Sediment-water coupling in permeable shallow water sediments

with special emphasis on carbonate sands and the cycling of coral exudates in reef environments

Dissertation

zur Erlangung des Doktorgrades der Naturwissenschaften

dem Fachbereich Biologie/Chemie der

Universität Bremen

vorgelegt von

Christian Wild

Bremen
August 2003

Die vorliegende Arbeit wurde in der Zeit von Oktober 2000 bis August 2003 am Max Planck Institut für marine Mikrobiologie in Bremen angefertigt. Abgabetermin: 15. August 2003.

1. Gutachter: Prof. Dr. Bo Barker Jørgensen
2. Gutachter: Prof. Dr. Wilhelm Hagen

weitere Prüfer:
Prof. Dr. Gunter Kirst
Dr. Claudio Richter

Tag des Promotionskolloquiums: 15. Oktober 2003

DANKSAGUNG

Mein herzlicher Dank geht an alle, die in irgendeiner Art und Weise zur Entstehung dieser Arbeit beigetragen haben.

Herrn Professor Dr. Bo Barker Jørgensen danke ich für die Begutachtung dieser Arbeit sowie hilfreiche Kommentare und Anregungen.

Herrn Professor Dr. Wilhelm Hagen danke ich für die Übernahme des Zweitgutachtens, sowie Professor Dr. Gunter Kirst, Dr. Claudio Richter, Markus Billerbeck, Maren Nickel und Andrea Peiter für Ihre Bereitschaft, ebenfalls dem Prüfungskomitee anzugehören.

Das größte Dankeschön geht an Professor Dr. Markus Hüttel für die Betreuung dieser Arbeit. Ich möchte ihm insbesondere danken für seine großartige Unterstützung, sein Engagement und seine zahlreichen Ideen, die entscheidend zum Gelingen dieser Arbeit beigetragen haben.

Vielen Dank auch an unsere TA's Martina Alisch und Susanne Menger, die sowohl im Feld als auch im Labor eine große Hilfe waren. Dies gilt auch für Linda Hönemann und Heiko Schütte im Labor. Stephan Kremb, Dr. Selina Ward und Dr. Ron Johnstone waren eine wertvolle Hilfe im Feld bei den Heron Island Expeditionen 2001 beziehungsweise 2002. Professor Dr. Ove Hoegh-Guldberg und das Personal der Heron Island Research Station, insbesondere Rod Forbes, haben unseren Aufenthalt möglich und sehr angenehm gemacht.

Dank gebührt auch allen meinen Co-Autoren auf den verschiedenen Manuskripten dieser Doktorarbeit für die gute Zusammenarbeit und fruchtbare Diskussionen.

Ich möchte mich ausserdem bei den Mitarbeitern des Max Planck Instituts bedanken, vor allem bei Perran Cook und Hans Røy für gute Anregungen und Tips, bei Bernd Stickfort für große Hilfe bei der Beschaffung exotischer Literatur, bei Jens Kallmeyer und Elke Allers für die kompetente Betreuung meines Aquariums in meiner Abwesenheit sowie insbesondere bei Maren Nickel, Perran Cook, Tomas Wilkop und Markus Billerbeck für eine schöne Zeit am MPI.

Nicht zuletzt möchte ich mich bei meinen Eltern, bei meiner Schwester Friederike sowie insbesondere bei meinen Freunden Andrea, Ines, Heike, Carin, Alexandra, Ute, Stephan, Michael, Dieter, Nick, Stefan, Herbert und Tristan bedanken, die mich unterstützt haben, für mich da waren und mir gut getan haben.

ZUSAMMENFASSUNG

Permeable Sande bedecken große Bereiche des Meeresbodens auf dem Kontinentalschelf. Diese Gebiete sind normalerweise stark durch den Eintrag von Partikeln und organischem Material durch das angrenzende Land beeinflusst. Relativ starke Wasserströmung und Wellenbewegung können die Grenzfläche zwischen Sediment und Wasser erreichen, wo die Wasserbewegung advektiven Porenwassertransport erzeugen kann. Transport und der Austausch von Wasser in oberflächlichen Schichten von permeablen Schelfsanden sind deshalb sehr eng mit der darüber liegenden Wassersäule verknüpft. Dies könnte den Abbau von Organik in solchen permeablen Sedimenten beeinflussen.

Im ersten Teil dieser Arbeit (Kapitel 2-4) haben wir die Verknüpfung zwischen Sediment und Wassersäule und seine biogeochemischen Konsequenzen in Silikatsedimenten von der deutschen Nordsee und dem nordamerikanischen Schelf untersucht.

Wir fanden, dass

a) die Permeabilität ein kontrollierender Faktor für den Abbau von Organik in der Oberflächenschicht von Sedimenten ist. Eine Erhöhung der Permeabilität führt auch zu einer erhöhten Mineralisierung von organischem Material (Kapitel 2). Das Ablegen von Kotpillen auf die Sedimentoberfläche von feinkörnigen Wattenmeersedimenten durch Polychaeten erhöhte die Permeabilität der Sedimentoberfläche um zwei Größenordnungen. Dies ermöglichte advektiven Transport durch die biologisch veränderte Sedimentoberfläche was zu einer erhöhten Sauerstoffverfügbarkeit und schnellerem Abbau von Organik führte.
b) Porenwasserflüsse ein weit verbreiteter Prozess in permeablen Schelfsanden sind, wie wir durch eine neue in-situ Messtechnik mit Jod als Indikator feststellen konnten (Kapitel 3). Dieses Ergebnis bestätigt die Hypothese, dass ausgedehnte sandige Schelfgebiete als riesiges Filtersystem fungieren können. Versuche mit Durchfluss-Säulen demonstrierten, dass die Sauerstoffaufnahme des inkubierten Sediments positiv mit der Durchflussgeschwindigkeit des Porenwassers korreliert war.
c) gelöstes organisches Material (DOM) in diesen Sanden sehr effektiv abgebaut werden kann (Kapitel 4). Obwohl die Bakterienzahlen pro Sedimentvolumen aufgrund der kleinen Sandkörneroberfläche relativ gering waren, scheinen die wenigen Bakterien, die auf den Sandkörnern leben, den mechanischen Sandfilter in einen biokatalytischen Filter zu verwandeln.

Die biokatalytische Effizienz von Karbonatsanden, die den Meeresboden der meisten Korallenriffe bedecken, übertrifft die von Silikatsanden mit einer ähnlichen Korngrößenverteilung. Dies liegt an einer höheren Permeabilität, einer höheren spezifischen Oberfläche und höheren Bakteriendichten in Karbonatsanden. Der Kernteil dieser Arbeit (Kapitel 5-9) beschäftigt sich deshalb mit Transportmechanismen und Reaktionen in Korallensanden und den Prozessen, die die Wassersäule und diese Karbonatsande miteinander verknüpfen. Feld und Laborarbeiten wurden vor allem auf Heron Island in der australischen Great Barrier Reef Region durchgeführt. In-situ und Laborexperimente mit benthischen Kammern zeigten einen sehr aktiven sedimentären Matabolismus in Karbonatsanden des Riffs. Die Sauerstoffverbrauchsraten gemessen in-situ waren 65 ± 15 mmol O_2 m^{-2} d^{-1} und stiegen mit erhöhter Permeabilität und advektivem Porenwasseraustausch an (Kapitel 5). Diese hohen Oxidationsraten in permeablen Karbonatsanden deuten darauf hin, dass diese Sedimente einen wichtigen Beitrag für den Abbau und die Regeneration von organischem Material in Rifflebensräumen leisten.

Wir fanden ausserdem, dass transparente exopolymere Partikel (TEP) und klebrige marine snow- Aggregate in Korallenriffen häufig und weit verbreitet sind. Diese Aggregate können das Leben und die Stoffwechselprozesse auf und im Meeresboden beeinflussen, weil sie die Sedimentationsraten erhöhen und vielfach absedimentieren (Kapitel 6).

Schleime, die ständig von Riffkorallen in die Wassersäule entlassen werden, in besonders grossen Mengen bei Umweltstress, verändern sich zum Teil zu diesen marine snow-Aggregaten und spielen eine wichtige Rolle für den Energietransport von Korallen zum benthischen Lebensraum. In-situ Inkubationen von Korallenschleim in benthischen Kammern zeigten, dass dieses organische Substrat von den Karbonatsanden mit einer Umsatzrate von mindestens 7% des zugegebenen Kohlenstoffs pro Stunde abgebaut wird (Kapitel 7). Durch die Klebrigkeit des Korallenschleims werden zusätzlich Partikel aus der Wassersäule eingefangen und so die Sinkgeschwindigkeit der entstehenden Aggregate erhöht.

Dies führt zu einer Sedimentation dieses partikulären Materials in der Rifflagune. Der Transport von Energie und Nährstoffen durch Korallenschleim kann 2-26%, 1-22% und 2-5% des C, N und P Bedarfs der Lagunensedimente abdecken, oder sogar mehr unter bestimmten Bedingungen. Dieser Mechanismus reduziert auch den Verlust von Organik für das Riffsystem (Kapitel 8).

Hinzu kommt, dass das jährliche massenweise Entlassen von Geschlechtsprodukten durch Riffkorallen Konsequenzen für den Metabolismus des Sediments hat. Die Sauerstoffverbrauchsraten des Sediments, in-situ gemessen vor, während und nach einem

solchen Ereignis, waren für 9 Tage nach dem Ereignis signifikant erhöht verglichen mit den Werten, die vorher gemessen wurden. Dabei wurden Sauerstoffverbrauchsraten von bis zu 230 mmol O_2 m^{-2} d^{-1} registriert (Kapitel 9). Das massenhafte Entlassen von organischem Material während dieses Ereignisses hat somit einen starken jahreszeitlichen Einfluss auf die sedimentären Prozesse, was darauf hindeutet, dass Teile der in die Wassersäule entlassenen Korallengeschlechtsprodukte schnell, entweder direkt oder indirekt (z.B. über Nahrungskettenprozesse) die Sedimentoberfläche erreicht haben und letztendlich auch in den Karbonatsanden abgebaut wurden.

Organisches Material, welches von Riffkorallen in die Wassersäule entlassen wird, hat demzufolge eine wichtige Funktion für die Ernährung der mikrobiellen Gemeinschaften und Fauna des Sediments. Dies liegt an einer sehr engen Verknüpfung zwischen Wassersäule und Sediment in Riff- Ökosystemen.

Zusammenfassend kann gesagt werden, dass advektiver Transport, der den pelagischen und benthischen Lebensraum verbindet, eine größere Wichtigkeit für Stoffkreisläufe in flachen Schelfgebieten zu haben scheint als bisher gedacht. Der Lebensraum Korallenriff stellt eine Extremsituation dar, weil durch Wind oder Wellen erzeugte Druckgradienten in der Lage sind die Filtration von Material durch Karbonatsande stark zu erhöhen. Dies macht diese aktiven Sande zu riesigen katalytischen Bioreaktoren, was zur Erklärung der hohen Produktivität von Riff-Ökosystemen beitragen könnte.

THESIS ABSTRACT

Permeable sands are covering large parts of the continental shelf areas. These areas are usually strongly affected by organic matter and particles imported from land. Relatively strong currents and waves can reach down to the sediment-water interface where the water movement can induce advective pore water transport. Transport and water exchanges in surface layers of permeable shelf sands thus are tightly coupled to the overlying water column. This should influence organic matter degradation in such permeable sediments.

