*
Arabinose (Ara)	50.8	13.9	36.7	63.2	24.6	25.4
Rhamnose (Rha)	nd	2.8	nd	nd	8.0	nd
Fucose (Fuc)	5.5	5.0	5.6	nd	6.6	7.8
Xylose (Xyl)	nd	4.0	nd	nd	4.7	9.8
Mannose (Man)	10.6	12.0	12.8	11.1	13.4	11.1
Galactose (Gal)	6.2	5.3	5.4	5.3	5.9	2.9
Glucose (Glc)	13.2	40.5	22.2	12.5	22.1	32.2
N-acetyl glucosamine (GlcNAc)	13.7	16.4	17.2	7.9	10.6	10.7

Table 3. *Acropora* spp. Carbon, nitrogen, protein and chlorophyll contents of coral mucus in comparison to the surrounding seawater. Values are means of triplicate measurements ± SD (nd = not detected, nm = not measured). The term mixed *Acropora* represents mucus collected from the 3 species *A. millepora*, *A. aspera* and *A. nobilis*

Sampling date (day.month.year)	Sample origin	C content (mg l^{-1})	N content (mg l^{-1})	C:N ratio	Protein content (mg l^{-1})	Chl *a* conc. (µg l^{-1})
14.01.2002	*A. millepora*	30.9 ± 0.4	2.2 ± 0.1	13.8	22.9 ± 0.4	
03.02.2001	Mixed *Acropora*	36.8 ± 7.2	3.8 ± 0.1	9.6	13.0 ± 0.3	7.3 ± 0.4
06.02.2001	Mixed *Acropora*	51.6 ± 7.7	5.1 ± 0.3	10.1	26.2 ± 0.3	7.7 ± 0.7
11.02.2001	Mixed *Acropora*	nm	nm	nm	17.9 ± 1.2	nm
12.02.2001	Mixed *Acropora*	nm	nm	nm	17.0 ± 0.6	nm
11.01.2002	Mixed *Acropora*	24.7 ± 0.8	3.1 ± 0.4	7.9	21.1 ± 0.4	nm
22.01.2002	Mixed *Acropora*	32.3 ± 2.6	4.0 ± 0.2	8.2	20.8 ± 0.1	nm
25.01.2002	Mixed *Acropora*	10.8 ± 0.8	1.3 ± 0.1	8.3	nm	nm
27.01.2002	Mixed *Acropora*	8.6 ± 0.4	0.67 ± 0.04	12.8	nm	nm
29.01.2002	Mixed *Acropora*	20.3	1.8	11.5	nm	nm
06.02.2001	SW control	nm	nm	nm	nd	0.6 ± 0.004
11.01.2002	SW control	2.7 ± 0.1	0.3 ± 0.1	9.0	nd	nm
14.01.2002	SW control	1.8 ± 0.1	0.2 ± 0.1	11.7	nm	nm
22.01.2002	SW control	0.3 ± 0.1	0.04 ± 0.01	7.8	nd	nm
25.01.2002	SW control	0.43 ± 0.03	0.03 ± 0.01	13.2	nd	nm
27.01.2002	SW control	0.5 ± 0.1	0.03 ± 0.004	17.6	nd	nm

Table 4. *Acropora* spp. Concentration of inorganic nutrients and pH values in *Acropora* mucus and the surrounding seawater. Values are means of triplicate measurements ± SD (nd = not detected, nm = not measured)

	Silicate (µM)	Phosphate (µM)	Ammonium (µM)	Nitrate + nitrite (µM)	pH
Mucus 06.02.2001	4.06 ± 0.11	21.65 ± 0.58	19.73 ± 0.72	0.95 ± 0.26	7.65 ± 0.02
Mucus 08.02.2001	3.92 ± 0.18	20.96 ± 4.04	49.96 ± 1.04	0.61 ± 0.05	7.73 ± 0.02
Mucus 22.01.2002	3.11 ± 0.04	19.29 ± 0.24	23.04 ± 1.58	1.51 ± 0.06	nm
Seawater 04.02.2001	1.97 ± 0.09	0.15 ± 0.06	1.53 ± 0.30	0.17 ± 0.11	8.29 ± 0.01
Seawater 13.01.2002	1.11 ± 0.32	0.23 ± 0.40	nd	1.15 ± 0.49	nm
Seawater 22.01.2002	1.20 ± 0.10	0.05 ± 0.16	nd	1.00 ± 0.03	nm
Seawater 27.01.2002	0.84 ± 0.09	0.19 ± 0.69	nd	0.78 ± 0.11	nm