In the first part of this thesis (chapters 2-4), we experimentally studied the sediment-water coupling and its biogeochemical consequences in silicate sediments from the German North Sea and the North American Atlantic Shelf. We found that

a) permeability is a controlling factor for organic matter degradation in the sediment surface layer, and mechanisms that enhance permeability thus enhance the sedimentary mineralization of organic matter (chapter 2). Deposition of fecal pellets by polychaetes on the surface of fine-grained sediments increased the permeability of the sediment surface layer by two orders of magnitude. This facilitated advective flow through the biologically altered sediment surface resulting in a higher oxygen availability and faster degradation of organic matter.
b) porewater flows are a common process in permeable shelf sands as assessed by a new measuring technique with iodide as tracer in-situ (chapter 3). This result supports the hypothesis that large sandy shelf areas function as gigantic filter systems. Flow-through column experiments demonstrated that the sedimentary O_2 consumption is positively correlated with the flow rate of the porewater through these permeable sediments.
c) dissolved organic matter (DOM) is efficiently degraded in these sands (chapter 4). Although the bacterial numbers per sediment volume are relatively low due to the small surface area for microbial growth, the bacteria attached to the sand grains seem to convert the mechanical sand filter into a biocatalytic filter.

The biocatalytical efficiency of carbonate sands covering the seafloor of most coral reef environments exceeds that of silicate sands with similar grain size spectrum, because of their higher permeability, specific surface area and bacterial densities. The core part of this thesis (chapters 5-9) addresses transport and reaction in coral sands and the processes that couple the water column and these carbonate sands. Field and laboratory studies were mostly conducted on Heron Island in the Australian Great Barrier Reef area. In-situ and laboratory chamber experiments revealed a very active sedimentary metabolism in the carbonate reef sands. O_2

consumption rates measured in-situ were 65 ± 15 mmol O_2 m^{-2} d^{-1} and increased with increasing permeability and advective porewater exchange (chapter 5). These high oxidation rates in permeable carbonate sands indicate that these sediments are an important site for the degradation and recycling of organic matter in reef environments. It is shown that transparent exopolymer particles (TEP) and sticky marine snow aggregates are common and widely distributed in the water column of reef environments. These aggregates can influence benthic life and metabolism by enhancing the sedimentation rate (chapter 6).

Mucus, continuously released by reef corals into the water column and in very high quantities under environmental stress changes partly to those sticky marine snow aggregates and is playing an important role for the transport of energy from the corals to the benthic environment. In-situ incubations of coral mucus in benthic chambers showed that coral mucus can be degraded by the carbonate sands with a carbon turnover rate of at least 7% per hour (chapter 7). Due to the stickiness of coral mucus, particles from the water column are trapped and increase the sinking rates of the ensuing aggregates. This leads to the sedimentation of this particulate material in the reef lagoon. The transport of energy and nutrients via coral mucus can cover 2-26%, 1-22% and 2-5% of the sedimentary C, N and P demand of the reef lagoon, or even more (chapter 8).

In addition, the release of sexual products by corals during the annual spawning event has consequences for the sedimentary metabolism. Sedimentary oxygen consumption rates measured in-situ before, during and after a small spawning event were significantly increased compared to pre-spawning values for 9 days after the spawning event, reaching very high rates of up to 230 mmol O_2 m^{-2} d^{-1} (chapter 9). The release of organic material by corals during the coral spawning event has a strong seasonal input on sedimentary processes. This indicates that parts of the spawning products in the water column reached the sediment surface rapidly either directly or indirectly (e.g. via food chain processes) and were degraded in the carbonate sands. Coral-derived organic matter released into the water column thus has an important function for the nutrition of sedimentary microbial communities and fauna, because of the close water-sediment coupling in reef ecosystems.

In summary, advective transport coupling pelagic and benthic environment seem to be more important than previously thought for the cycles of matter in shallow shelf areas. An even more extreme situation applies for coral reefs environments where pressure gradients induced by wind and waves may strongly increase the filtration of matter through the carbonate sands, making them to gigantic catalytic bioreactors. This may contribute to explain the high productivity of these ecosystems.

TABLE OF CONTENTS

Chapter 1

General Introduction

GENERAL INTRODUCTION

This study is dealing with the coupling between permeable sediments and the water column as well as sedimentary processes in shallow water shelf areas. In this context, coral reefs and their carbonate sediments display extreme environments. Sediment-water coupling and processes in the highly permeable carbonate reef sands appear very clearly and may have an enormous importance for the recycling of matter in the oligotrophic environment.

In chapter 2 of this study, „The role of pelletization for mineralization in fine-grained coastal sediments“, it will be shown which importance the factor permeability can have for benthic degradation processes. It also will demonstrate the effect of benthic fauna for benthic degradation of organic matter in fine-grained Wadden-Sea sediments.

Chapter 3, „In-situ measurements of advective solute transport in permeable shelf sands“, is connected to chapter 2 by the O_2 measurements and will point out that transport of pore water is a common process in permeable shelf sands.

The chapter 4, „Sedimentary oxygen consumption and organic matter turnover in organic-poor, permeable shelf sands“, will confirm the results of chapter 3 and also point out the efficient degradation of organic matter in permeable shelf sediments.

While chapters 2-4 will deal with general processes between water column and permeable shelf sediments, and add more insights concerning permeability, advection, pore water flow and DOM degradation, chapter 5 „Benthic respiration and photosynthesis in permeable carbonate sediments from Heron Island, Great Barrier Reef, Australia“ then will specialize on processes in carbonate sediments in contrast to the silicate sediments studied in the chapters 2-4. It will show the extreme reactivity of carbonate sands and also justify why it is especially important to do studies on sediment-water coupling and permeable sediments in a coral reef environment.

Chapter 6, “Effects of marine snow and muddy terrigenous sediments on the survival of hard coral recruits”, was included in the thesis, because the work for this chapter is the fundament for the subsequent chapters by observing the eminent role of exopolysaccharides and ensuing mucus aggregates in reef waters. Chapter 6 thus leads over to sediment-water coupling by

marine snow and mucus aggregates. Particles from the water column are influencing benthic life and processes.

Chapter 7, “Degradation of coral mucus in reef environments”, will study one of the dominant natural organic matter in reef environments and its turnover in the sediments as an end point of the water-sediment coupling.

Chapter 8, “Coral mucus functions as energy carrier and nutrient trap in the reef”, will comprehend the cycle of coral mucus in reef systems and give an overview of the contributing processes. It will also propose a quantitative budget about the importance of coral mucus for the nutrition of the reef.

Chapter 9, “Rapid recycling of coral mass spawning products in permeable reef sediments”, will finally study another coral-derived source of organic matter in the reef system: sexual products released once or twice a year in very high amounts. The effect of this organic matter pulse on sedimentary processes is also an important aspect for the coupling between water column and permeable sediments.

The following “General Introduction” is organised as connecting text between the different subsequent chapters (manuscripts) as required for a cumulative thesis. Sentences in *Italics* label the textual contexts.

Shelf sediments

Continental shelf areas account for only 7.6% or 27.1 million km² (Tardent 1979, Wollast 2003) of the total ocean area (Figure 1). The thickness of the overlying water column is usually less than 250 m (average 130 m) indicating that the seafloor of many shelf areas is still located within the euphotic zone. If water turbidity is low, sediments deposited in shelf areas are therefore subjected to the influence of light intruding through the shallow water column and allowing photosynthesis. Due to the water column shallowness, shelf sediments are also often influenced by water turbulence caused by wind and waves (Precht & Huettel 2003). In some areas located at the West coasts of Africa and South America the continental shelf areas are affected by upwelling of nutrient rich water from the deep sea due to oceanic currents (e.g. Benguela and Humboldt current). Upwelling also occurs in several other shelf areas.

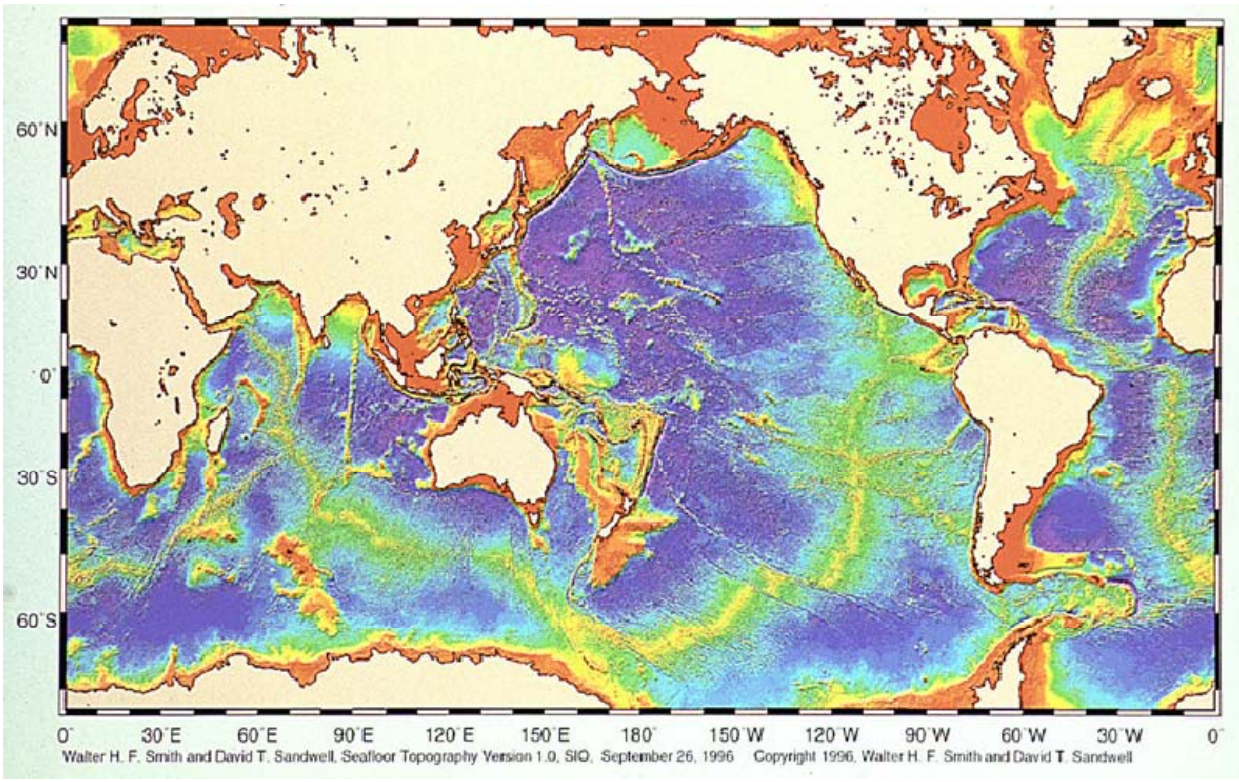

Figure 1. Global Distribution of shelf areas (indicated in orange).

Additionally, shelf areas are strongly influenced by the close landmasses because of nutrient and organic matter input via rivers. Gibbs (1981) reported that approximately 90% of the particles and organic carbon transported by the world rivers are finally trapped in the delta and shelf area. Shelf sediments can store a large fraction of this material and, thus, have an important regulatory and buffering function in coastal ecosystems (Jørgensen 1996). Remineralization of the deposited material leads to a release of nutrients from these sediments to the water column.

Due to light availability on the sea floor and often high nutrient concentrations in the overlying waters, shelf areas contribute 18-33% of the global oceanic primary production (Wollast 1991, Jørgensen 1996). These factors in addition to a close coupling between benthic and pelagic systems make shelf areas to the most productive regions of the ocean (see Tables 1 and 2).

Table 1. Oceanic primary production rates for different areas. Data derive from Lalli & Parsons (1997).

Location	Mean annual primary productivity ($g\ C\ m^{-2}\ y^{-1}$)
Continental upwelling (e.g. Peru current, Benguela current)	500-600
Continental shelf-breaks (e.g. European shelf, Grand Banks)	300-500
Subarctic oceans (e.g. North Atlantic, North Pacific)	150-300
Anticyclonic gyres (e.g. Sargasso Sea, subtropical Pacific)	50-150
Arctic Ocean (ice-covered)	less than 50

Table 2. Benthic primary production rates for different seafloor communities. Data are summarised from Sommer (1998).

Location	Mean annual primary productivity ($g\ C\ m^{-2}\ y^{-1}$)
Microalgae on sediment surface	30-400
Seegrases	130-2300
Macroalgae	400-3000
Coral reefs	1500-5000

Photosynthetic organisms in shelf areas driving high primary production rates are first of all phytoplankton organisms (e.g. diatoms, cyanobacteria, dinoflagellates), but also benthic communities of seagrasses (e.g. the endemic *Posidonia oceanica* in the Mediterranean), macroalgae (e.g. kelp forests of the Westcoast of North America), benthic microalgae (Jahnke et al. 2000) and symbiotic dinoflagellates living in the tissue of many benthic invertebrates. *Especially, the latter will have relevance for the coral mucus studies presented in the chapters 7 and 8.*

The high kinetic energy in the water column above shelf sediments in most cases prevents a deposition of muddy fine-grained material. The seafloor of shallow shelf areas is therefore often dominated by fine to coarse sands.

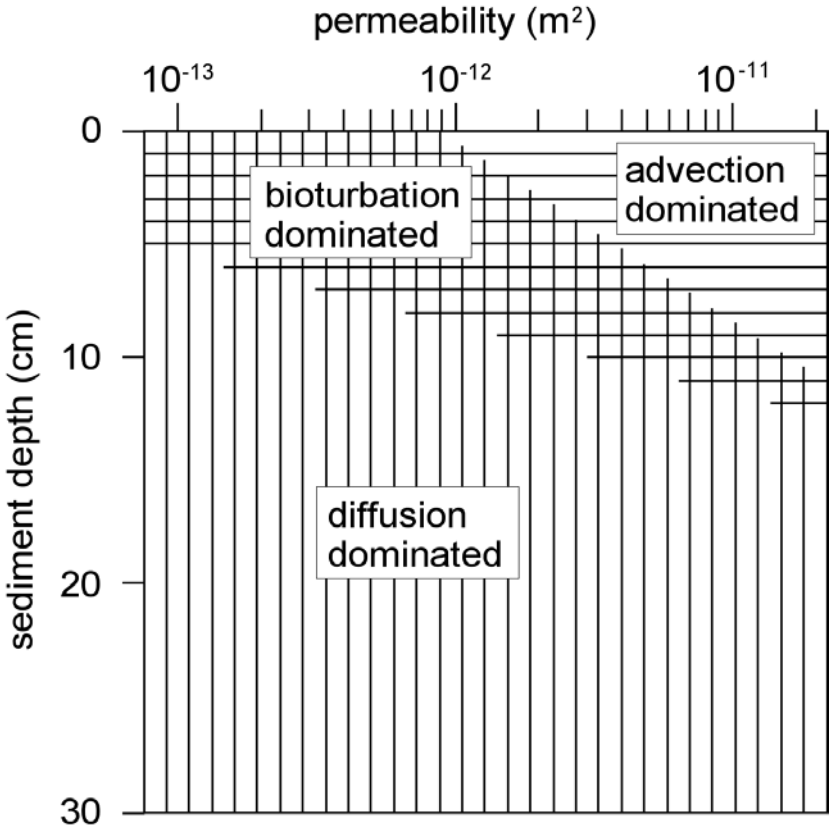

Figure 2. The transport mechanisms in aquatic environments and their depth and permeability related distribution. Molecular diffusion is dominant in muddy sediments where benthic organisms are absent (great sediment depths, anoxic conditions). Biological transport via bioturbation/bioirrigation is most intense near the oxic sediment-water interface where benthic organisms are numerous. Graph derived from Huettel et al. (2003), submitted to Hydrobiologia, with permission.

Permeable sands

These shelf sands are characterised by grain sizes of up to 2000 µm in contrast to fine muddy cohesive sediments (grain size less than 63 µm) covering large areas with calm hydrodynamic conditions (e.g. the deep sea where hydrodynamic forces are usually very low). Because of their large grain size, shelf sands are often permeable for water flowing through them (Shum & Sundby 1996). Permeability is determined mainly by the grain size, but also by other

factors like the sediment sorting (Hsü 1989), bioturbation (Ziebis et al. 1996a) and exopolymers of biological origin (Yallop et al. 1994). Riedl et al. (1972) stated that permeable sediments cover approximately 40% of the shelf seafloor.

In cohesive fine-grained sediments (permeability < 10^{-12} m²) transport of water and solutes into and out of the sediment takes place via molecular diffusion or bioturbation/bioirrigation (Aller 1982, Huettel & Gust 1992).

In addition to these processes, solute transport caused by pore water flows can occur in permeable shelf sands. Boundary flows and surface gravity waves interacting with the sea bed topography induce pressure differences at the sediment-water interface leading to advective pore water motion in permeable sediments (Riedl et al. 1972, Huettel & Gust 1992), and the pore water flow rate is proportional to permeability and occurring pressure gradients (Darcy 1856).

Permeability is the key factor for pressure-driven porewater exchange (Huettel & Gust 1992) and thus the intense coupling between water column and sediments. In surface sediments with permeabilities larger than 10^{-12} m^2 (Figure 2), solute transport via advection exceeds that of diffusion. Advection can also take place in sediments with permeabilities lower than 10^{-12} m^2, but then is slower than diffusion.

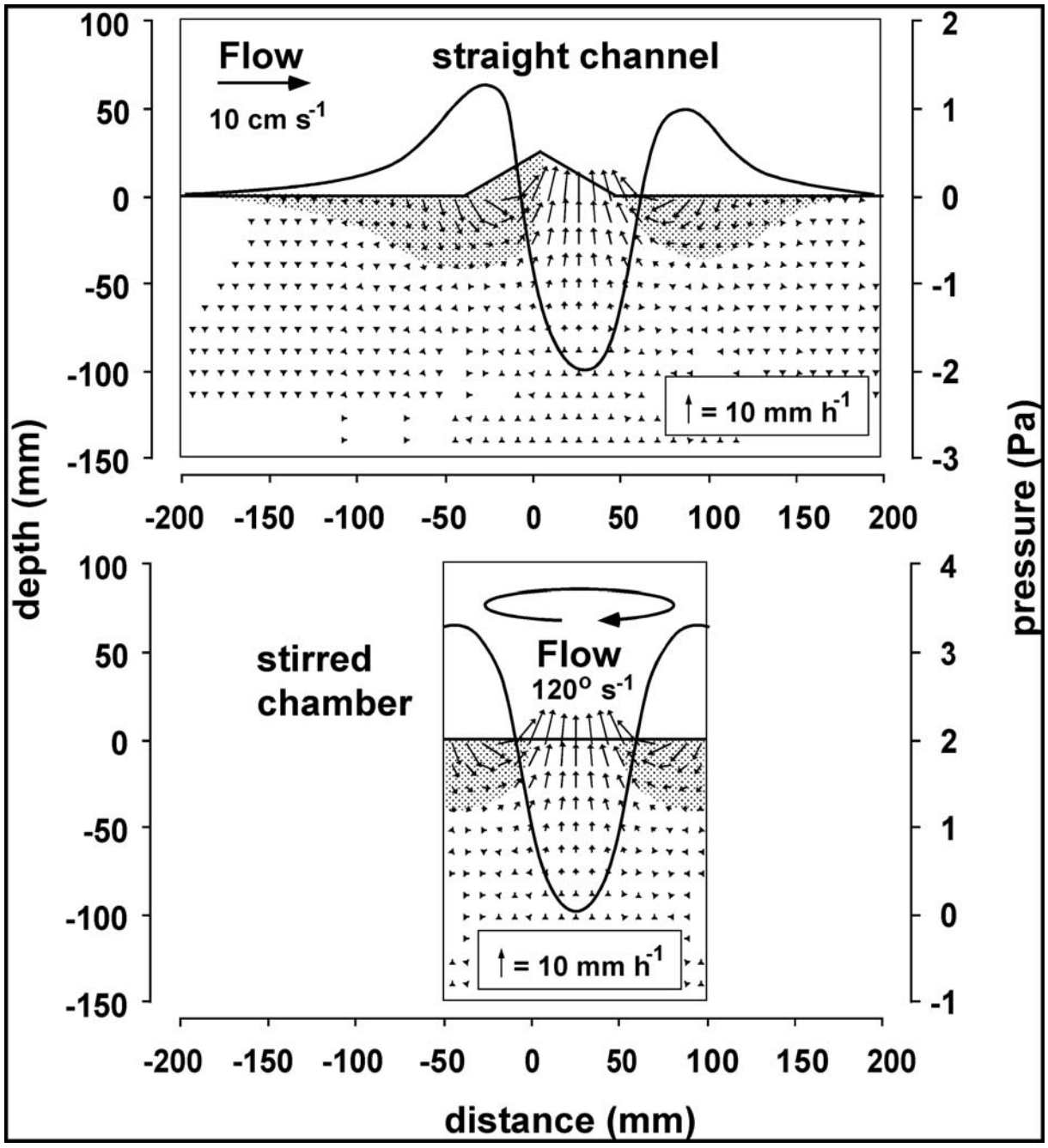

Figure 3. Advective pore water flow fields in a flume and a stirred benthic chamber either caused by sediment topography exposed to unidirectional flow in the flume (above) or by the rotating water column in the stirred benthic chamber that were used for the work presented in this study. Solid lines represent the pressure distribution at the sediment-water interface. The shaded areas are indicating the zones and penetration depths of intruding water. Small arrows show direction and strength of advective pore water flows. Graph derived from Huettel & Rusch (2000), Limnology and Oceanography, Vol. 45 (3), page 535, © by the American Society of Limnology and Oceanography, with permission.

Advective transport (see Figure 3) can be several orders of magnitude higher than the transport by molecular diffusion (Huettel & Webster 2001). Precht & Huettel (2003) showed that shallow water waves can increase the fluid exchange between the sandy sediments and the overlying water 50-fold relative to the exchange of molecular diffusion due to pressure gradients generated by the interaction of oscillating boundary flows and wave ripples. This kind of sea floor topography, but also other roughness elements at the sediment surface like burrows, mounds, mollusc shells or benthic organism resting on the sediment, can alter the small-scale flow regime and thus increase advective transport caused by pressure gradients (Huettel & Gust 1992, Ziebis et al. 1996b). Figure 3 (above) represents an example for bioroughness creating low and high-pressure zones around the topography.

In this context, we studied the role of fecal pellets positioned on the surface of fine-grained Wadden Sea sediments. These pellet accumulations increase the permeability of practically impermeable sediment. The results of this study are shown in Chapter 2.

The chapter 3 of this study gives information about a new method for measuring advective transport and in particular the dependence of O_2 distribution on pore water flow.