phosphate in coral mucus (20.6 ± 1.2 µM, mean ± SD, n = 3), exceeding seawater concentrations (0.16 ± 0.08 µM), on average, by a factor of 133. The pH value of liquid coral mucus was significantly lower by 0.56 to 0.64 (2-sided *U*-test, $\alpha < 0.05$) than that of the seawater (Table 4).

Nutrient fluxes in chamber experiments with mucus addition

In the control chambers of the *in situ* experiment, a low flux of phosphate and nitrate + nitrite into the sediment was recorded (Fig. 3). The addition of coral mucus to 3 of

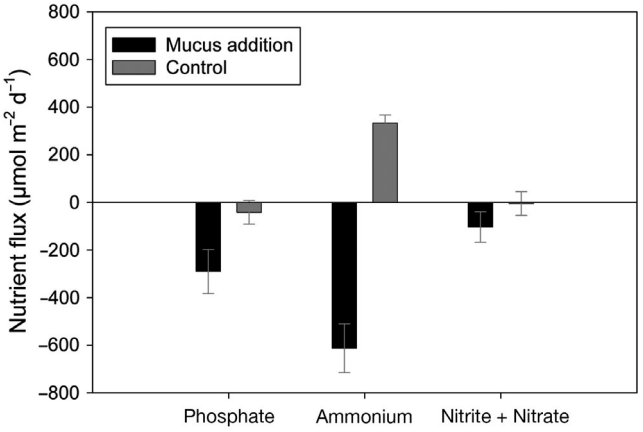

Fig. 3. *In situ* experiment with natural sediment: net fluxes of inorganic nutrients between water column and reef sands with and without the addition of coral mucus. Positive values are effluxes out of the sediment and negative values are influxes into the sediment. Error bars indicate the SD of 3 replicate measurements

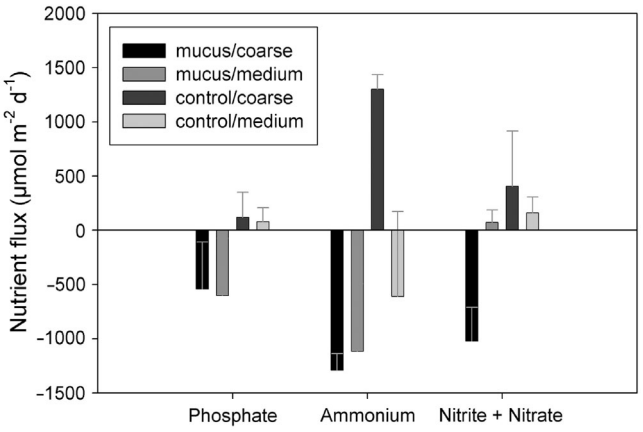

Fig. 4. Laboratory experiments with sieved natural sediment (median grain sizes were 538 µm for the medium and 838 µm for the coarse sand fraction): net fluxes of inorganic nutrients between water column and reef sands with and without the addition of coral mucus. Positive values are effluxes out of the sediment and negative values are influxes into the sediment. Error bars indicate the SD of 3 replicate measurements

the 6 chambers increased these fluxes by factors of 7 and 20 for phosphate and nitrate + nitrite, respectively. Mucus reversed the flux of ammonium from an ammonium release of 333 ± 34 µmol m^{-2} d^{-1} in the control chambers to an ammonium uptake of 613 ± 102 µmol m^{-2} d^{-1} in the mucus chambers (Fig. 3). A 2-sided *U*-test showed that fluxes of phosphate and ammonium were significantly different ($\alpha = 0.1$) with the addition of coral mucus relative to the controls.

The laboratory chamber experiments with sieved sediments from Shark Bay showed effluxes of all measured inorganic nutrients from both sand fractions in the control chambers, except of ammonium influxes in the chambers filled with medium sands (Fig. 4). In the chambers filled with coarse sands, with the addition of coral mucus, these effluxes in the control chambers were always reversed and changed to fluxes into the sediment. A 2-sided *U*-test showed that fluxes of phosphate, ammonium and nitrate-nitrite were significantly ($\alpha = 0.1$) different in the chambers with mucus addition compared to the control chambers. Only the fluxes of silicate were not significantly different.

A similar, but weaker effect could be observed in the chambers with the medium sand fraction. Addition of coral mucus reduced the efflux of nitrate + nitrite and reversed the flux of phosphate significantly ($\alpha = 0.1$, 2-sided *U*-test) to an influx. However, fluxes of silicate, ammonium and nitrate + nitrite were not significantly different between mucus and control chamber filled with medium sand (2-sided *U*-test), but the mean influx of ammonium was increased by approximately a factor of 2. Thus, addition of coral mucus in general moved the direction of nutrient fluxes towards the sediments. This effect was more pronounced in the experiments with the coarse sand fraction.

DISCUSSION

Quantitative release of coral mucus

It was known from observations that corals release large amounts of mucus during tide-related exposure to air (Krupp 1984). Our experiments quantify this release and highlight the significance of this phenomenon, which causes a strong increase of the normal mucus production rates by *Acropora millepora* from approximately 0.3 to 3.8 l mucus m^{-2} coral surface h^{-1}. This is equivalent to a mucus layer of 0.3 to 3.8 mm thickness over the coral surface released per hour. These volumes were calculated using an average C content of 30.9 mg l^{-1} as derived from Table 3, and the mucus production rates presented in Table 1. During a day with air exposure of the coral on the Heron Island reef flat (duration ca. 2 h d^{-1} for about 6 d per month), this would result in a daily mucus release of 14.2 l m^{-2} compared to 7.2 l m^{-2} coral surface during a normal day with totally submersed corals.

The quantification of coral mucus release by measurements of particulate organic C and N contents turned out to be a more sensitive method than the quantification of mucus via dry mass determination. A summary of mucus release studies is given in Table 5. The mucus production rates under submersed conditions, as quantified in our study, are of the same order of magnitude as reported by other researchers. We, for the first time, could quantify mucus production during

Table 5. Summary of coral mucus release (as C, N and dry mass) studies at different reef locations. Values are means of triplicate measurements ± SD

Study site	Species	Mucus C release (mg^{-2} coral surface h^{-1})	Mucus N release (mg^{-2} coral surface h^{-1})	Mucus release (mg m^{-2} reef area d^{-1})	Mucus C release (mg C m^{-2} reef area d^{-1})	N	Method	Reference
Heron Island	*Acropora millepora*	117 ± 79	13 ± 8			8	Container	This study
Heron Island	*Acropora millepora*	10 ± 5	1.3 ± 0.8			5	Beaker	This study
Heron Island	*Acropora aspera*	7 ± 3	0.8 ± 0.4			8	Beaker	This study
Eilat	*Acropora variabilis*			51			Plastic bags	Richman et al. (1975)
Eilat	*Acropora hemiprichi*						Plastic bags	Richman et al. (1975)
Eilat	*Acropora variabilis*	1.4–4.2					Perspex chamber	Crossland (1987)
Eilat	*Stylophora pistillata*	2.7–4.0					Perspex chamber	Crossland (1987)
Jamaica	*Acropora palmata*	18			20	3	Stirred chamber	Means & Sigleo (1986)
Bight of Piran	*Cladocora cespitosa*	6		320	32	12	Beaker	Herndl & Velimirov (1986)
Eniwetok	Reef corals			480				Johannes (1967)

natural occurring air exposure and prove that this production increases by 1 order of magnitude relative to the normal submerged condition. Coffroth (1990) found mucus sheet production rates of 0.17 mg C and 0.034 mg N m^{-2} h^{-1}, which were 1 order of magnitude less than the range of data for liquid mucus derived from the studies presented in Table 5. This suggests that liquid mucus has a more important function for energy and nutrient cycles than mucus sheets.