Sands as biofilters

Shelf sands are characterised by a high permeability and high advective flushing (Rusch & Huettel 2000, Rusch et al. 2001). Thus, the exchange between the overlying water and the pore water is very intense. A large volume of water is pumped through these sediments (Hutchinson & Webster 1998, Precht & Huettel 2003). With the water, organic matter is transported into the sands (Huettel et al. 1996). It was found that penetration depths of suspended phytoplankton increase with increasing permeability (Huettel & Rusch 2000, Ehrenhauß & Huettel 2003) and increased seabed topography (Huettel & Rusch 2000). Permeable sediments therefore may act as biofilters for organic material (Huettel & Rusch 2000, D`Andrea et al. 2002). In addition, filtration and subsequent trapping of matter by the sands prevent a removal or resuspension of this material by hydrodynamic forces like waves or bottom currents (Huettel & Rusch 2000). The low organic content in permeable sands is rather attributed to high turnover rates than to low activities (Shum & Sundby 1996). Thus, the filtration of organic matter by permeable shelf sands efficiently links pelagic and benthic systems and may have a particular importance for the cycling of matter in the ocean.

Organic matter degradation in permeable sands (sands as biocatalysators)

Shelf sediments are subjected to about 83% of the total organic matter sedimentation (Jørgensen 1996). In addition, continental shelf areas are dominated by permeable sediments (Shum & Sundby 1996). Suspended organic matter is transported into the permeable sediments and not buried to a large extent as indicated by the low organic content of these sediments (Shum & Sundby 1996).

Oxygen, as the terminal electron acceptor of aerobic degradation of organic matter can penetrate deeper into permeable sediments because of the advective flushing (Ziebis et al. 1996b, Falter & Sansone 2000). Advective flow maintains an oxic sediment volume larger than that in less permeable sediments leading to a flow-enhanced oxygen utilisation in permeable beds of coastal and shelf regions, in contrast to the situation in cohesive sediments limited by predominantly diffusive oxygen supply (Forster et al. 1996).

Increased oxygen availability in permeable sediments has consequences for the biogeochemical sediment stratification leading to primarily aerobic degradation of organic material within the upper sediment layer. Nevertheless, reduced metal species (Fe^{2+}, Mn^{2+}) can be released to the water column by flow-topography interactions (Huettel et al. 1998). The anaerobic degradation of organic matter with other terminal electron acceptors than oxygen (e.g. nitrate, Fe^{3+}, Mn^{4+}) in the suboxic layer can possibly be enhanced due to reoxidation of reduced compounds via oxygen.

In general, advective transport of solutes through the sediment can enhance benthic exchange (Jahnke et al. 2000, D`Andrea et al. 2002). The mineralization of organic matter is increased due to higher oxygen availability and a fast removal of metabolic end products. Jørgensen & Sørensen (1985) and Enoksson & Samuelsson (1987) found that the transport of oxygen and sulfate into the sediments enhances organic matter decomposition and nitrification and Dauwe et al. (2001) stated that aerobic mineralization of organic matter at low rates is faster than anaerobic mineralization. Permeable shelf sands may therefore have a biocatalytic function for the degradation of organic matter.

The chapter 4 of this study provides some information about the degradation of dissolved organic matter (DOM) in permeable sands of the North American East Coast shelf. To quantify this, flow trough column experiments were used. Flow trough column experiments represent a new method to assess porewater fluxes and organic matter degradation.

Special role of carbonate sands for organic matter degradation

Permeable sediments do either consist out of silicates or carbonates. Most of the continental shelves are covered with different kinds of silicate sediments, but in some areas, especially subtropical and tropical coral reefs environments, carbonate sediments are predominant. These carbonates mainly originate from the biological production of hermatypic corals, coralline algae and coccolithophorids (Gattuso & Buddemeier 2000), but also gastropods, bivalves and foraminifera contribute with their skeletal elements.

Carbonate sediments show some distinct differences concerning their physical and chemical characteristics in comparison to silicate sediments. Schroeder & Purser (1986) summarised that besides the mineral composition also the surfaces structure, porosity, light attenuation and sorption/desorption behaviour is different between the two kinds of sediments. Rasheed et al. (2003b) measured a 2-fold higher permeability in carbonate sands compared to silicate sands with the same grain size.

In contrast to silicate sediments, carbonate sediments are very reactive and can function as a buffer for a variety of chemical reactions by precipitation and dissolution of carbonates within the oceanic carbonate buffer system.

Carbonate sediments have a higher specific surface area than silicate sediments due to the occurrence of channels and holes in the matrix of carbonate grains (Rasheed at al. 2003a, *see also chapter 5*).

This relatively large surface area of carbonate grains provides a habitat for dense communities of bacteria. Hüttel & Wild (unpublished data) found bacteria numbers in the range of 10^9 – 10^{10} cm^{-3} in carbonate sediments from the Great Barrier Reef (Australia), Hawaii and the Northern Red Sea. These bacteria counts are about 1-2 orders of magnitude higher compared to silicate sands (Rusch et al. 2001).

High bacteria numbers, high rates of advective flushing often combined with water temperatures exceeding 20°C make carbonate sediments sites of intense mineralization of organic matter. Rasheed et al. (2003b) found that carbonate sediments accumulated more organic matter and developed higher nutrient concentrations than silicate sediment incubated under the same conditions.

In addition, the highly permeable carbonate framework of coral reefs acts as biofilter and contributes significantly to the efficient mineralization of organic matter (Richter et al. 2001, Rasheed et al. 2002).

Sediment-water coupling in coral reef environments with their highly permeable carbonate sediments thus appears very intelligibly and may be especially important for the cycling of matter in the oligotrophic reef systems.

As initial part of the thesis core work on sediment-water coupling in coral reef systems we did research on the benthic metabolism in carbonate lagoon sands from Heron Island and quantified benthic photosynthesis and O_2 consumption with the use of stirred benthic chambers. These results are presented in chapter 5.

The ecosystem coral reef

A coral reef represents the net accumulation of calcium carbonate ($CaCO_3$) produced by corals and other calcifying organisms (Kleypas et al. 1999). Coral reefs account for 15% of the continental shelf areas (0-30 m depth range) and about 30% of the world's coastline (Smith 1978). The total area covered by coral reefs was estimated as 6 x 10^5 km^2 (Smith 1978). Their geographical distribution is restricted to an area within the Tropic of Capricorn and Tropic of Cancer (ca. 30° South and North) and to average winter temperatures of at least 18°C (Schuhmacher 1976).

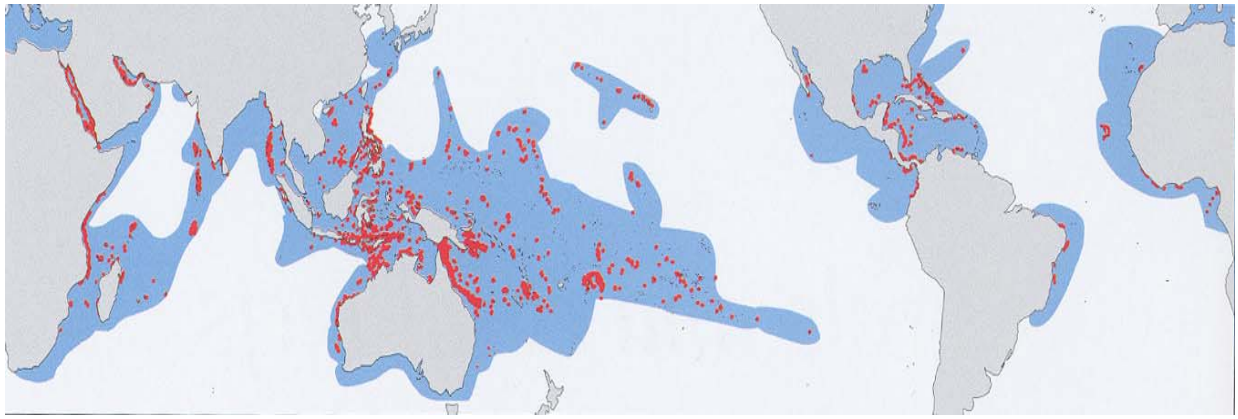

Figure 4. World-wide distribution of warm water coral reefs (indicated as red spots). From (Veron 2000).

Johannes et al. (1983b) attributed these latitudinal limits of coral reef growth rather to a competition between coral and macroalgae than to a direct temperature effect.

In contrast to warm water reefs it is also known that cold water reefs built by the coral *Lophelia pertusa* exist off the coast of Norway in a water depth of about 200-600 m (Mortensen et al. 2001). The main difference between warm and cold water coral reefs is that reef-building warm water corals are zooxanthellate (posse endosymbiotic algae) and reef-building cold water corals are azooxanthellate (no endosymbiotic algae in the coral tissue).

Warm water corals are therefore also restricted to water depths within the euphotic zone (< 100m in tropical oceans) and to waters with a low turbidity.
The existence of large warm water reefs thus depends on the photosynthetic activity of the zooxanthellae leading to calcification rates equalling or exceeding carbonate dissolution and reef erosion. A 5% decrease in the rate of calcification is leading to a net loss of calcium carbonate (Hoegh-Guldberg 1999).
In addition, corals can naturally only exist at salinities between 32 and 34 PSU (Veron 1986). Low salinity and high turbidity prevents the distribution of corals close to the mouths of large rivers, e.g. Northeast coast of South America (see Figure 4).

Coral reefs appear in different kinds of types after Schuhmacher (1976):
The most common reef type is the fringing reef, a reef belt orientated parallel and close to the coastline usually with a width of less than 100 m. A lagoon can develop between the coast and the reef belt if erosion deepened the landward part of the reef belt. Almost all reefs in the Red Sea are fringing reefs.
Barrier reefs develop on shallow areas of the continental shelf and reach their often enormous size because of a sea floor depression or seawater level rise, slow enough that coral growth can follow. Typical barrier reefs can be found of the coasts of Queensland (Australia) and Belize (Central America).
The atoll reef is characterised by a reef ring around a lagoon. After Darwins theory do atolls form if an island with fringing reef is sinking down slowly enough that the corals of the fringing reef can sustain their growth towards the water surface. Atoll reefs usually do not form on the continental shelf and their reef slope is often dropping down to several hundred meters depth.
A platform reef can grow where the water depth is shallow enough to allow coral growth. It can develop in all outside directions. Erosion often leads to a deepening of the central reef part forming a so-called pseudo lagoon in contrast to the true lagoons of atoll reefs. In many cases, a platform reef also hosts a sandbank building a sand cay or even a little island. Platform reefs mostly occur on the continental shelf, e.g. the reefs of the Swain and Capricorn group in the Southern Great Barrier Reef. *The main field station of this study Heron Island is a typical platform reef and part of the Capricorn Bunker group in the Central Section of the Great Barrier Reef National Park.*

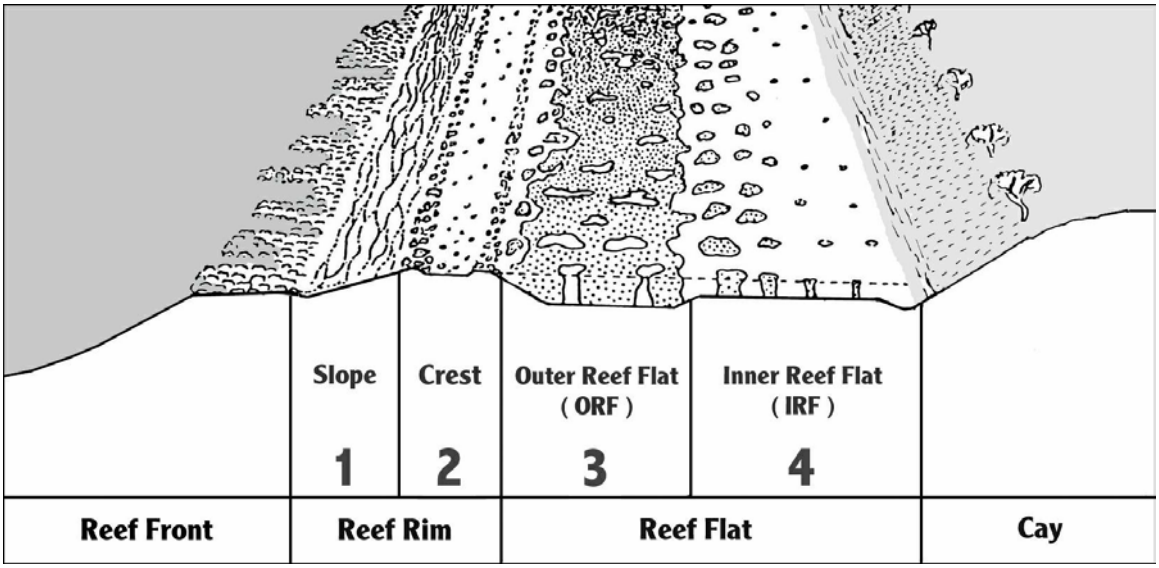

Figure 5. Schematic structure of the platform reef including Heron Island as coral cay. Graph modified from Mather & Bennet (1993).