Crossland (1987) discovered that more mucus was released by corals from 5 compared to 23 m water depth, and also discovered that the scleractinian corals *Acropora variabilis* and *Stylophora pistillata* produce only 30% of total mucus during the night. The carbohydrate components of mucus released by hermatypic corals, therefore, seem to originate to a large extent from zooxanthellate photosynthesis via the transfer of metabolites from the endosymbionts to the coral. Quantitatively, up to 50% of the C fixed by the zooxanthellae can be released as coral mucus (Crossland et al. 1980, Davies 1984).

Richman et al. (1975) detected that mucus production depends on coral morphology, with a greater production by massive species than by branching species, which was attributed to higher loads of material that accumulate on corals with large horizontal structures. Kato (1987) reported that exposure to air, heavy sedimentation and high temperatures lead to increased mucus production. Liquid mucus production, thus, depends on different factors, of which the degree of air exposure, daytime, amount of sediment load, temperature and coral morphology could be identified. Mucus sheet production, on the other hand, seems to be independent of the environmental parameters salinity, turbidity and sedimentation (Coffroth 1983, 1991).

Qualitative components of coral mucus

The relatively large volumes of particulate carbon released in the form of mucus to the reef ecosystem highlight the function of coral mucus as an energy carrier. This carrier function was studied in detail in Wild et al. (2004b). A C:N ratio in coral mucus similar to particulate matter in the surrounding water indicates that either the suspended particulate matter was largely composed of coral mucus or that N components in coral mucus increased parallel to the C components in coral mucus, which may also be reflected by the high protein content of coral mucus. Our high concentrations of chlorophyll in mucus are in agreement with Coffroth (1990), who also detected higher concentrations of chlorophyll in coral mucus than in the surrounding seawater. Chlorophyll in coral mucus can indicate the presence of zooxanthellae or attached algae. This was

confirmed by microscopic studies presented in Wild et al. (2004a), who even found cells of algae (diatoms and dinoflagellates) in freshly released coral mucus. Free-living active zooxanthellae in the coral mucus layer have also been found by Paul et al. (1986).

Inorganic nutrients in coral mucus

The relatively high silicate concentrations in coral mucus probably originate from diatoms and radiolarians attached to the sticky mucus matrix. Diatoms and radiolarians have been microscopically detected on most coral mucus samples (Wild et al. 2004a).

Ammonium is a typical excretion product of many marine invertebrates including corals, but usually ammonium in a zooxanthellae/coral symbiosis is not released, because of an intense use of the released ammonium by the endosymbionts (e.g. Grover et al. 2002). Ammonium could also originate from dissimilatory metabolism of an active microbial community inhabiting and degrading the mucus-rich coral surface microlayer extending a few micrometres from the coral surface (Paul et al. 1986). In addition, Nozais et al. (1997) suggested a possible function of invertebrate mucus as a trap of nutrients; however, higher concentrations of ammonium, nitrate and phosphate compared to the surrounding water were also found by Shanks & Trent (1979) in marine snow aggregates, indicating a possible role of mucus aggregates as adsorption sites for nutrients.

The low pH values of coral mucus may be the result of the chemical composition, e.g. the existence of acidic components in coral mucus. Richards et al. (1983) and Meikle et al. (1987, 1988) suggested that coral mucus consists of a glycoprotein chain with sulfated oligosaccharide side chains probably occurring as acid sulfate esters. Krupp (1985) found that the main component of coral mucus is very likely a sulfated acid polysaccharide strongly associated with a protein or peptide. Another possibility for the comparatively low pH values in coral mucus may be intensive degradation processes as indicated by high bacterial numbers and high O_2 consumption rates measured in the mucus (Wild et al. 2004b). The associated production of CO_2 can lower the pH value. However, repetitive measurements in very fresh mucus (within 10 min after release) collected from corals kept in an aquarium resulted in a pH value of 7.8 ± 0.03 (mean ± SD, n = 6; data not shown). These values are very similar to the values measured in coral mucus collected from Heron Island, and indicate that the chemical composition rather than the intense microbial metabolism is responsible for the low pH value. However, it is also possible that ionic properties of coral mucus had an effect on the measurement of pH.