Both platform and atoll reefs show a reef belt around a lagoon. The water in the lagoon is connected to the surrounding water via only one or a few channels. *This feature will have some importance for the studies presented in the chapters 7-9 as these chapters present results about the degradation and trapping of organic matter within the reef system.*

The morphological structure differs between the 4 described reef types. Figure 5 shows the situation for a platform reef like Heron Island. Typical is an extended reef flat with a water depth of between 1-3 m. This pseudo lagoon often harbours a small and slightly deeper shore channel orientated parallel to the beach. Coral abundance in the reef flat area, in particular the inner reef flat is usually low, because of a long water residence time leading to high water temperature and high salinity. Carbonate sediments instead of living corals thus mainly cover the reef flat seafloor.

The reef crest seafloor is slightly elevated compared to the reef flat area. Here, corals are subjected to strong tidal currents and enjoy a continuous renewal of the overlying water body. That is the reason why coral growth on the reef rim (crest and slope) usually is extensive.

Importance and productivity of coral reefs

Coral reefs show a very high biodiversity with ca. 350 species of hard corals, 4000 species of molluscs, 1500 species of fish and 240 species of associated seabirds (Lalli & Parsons 1997). In total, potentially hundreds of thousands of species live in the reef, many of which are not

yet scientifically described (Hoegh-Guldberg 1999). Coral diversity is greatest in the Western Pacific with more than 180 known coral genera (Thurman 1993, see Figure 6).

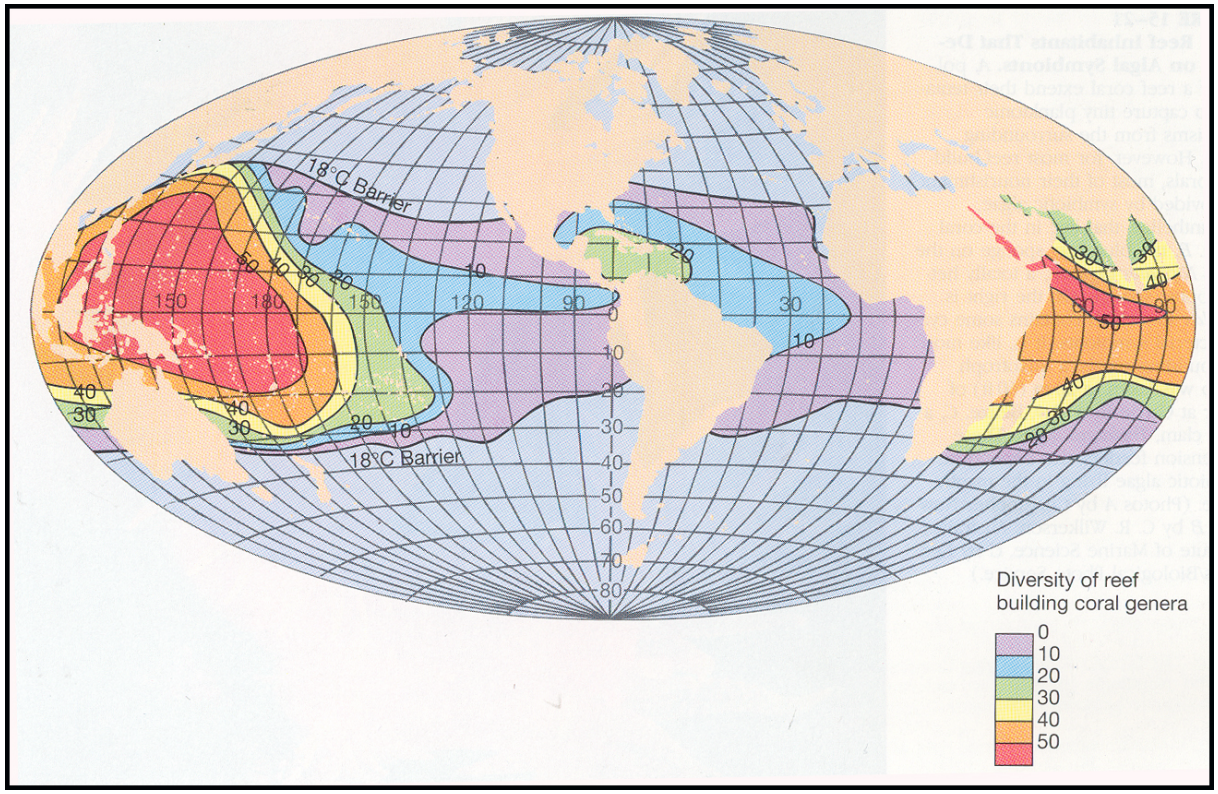

Figure 6. Global distribution of reef-building genera. Graph derived from Thurman (1993).

Gross primary production in reef ecosystems was estimated as between 300 and 5000 g C m^{-2} y^{-1} (Lewis 1977, see also Table 2) exceeding primary production rates in the neighbouring open seas by one to three orders of magnitude (Hatcher et al. 1987, D`Elia & Wiebe 1990, Adey 1998). Hatcher (1988) even estimated a productivity of 14.600 g C m^{-2} d^{-1} for corals. In comparison to other shelf areas, the primary production in coral reefs is also much higher (see Table 1). This is surprising, because coral reefs are located in usually clear and oligotrophic waters with nutrient concentrations lower than 1.5 µM for inorganic nitrogen, lower then 0.5 µM for phosphate and lower than 2.5 µM for silicate (Johannes et al. 1983a, D`Elia & Wiebe 1990, Rasheed et al. 2002), a contradiction which is commonly called Darwins Paradox.

The main explanation for this paradox is that the few nutrients available in the reef are kept in the system via an effective and tight internal recycling of matter. From the literature the following main mechanisms for such a recycling are known:

(1) Internal cycle of nutrients between heterotrophic and autotrophic organisms, in particular between corals and their endosymbiotic zooxanthellae (Muscatine & Porter 1977, Trench 1979, Schlichter et al. 1983)
(2) Rapid turnover of organic and inorganic nutrients within the reef system (Crossland & Barnes 1983)
(3) Filtering of fine particulate matter by the reef frame work colonised with dense communities of filtering organisms, e.g. sponges (Richter et al. 2001)

In addition, nitrogen fixation by benthic cyanobacteria (Larkum et al. 1988) and phosphate input trough guano by coral reef associated birds (Littler et al. 1991) both contribute to the nutrient availability in coral reefs.
It is one goal of this thesis to get new insights in reef recycling processes by studying the contribution of the coupling between reef waters and permeable reef sands (chapters 5 and 7-9).

Because of their high productivity, coral reefs have an enormous economical importance, e.g. for the fishery industry (Smith 1978), the tourism and also recently for the pharmaceutical industry discovering new chemicals and drugs from the highly diverse reef organisms (Carte 1996, Fung et al. 1997, Fung & Ding 1998, Ding et al. 1999). About 15% of the world population live within 100 km to coral reefs and many of those people depend in part or wholly on coral reefs for their livelihood (Hoegh-Guldberg 1999). The tourism in the Australian Great Barrier Reef generates $US 1 billion annually (Done et al. 1996). In addition, coral reefs have an important role for coastal protection against storm damage, erosion and flooding by reducing the wave energy.

In the following two paragraphs some information about coral metabolism and stress factors affecting corals are given in order to introduce the main natural organic substrate studied in this thesis: coral mucus. It is important to be familiar with coral metabolism and stress factors to corals in order to understand the chemical composition and quantitative release of mucus by corals.

The reef-building corals

Coral reefs are primarily build by reef building (hermatypic) hard corals (Scleractinia) belonging to the class Anthozoa within the phylum Cnidaria. Reef building warm water corals are able to produce 6 x 10^{12} mol $CaCO_3$ per year (Smith 1978) or between 1 and 35 kg $CaCO_3$ m^{-2} y^{-1} (Barnes & Chalker 1990) due to high photosynthetic rates of their endosymbiotic zooxanthellae (Muscatine 1980, Muscatine 1990, Al-Horani et al. 2003a, Al-Horani et al. 2003b).

Hermatypic hard corals use 3 different processes to fulfil their energy and nutrient demand:

- Feeding particulate organic matter (POM) from the water column by the use of specialised cells (nematocysts) or the secretion of mucus entangling the prey (Hubbard & Pocock 1972, Schuhmacher 1977).
- Uptake of dissolved organic matter (DOM) via the oral ectoderm (Ferrier 1991)
- Transfer of metabolites (sugars, amino acids, carbohydrates, and small peptides) from the zooxanthellae. Zooxanthellae translocate up to 95% of their photosynthetic production to the coral (Muscatine 1990). Up to 90% of the coral nutrition is provided by the zooxanthellae (Thurman 1993), which appear in population densities of 0.5 – 5.0 x 10^6 cells cm^{-2} coral (Hoegh-Guldberg & Jones 1999).

The upper 2 mechanisms characterise a coral as heterotrophic organism, the last one as functional autotrophic, because of the close metabolic dependence on the endosymbiotic algae (Schlichter et al. 1983, Muscatine 1990).

All 3 processes contribute simultaneously to the fulfilment of the energy demand, but in varying proportions. Anthony & Fabricius (2000) for example showed that the contribution of autotrophy and heterotrophy to the overall energy budget varies in the presence of a changing environmental factor (in this case the amount of particles in the water). However, coral growth, calcification and productivity strongly depend on the vitality of the endosymbiotic zooxanthellae (Muscatine 1990, Glynn 1993, Hoegh-Guldberg & Jones 1999).

Natural and man-made stress factors on corals

Coral reefs are menaced by a variety of stress factors affecting either the heterotrophic coral or the autotrophic zooxanthellae, but in last consequence both because of the mutualistic relationship. This powerful symbiosis still is very sensitive to a variety of natural and anthropogenic stress factors. Between 50 and 70% of all coral reefs are directly threatened from human activities (Hoegh-Guldberg 1999).

Environmental stress factors affecting corals are first of all sedimentation of material, high water turbidity, air exposure, changes in salinity caused by fresh water input, rain storms or evaporation and high water temperatures. Storms and high water turbulence can cause a breaking of coral colonies. In addition, outbreaks of the crown-of-thorns starfish *Acanthaster planci* have destroyed large reef areas in the Pacific and the Red Sea (Moran 1986). It is so far not clear if *Acanthaster* outbreaks are caused by man-made activities (e.g. exploitation of predators like the triton snail) or periodically occurring events. Hoegh-Guldberg & Pearse (1995) suggested a more rapid growth of crown-of-thorn larvae due to increased sea temperatures.