Coral mucus as a carrier of nutrients?

Crossland (1987) and Coffroth (1990) suggested that corals release large amounts of nutrients as POC and PON in the form of mucus. Our chamber experiments showed that, with the addition of coral mucus, fluxes of nutrients are turned towards the sediment. Higher nutrient fluxes in the chambers were likely caused by the addition of nutrient-rich mucus. However, the direction of fluxes changed with the addition of coral mucus. This means that nutrients contained in coral mucus are transported into the permeable reef sands, where the particulate mucus fraction is trapped in the porous sediment matrix, while benthic microorganisms readily consume the dissolved mucus fraction. This is supported by the observation that advection flushes the upper layers of the sediments at the study site, as revealed by inert bromide tracer addition (Rasheed et al. 2004). Mucus added to the chambers was homogenized and, thus, could easily penetrate into the coarse sand.

Over time, sedimentary decomposition will lead to release of inorganic nutrients from the reef sands, but our incubation times of 5 to 6 h were too short to demonstrate this release. In the laboratory chamber experiments, the water-sediment fluxes of nutrients were more pronounced in the coarse sand compared to the medium sand. This was caused by the higher permeability of the coarse sands, promoting advective water exchange and, thus, an intense sediment-water coupling and a more rapid transport of the mucus into the sand. We, therefore, can confirm the hypothesis of Ducklow & Mitchell (1979b) that coral mucus may be an important source of nutrients.

The special role of phosphate

Phosphorus, like nitrogen, can be a limiting element in coral reef ecosystems (Crossland & Barnes 1983). It is not easily explainable, therefore, why corals release high concentrations of phosphate with the mucus, as revealed by our measurements. Sorokin (1992) reported phosphate concentrations of 0.1 to 0.3 µmol l^{-1} in Heron Island reef waters, which is similar to the 0.05 to 0.23 µmol l^{-1} we found in this study. In comparison, phosphate concentrations in coral mucus were 2 orders of magnitude higher (20 to 22 µmol l^{-1}).

X-ray microanalyses of elemental composition in coral mucocytes and on the external surface layer of corals (Marshall & Wright 1995, Clode & Marshall 2002) may hint at the source of the high mucus phosphorus concentrations. The P content of oral ectoderm mucocytes of the coral *Galaxea fascicularis* reaches approximately 2% of its sulfur content, and S ranges between 1 to 2 mol kg^{-1} wet wt (P. L. Clode & A. T. Mar-

shall unpubl. data). In Clode & Marshall (2002), it was found that the S concentration in secreted mucus on the external surface of the polyp was about 60 mmol kg^{-1}. Assuming a seawater S concentration of 28 mmol kg^{-1}, the concentration of S caused by mucus ranges from 32 to 60 mmol kg^{-1}. This gives a dilution factor of 17 to 31 using a S concentration of 1000 mmol kg^{-1} in the mucocytes. By using these factors, the P concentrations in the exuded mucus can be calculated as 0.8 to 1.5 mmol kg^{-1}, which is even higher than our measured phosphate concentrations of 0.02 mmol l^{-1}. The concentration of P in exuded coral mucus depends on the degree of dispersion and dilution, so that the data of Clode & Marshall (2002) seem to agree with our data. We can, therefore, conclude that there are indications that the P is coming from the mucus itself (maybe phospholipids essential for modifying the viscosity of mucins; Daumas et al. 1982), but not from the adsorption of phosphate and cellular material (containing DNA with phosphate as a main constituent) from the water column or the remineralization of P containing mucus compounds. Sorokin (1992), during his work at Heron Island, estimated P fluxes between coral sand and water column ranging from sedimentary uptake rates of 65 to 226 µmol m^{-2} d^{-1}. This is in agreement with our *in situ* measured phosphate fluxes into the sediment of 42 ± 50 µmol m^{-2} d^{-1} in the control chambers and 290 ± 92 µmol m^{-2} d^{-1} in chambers with the addition of coral mucus. This indicates that coral mucus plays a major role as a carrier of phosphorus to the sediment community in reef environments.

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