The global increase in atmospheric CO_2 is associated with a decrease in aragonite and calcite saturation states (Gattuso et al. 1998), a decreased alkalinity and also with increasing water temperatures and higher UV radiation. The sea temperatures increased by almost 1° C over the past hundred years and are currently increasing at 1-2° C per century (Hoegh-Guldberg 1999). It was shown that the calcification of a variety of organisms, including coccolithoporids (Riebesell et al. 2000), coralline algae and reef-building corals (Gattuso et al. 1999, Marubini & Thake 1999, Gattuso & Buddemeier 2000) is depressed by increased levels of atmospheric CO_2.

Man made stress factors are also increased nutrient inputs by eutrophication, pollution, cyanide fishing, over exploitation of marine species, mining and tourist activities mechanically disturbing the corals (Sebens 1994). Nutrient addition to corals additionally decreased their growth rate (Marubini & Atkinson 1999, Marubini & Thake 1999).

Reaction of corals to stress

Corals react very sensitive to environmental changes as the are adapted to an environment with relatively constant conditions. The mean sea surface temperature in tropical oceans varied by less than 2° C over the past 18.000 years (Thunnel et al. 1994).

Their temperature tolerance has its upper boundary by a maximum of 32° C or less (Iglesias-Prieto et al. 1992, Warner et al. 1996, Hoegh-Guldberg 1999). If temperature increases to this

level or earlier corals start to expel their zooxanthellae (Glynn 1984) what is commonly called coral bleaching. Bleaching is described as a generalised and reversible response to a variety of environmental stress factors (Brown & L.S. 1985). These are known as sedimentation/high water turbidity (Bak 1978, Dallmeyer et al. 1982, Rogers 1983, Acevedo et al. 1989, Glynn 1993), hypoosmotic conditions (Goreau 1964) and high UV radiation (Lesser et al. 1990) or mechanical disturbance (own observations). The mechanisms of coral bleaching are not entirely understood, but it is discussed that reduced photosynthetic rates lead to a decrease in exchange of metabolites between the zooxanthellae and the coral (Iglesias-Prieto et al. 1992). This leads to an interruption of the chemical transfer of signals and finally causes the release of zooxanthellae by the coral (Markell et al. 1992). Kushmaro et al. (1997) also found that the coral surface inhabiting bacterium *Vibrio alginolyticus* may be involved by producing extracellular toxins that inhibit photosynthesis, bleach and lyse the zooxanthellae. However, mass coral bleaching and associated coral mortality is a major contribution to the global decline of coral reefs (Brown 1997, Hoegh-Guldberg 1999).

Besides coral bleaching there is another mechanism taking place in response to unspecific environmental stress: the production of **coral mucus**. Strong mucus production was observed after sedimentation of carbonate sediment (Hubbard & Pocock 1972, Schuhmacher 1977) and marine snow sediment (*see chapter 6 of this study*) as well as aerial exposure (Krupp 1984 *and chapters 7+8 of this study*).

It is also reported that the tissue thickness of corals is an indicator for stress as that it decreases in response to environmental stress (Barnes & Lough 1999, Lough & Barnes 2000).

In general, the metabolic performance of corals is decreased because of stress. This includes a reduced production of gametes (Szmant & Gassman 1990, Sier & Olive 1994) and a reduced survival of coral recruits (*see in this context chapter 6 of this study*).

Environmental stress weakens the condition of corals. They are subjected to a range of coral diseases, some of them recently discovered: black and white band, virus infections, ciliates (Peters 1983, Szmant 2002). Hoegh-Guldberg (1999) expects severe and negative effects on the health of coral reefs by the middle of this century. Bleaching events are supposed to increase in frequency and intensity until they become annually by 2050 in most oceans. The bleaching events then exceed the frequency at which corals can recover from bleaching related mortality. Global warming and its consequences are thus expected to kill most of the coral reefs by the end of this century (Pockley 1999). These dramatic visions highlight the

necessarily to put strong effort in coral reef research in order to understand the functioning of this complex ecosystem.

Coral exudates and their influence on life in the reef

The symbiosis between hard or soft corals on the one hand and the zooxanthellate dinoflagellate *Gymnodinium* spec. on the other hand is well-known. Hermatypic corals host a large number of algal endosymbionts (ca. 1 million cells per cm²). The zooxanthellae account for up to 75% of the coral biomass (Thurman 1993). Exudates of corals therefore display a combination of both autotrophic and heterotrophic metabolism.

Corals are continuously exuding dissolved organic material (DOM) including typical products of photosynthesis like amino acids or sugars (Schlichter & Liebezeit 1991, Ferrier-Pages et al. 1998) and products of respiration like ammonia (Muscatine & D´Elia 1978). Polysaccharides are a dominant component of DOM found in surface waters of the ocean (Benner et al. 1992). Dissolved organic carbon (DOC) release of *Galaxea fascicularis* represented ca. 14% of the net daily photosynthetically fixed carbon (Ferrier-Pages et al. 1998). These exudates can enhance the growth of pico- and nanoplankton (Ferrier-Pages et al. 2000). In transect studies over the reef flat the highest pico- and nanoplankton production rates have been measured directly above corals (Sorokin 1993, Sorokin 1994). Bacterial productivity in reef waters was found to be much higher than in the open ocean (Moriarty et al. 1985, Ducklow 1990).

Thus, DOM exuded by corals seems to be important for the nutrition of heterotrophic consumers, e.g. bacteria which are important organisms for the C and N cycles in coral reefs (Sorokin 1994, Charpy-Roubaud et al. 1996).

Corals are also exuding particulate organic material (POM) in form of mucus and gametes. Coral mucus was identified as the major component of coral derived POM (e.g. Krupp 1984). It was assumed that coral mucus can only be used by reef microbes if it is retained long enough in the reef system that decomposition can take place (Capone et al. 1992). Hatcher & Sanmarco (1983) further suggested that a large fraction of coral mucus may be refractory and not consumed in the reef during the short transit time across the reef.

In the literature, thus, POM released as mucus by corals was rather stated as a loss from the reef system than important for the support of microbial growth.

Coral mucus as source of organic carbon and nutrients

Reef-building corals provide much of the reef primary production of coral reef ecosystems. Solar energy captured by the zooxanthellae is released to the water column as mucus (Hoegh-Guldberg 1999). Coral mucus is produced in large quantities in response to environmental stress (see above), but also continuously on a species-specific level under normal undisturbed conditions (Coles & Strathman 1973, Crossland et al. 1980, Crossland 1987).

Hard and soft corals continuously produce fluid mucus or mucus sheets in ectodermal cells (Coffroth 1983) and release it as dissolved or particulate matter. The transparent mucus initially is produced and transported over the coral surface via ciliary currents. Due to the sticky nature of coral mucus soon particles from the water column attach to it and make it visible. On various dives in reefs of the Great Barrier Reef (Australia) and the Northern Red Sea (Egypt) mucus strings attached to colonies of hard and soft corals were observed (see Figure 7).

The 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).

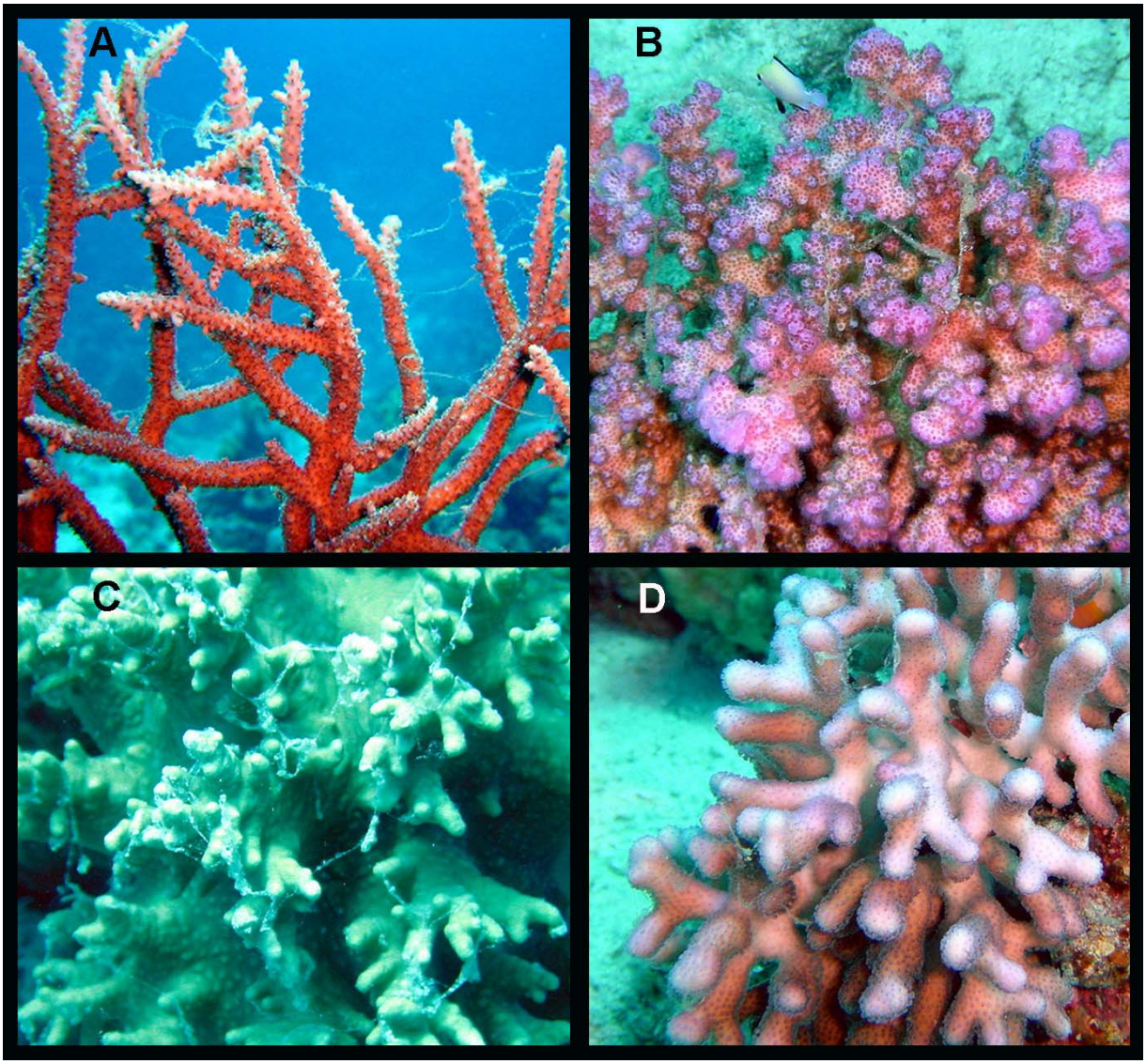

Figure 7. Mucus visible as strings attached to colonies of *Acropora* (A), *Pocillopora* (B), *Sinularia* (C) and *Stylophora* (D) coral colonies (All photographs were made in reefs of the Northern Red Sea, Egypt, by the author).

Coral mucus is exuded in such large quantities that it is a dominant component of the particulate organic matter (POM) in reef systems (Johannes 1967, Marshall 1968). *In the work for chapter 6 (sedimentation response of corals), we observed that coral mucus aggregate densities in the water column especially after low tide was so high that visibility was decreased from 10 m to less than a meter.* These observations were made at different locations in the Cairns section and the Central Section of the Great Barrier Reef National Park.

Despite the large abundance of coral mucus in reef waters its role for the cycle of matter and the nutrition of the reef is still largely unknown.

External mucus layers of corals are inhabited by communities of marine heterotrophic bacteria (Ducklow & Mitchell 1979). They also postulated that these bacteria are increasing the detrital value of coral mucus.

Coffroth (1990) summarised in her work about *Porites* mucous sheets that their contribution for the nutrition of the reef is very small. However, the role of fluid coral mucus, often observed as particulate matter in reef ecosystems, is controversial. The main goal of this work is therefore to evaluate the significance of coral mucus as carrier and source of carbon and nutrients in the different reef environments. *The corresponding results will be shown in the chapters 7 and 8.*

The coral spawning event

Another kind of particulate matters released by corals are sexual products. Corals are gonochoric (single individuals or colonies have separate sexes), e.g. hydrozoan fire corals (Soong & Cho 1998) or hermaphroditic, e.g. Pocilloporidae and Acroporidae (Steiner & Cortes 1996). A few species (e.g. *Pocillopora*, *Stylophora*, *Seriatopora, Xenia, Heteroxenia*) are brooder, which means that sperms, released into the water, fertilise eggs within the females. Eggs develop to planula larvae within the female polyp and are then released.

But the majority of all reef corals are so-called broadcasting spawner, meaning that they release their gametes (eggs and sperms) directly into the water (Fig. 8 A). Eggs and sperms are released from hermaphrodites as egg-sperm bundles (Fig. 8 C). The eggs are fertilised in the water column and develop to planula larvae, which then settle down at an appropriate place on the seafloor growing up to a polyp which is then budding asexually to a colony.

In the Great Barrier Reef area, but also at many other places in the world word, it was observed that many different broadcasting spawning corals release their gametes synchronously within a very short time.

This so-called coral spawning event is reported to happen just once a year for a few hours and is obviously dependent on a combination of triggering factors (moon phase, water temperature, weather conditions, chemical signalling). This study is mainly interested on the coral spawning event, because during this time period large quantities of energy-rich organic matter are released into the reef waters. It is not really clear what happens to this material, especially if it plays a quantitative role for the nutrition of the reef system, in particular the benthic environment. Therefore, we undertook one expedition to the Australian Great Barrier Reef to exclusively study the effect of the spawning event on benthic metabolism. *The results of this study will be presented in Chapter 9.*

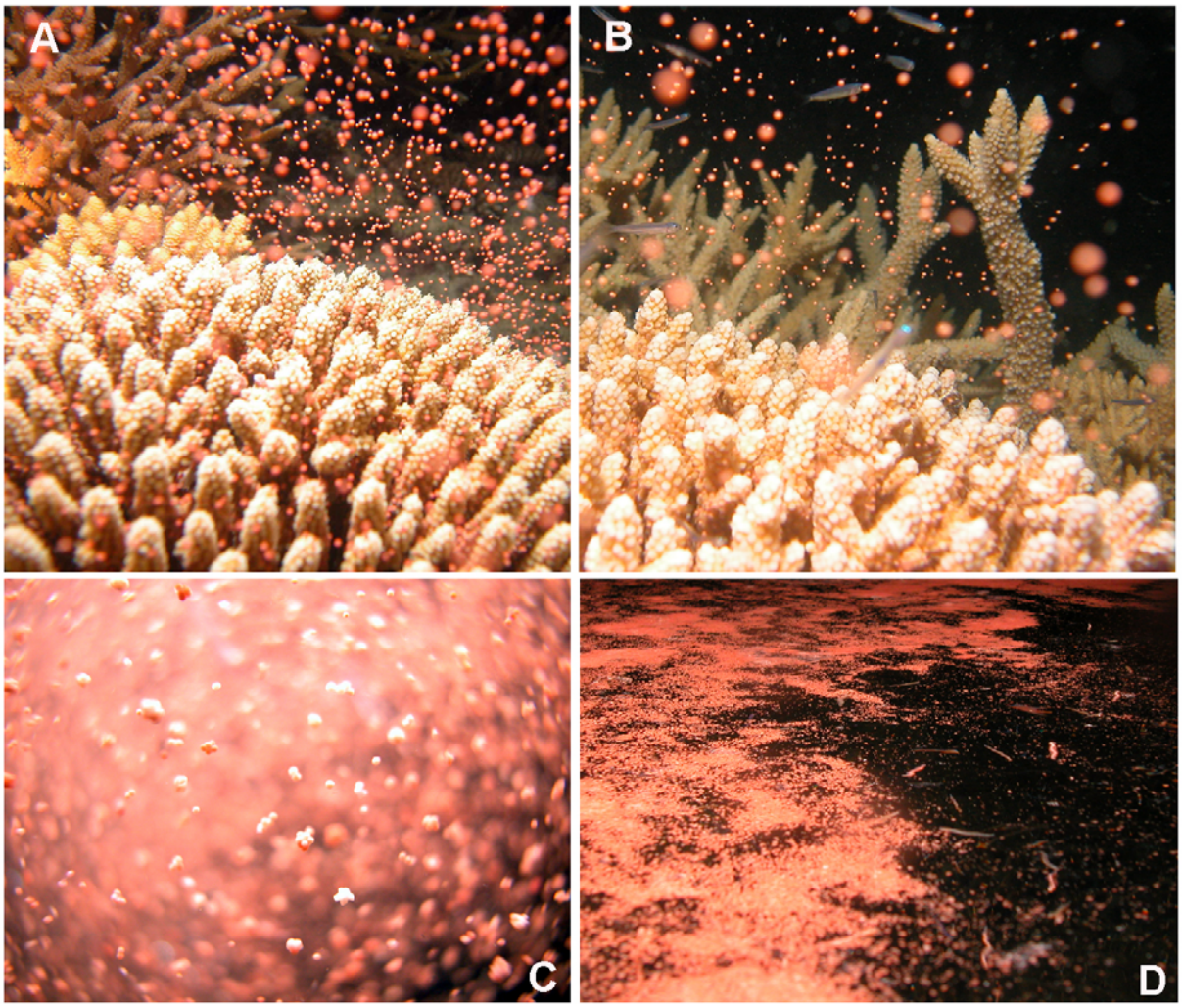

Figure 8. Coral spawning on the reef flat of the Great Barrier Reef location Heron Island in November 2002. A) Massive gamete release by different species of *Acropora*. B) Swarms of fish are feeding on the spawning products. C) High density of egg-sperm bundles in the water column. D) Carpets of egg-sperm bundles on the water surface. All photographs were made by R. Tollrian and kindly provided.

Objectives

This study has two main goals, a general and a more particular one. The general one was to contribute to the ongoing research in the flux group at MPI about permeable shelf sediments, transport processes in these sediments and their importance for organic matter degradation. All work presented in the chapters of this study (except Chapter 6) can be seen in this context. This includes work in shelf areas of the United States East coast, the German Wadden Sea, the Australian Great Barrier Reef and the Northern Read Sea (Egypt).

The particular and core part of this study were the studies in coral reef environments. Here, it was the main goal to investigate the role of carbonate sediments for the degradation of organic matter. As our study object we chose coral exudates as important fraction of the naturally occurring particulate matter in reef environments. We aimed to quantify both, the significance of coral mucus and the seasonal importance of coral sexual products for the nutrition of the reef.

In summary, the objectives of this study are:

1) Investigating the importance of permeability for mineralization of organic matter
2) Quantifying advective pore water flow in permeable sediments by the use of a new tracer method
3) Quantifying the dependence of O_2 consumption in permeable sands on the flow velocity through these sediments
4) Investigating the metabolic reaction of permeable sediments to the supply of dissolved organic matter
5) Quantifying metabolism in carbonate reef sediments
6) Investigating the degradation of the natural substrate coral mucus in carbonate sediments
7) Estimating the importance of coral mucus for energy and nutrient cycles in coral reefs
8) Quantifying the seasonal effect of the coral spawning event on metabolism in carbonate reef sediment

Publications outline

This thesis includes 8 articles. Six of them have been submitted to international journals, whereof four are already accepted for publication. The other two articles will be submitted within the next 3 months. Like mentioned above, should the work with carbonate sediments and coral exudates be understood as the core part of the thesis, including 5 articles presented in the chapters 5-9. The other 3 articles are therefore located in front of the core part of the study, because they contribute importantly to understand the special role of permeable sediments and should be seen in close context to the core work. Two of these introductory articles are the result from studies on the permeable shelf sands of the New Jersey Coast (chapters 3+4), the third one deals with the role of fecal pellets making an otherwise almost impermeable sediment permeable and shows the consequences of higher permeability for organic matter mineralization (chapter 2). All articles appear in the order described in the general introduction (chapter 1).

Within the core work, the first two articles are providing background information about metabolism in coral reef sands (chapter 5) and stress management/mucus production of corals as well about the occurrence of marine snow aggregates in reef waters and their influence on benthic life (chapter 6). The following 2 articles (chapters 7 and 8) are showing the results of the coral mucus studies, including work on the degradation of mucus (chapter 7) and a summary of the coral mucus study including an overall budget for the reef system (chapter 8). Chapter 9, finally, presents the work during and after the coral spawning event.

Publication 1) Wild C., Røy H., Huettel M.

The role of pelletization for mineralization in fine-grained coastal sediments

This study was initiated by M. Huettel. The experiments were carried out by C. Wild and M. Huettel. C. Wild evaluated the data and wrote the manuscript with help and input of M. Huettel and H. Røy. This article will be submitted to Marine Ecology Progress Series.

Publication 2) Reimers C.E., Stecher H.A., Taghorn G.L., Fuller C.M., Huettel M., Rusch A., Ryckelynck N., Wild C.

In-situ measurements of advective solute transport in permeable shelf sands

This study was initiated by C.E. Reimers and M. Huettel. The experiments were carried out by all co-authors, C. Wild contributed with flow-through column experiments. C.E. Reimers evaluated the data and wrote the manuscript with input of all co-authors. This article has been accepted for publication in Continental Shelf Research.

Publication 3) Rusch A., Huettel M., Wild C., Reimers C.E.

Sedimentary oxygen consumption and organic matter turnover in organic-poor, permeable shelf sands

This study was initiated by M. Huettel. The experiments were carried out by M. Huettel, C. Wild. and A. Rusch. A. Rusch and M. Huettel evaluated the data. The manuscript was written by A. Rusch, M. Huettel and C. Wild with input of C.E. Reimers. This article will be submitted to Aquatic Geochemistry.

Publication 4) Rasheed M., Wild C., Franke U., Huettel M.

Benthic respiration and photosynthesis in permeable carbonate sediments from Heron Island, Great Barrier Reef, Australia

This study was initiated by M. Huettel. The experiments were carried out by M. Huettel, C. Wild, U. Franke and M. Rasheed. M. Rasheed evaluated the data and wrote the manuscript with help and input of M. Huettel and C. Wild. This article has been accepted for publication in Estuarine Coastal Shelf Science.

Publication 5) Fabricius K.E., Wild C., Wolanski E., Abele D.

Effects of marine snow and muddy terrigenous sediments on the survival of hard coral recruits

This study was initiated by K. Fabricius, C. Wild and E. Wolanski. The experiments were carried out by C. Wild. C. Wild and K. Fabricius evaluated the data. The manuscript was written by K. Fabricius with input of C. Wild, E. Wolanski and D. Abele. This article has been published in Estuarine Coastal Shelf Science 57 (2003): 613-621.

Publication 6) Wild C., Rasheed M., Werner U., Franke U., Johnstone R., Huettel M.

Degradation and mineralization of coral mucus in reef environments

This study was initiated by M. Huettel and C. Wild. The experiments were carried out by C. Wild, M. Huettel, M. Rasheed, U. Werner, U. Franke and R. Johnstone. C. Wild evaluated the data and wrote the manuscript with help and input of M. Huettel. This article has been accepted for publication in Marine Ecology Progress Series.

Publication 7) Wild C., Huettel M., Kremb S.G., Klueter A., Rasheed M., Jørgensen B.B.

Coral mucus functions as energy carrier and nutrient trap in the reef ecosystem

For this study M. Hüttel and C. Wild did the conceptual design and co-ordination of all experimental work, the main part of all measurements and wrote the manuscript. S. Kremb and M. Rasheed helped with the chamber incubations and subsequent water analyses. A.K. quantified coral distribution on Heron Island. B. Jørgensen contributed with good ideas and advice significantly to the improvement of the manuscript. This article has been submitted to Nature.

Publication 8) Wild C., Huettel M., Tollrian R.

Rapid recycling of coral mass spawning products in permeable reef sediments

This study was initiated by M. Huettel and C. Wild. The experiments were carried out by C. Wild, who also evaluated the data and wrote the manuscript with help of M. Huettel and input of R. Tollrian. This article has been submitted to Marine Ecology Progress Series.

LITERATURE CITED

Acevedo R, Morelock J, Olivieri RA (1989) Modification of coral reef zonation by terrigenous sediment stress. Palaios 4:92-100

Adey WH (1998) Coral reefs: Algal structured and mediated ecosystems in shallow, turbulent, alkaline waters. J Phycol 34:393-406

Al-Horani FA, Al-Moghrabi SM, de Beer D (2003a) The mechanism of calcification and its relation to photosynthesis and respiration in the scleractinian coral *Galaxea fascicularis*. Mar Biol 142:419-426

Al-Horani FA, Al-Moghrabi SM, de Beer D (2003b) Microsensor study of photosynthesis and calcification in the scleractinian coral, *Galaxea fascicularis*: active internal carbon cycle. J Exp Mar Biol Ecol 288:1-15

Aller RC (1982) The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: McCall PL, Tevesz MJS (eds) Animal-sediment relations. Plenum Press, p 53-102

Anthony KRN, Fabricius KE (2000) Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. J Exp Mar Biol Ecol 252:221-253

Bak RP (1978) Lethal and sublethal effects of dredging on reef corals. Mar Poll Bull 1:14-17

Barnes DJ, Chalker BE (1990) Calcification and photosynthesis in reef-building corals and algae. In: Dubinsky Z (ed) Coral reefs. Elsevier, Amsterdam, p 109-131

Barnes DJ, Lough JM (1999) Porites growth characteristics in a changed environment: Misima Island, Papua New Guinea. Coral Reefs 18:213-218

Benner R, Pakulski JD, McCarthy M, Hedges JI, Hatcher PG (1992) Bulk chemical characteristics of dissolved organic matter in the ocean. Science 255:1561-1564

Benson A, Muscatine L (1974) Wax in coral mucus - energy transfer from corals to reef fishes. Limnol Oceanogr 19:810-814

Brown BE (1997) Coral bleaching: causes and consequences. Coral Reefs 16:S129-S138

Brown BE, L.S. H (1985) Assessing the effects of "stress" on reef corals. Adv Mar Biol 22:1-63

Capone DG, Dunham SE, Horrigan SG, Duguay LE (1992) Microbial nitrogen transformations in unconsolidated coral reef sediments. Mar Ecol Prog Ser 80:75-88

Carte BK (1996) Biomedical potential of marine natural products. Bioscience 46:271-286

Charpy-Roubaud C, Charpy L, Sarazin G (1996) Diffusional nutrient fluxes at the sediment-water interface and organic matter mineralization in an atoll lagoon (Tikehau, Tuamotu Archipelago, French Polynesia). Mar Ecol Prog Ser 132:181-190

Coffroth MA (1983) Cyclical formation of mucus sheets by 3 coral species. Amer Zool 23:960-960

Coffroth MA (1990) Mucous sheet formation on poritid corals - an evaluation of coral mucus as a nutrient source on reefs. Mar Biol 105:39-49

Coles S, Strathman R (1973) Observations on coral mucus flocs and their potential trophic significance. Limnol Oceanogr 18:673-678

Crossland C (1987) In situ release of mucus and DOC-lipid from the corals *Acropora variabilis* and *Stylophora pistillata* in different light regimes. Coral Reefs 6:35-42

Crossland C, Barnes D, Borowitzka M (1980) Diurnal lipid and mucus production in the staghorn coral *Acropora acuminata*. Mar Biol 60:81-90

Crossland CJ, Barnes DJ (1983) Dissolved nutrients and organic particulates in water flowing over coral reefs at Lizard-Island. Austr J Mar Freshw Res 34:835-844

D`Andrea AFD, Aller RC, Lopez GR (2002) Organic matter flux and reactivity on a South Carolina sandflat: The impacts of porewater advection and macrobiological structures. Limnol Oceanogr 47:1056-1070

D`Elia CF, Wiebe WJ (1990) Biogeochemical nutrient cycles in coral-reef ecosystem. In: Dubinsky Z (ed) Ecosystems of the world. Coral reef. Elsevier, Amsterdam, p 49-74

Dallmeyer DG, Porter JW, Smith GJ (1982) Effects of particulate peat on the behavior and physiology of the Jamaican reef-building coral *Montastrea annularis*. Mar Biol 68:229-233

Darcy H (1856) Les fontaines publiques de la ville de Dijon. Dalmont

Dauwe B, Middelburg J, Herman P (2001) The effect of oxygen on the degradability of organic matter in subtidal and intertidal sediments of the North Sea area. Mar Ecol Prog Ser 215:13-22

Ding JL, Fung FMY, Chou LM (1999) Novel bioactivities from a coral, *Galaxea fascicularis*: DNase- litte activity and apoptotic activity against a multiple-drug- resistant leukemia cell line. Mar Biotechnolog 1:328-336

Done TJ, Ogden JC, Wiebe WJ (1996) Biodiversity and ecosystem function of coral reefs. In: Mooney HA, Cushman JH, Medina E, Sala OE, Schulze ED (eds) Functional roles of biodiversity: a global perspective. Wiley: Chichester, p 392-429

Ducklow H, Mitchell R (1979) Bacterial populations and adaptations in the mucus layers on living corals. Limnol Oceanogr 24:715-725

Ducklow HW (1990) The biomass, production and fate of bacteria in coral reefs. In: Dubinsky Z (ed) Coral reefs, ecosystems of the world. Elsevier, Amsterdam, p 265-289

Ehrenhauß S, Huettel M (2003) Advective transport and decomposition of chain-forming planktonic diatoms in permeable sediments. Submitted to J Sea Research

Enoksson V, Samuelsson MO (1987) Nitrification and dissimilatory ammonium production and their effects on nitrogen flux over the sediment-water interface in bioturbated coastal sediments. Mar Ecol Prog Ser 36:181-189

Falter JL, Sansone FJ (2000) Hydraulic control of pore water geochemistry within the oxic-suboxic zone of a permeable sediment. Limnol Oceanogr 45:550-557

Ferrier MD (1991) Net uptake of dissolved free amino acids by 4 Scleractinian corals. Coral Reef 10:183-187

Ferrier-Pages C, Gattuso JP, Cauwet G, Jaubert J, Allemand D (1998) Release of dissolved organic carbon and nitrogen by the zooxanthellate coral *Galaxea fascicularis*. Mar Ecol Progr Ser 172:265-274

Ferrier-Pages C, Leclercq N, Jaubert J, Pelegri SP (2000) Enhancement of pico- and nanoplankton growth by coral exudates. Aquat Microb Ecol 21:203-209

Forster S, Huettel M, Ziebis W (1996) Impact of boundary layer flow velocity on oxygen utilisation in coastal sediments. Mar Ecol Prog Ser 143:173-185

Fung FMY, Ding JL (1998) A novel antitumour compound from the mucus of a coral, *Galaxea fascicularis*, inhibits topoisomerase I and II. Toxicon 36:1053-1058

Fung FMY, Tachibana S, Chou LM, Ding JL (1997) Cytotoxic and anticancer agents in mucus of *Galaxea fascicularis*: Purification and characterization. J Mar Biotechnol 5:50-57

Gattuso JP, Buddemeier RW (2000) Ocean biogeochemistry - Calcification and CO_2. Nature 407:311-313

Gattuso JP, Frankignoulle M, Bourge I, Romaine S, Buddemeier RW (1998) Effect of calcium carbonate saturation of seawater on coral calcification. Glob Planet Change 18:37-46

Gattuso JP, Frankignoulle M, Smith SV (1999) Measurement of community metabolism and significance in the coral reef CO_2 source-sink debate. Proc Natl Acad Sci U. S. A. 96:13017-13022

Gibbs RJ (1981) Sites of river-derived sedimentation in the ocean. Geology 9:77-80

Glynn PW (1984) Widespread coral mortality and the 1982-83 El Nino warming event. Environm Conserv 11:133-146

Glynn PW (1993) Coral reef bleaching-ecological perspectives. Coral Reefs 8:181-191

Goreau TF (1964) Mass expulsion of zooxanthellae from Jamaican reef communities after hurricane Flora. Science 145:383-386

Hatcher BG (1988) Coral-reef primary productivity - a beggars banquet. Trends Ecol Evol 3:106-111

Hatcher BG, Imberger J, Smith SV (1987) Scaling analysis of coral reef systems - an approach to problems of scale. Coral Reefs 5:171-181

Hatcher BG, Sanmarco PW (1983) The role of detritus in the metabolism and secondary production of coral reef ecosystems. In: Baker JT, R.M. C, Stark KP (eds) Proceedings Inaugural Great Barrier Reef conference. James Cook University, Townsville, p 317-326

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res 50:839-866

Hoegh-Guldberg O, Jones RJ (1999) Photoinhibition and photoprotection in symbiotic dinoflagellates from reef-building corals. Mar Ecol Prog Ser 183:73-86

Hoegh-Guldberg O, Pearse JS (1995) Temperature, food availability, and the development of marine invertebrate larvae. Am Zool 35:415-425

Hsü K (1989) Physical principles of sedimentology. Springer, Berlin

Hubbard JAE, Pocock YP (1972) Sediment-rejection by recent scleractinian corals: a key to palaeo-environmental reconstruction. Geol Rundschau 61:598-626

Huettel M, Gust G (1992) Impact of bioroughness on interfacial solute exchange in permeable sediments. Mar Ecol Prog Ser 89:253-267

Huettel M, Rusch A (2000) Transport and degradation of phytoplankton in permeable sediment. Limnol Oceanogr 45:534-549

Huettel M, Webster IT (2001) Porewater flow in permeable sediments. In: Boudreau BP, Jørgensen BB (eds) The benthic boundary layer. Oxyford University Press

Huettel M, Ziebis W, Forster S (1996) Flow-induced uptake of particulate matter in permeable sediments. Limnol Oceanogr 41:309-322

Huettel M, Ziebis W, Forster S, Luther GW (1998) Advective transport affecting metal and nutrient distributions and interfacial fluxes in permeable sediments. Geochim Cosmochim Acta 62:613-631

Hutchinson PA, Webster IT (1998) Solute uptake in aquatic sediments due to current-obstacle interactions. J Environ Eng ASCE 124:419-426

Iglesias-Prieto R, Matta JL, Robins WA, Trench RK (1992) Photosynthetic response to elevated temperature in the symbiotic dinoflagellate *Symbiodinium microadriaticum* in culture. Proc Nat Acad Sci USA:302-305

Jahnke RA, Nelson JR, Marinelli RL, Eckman JE (2000) Benthic flux of biogenic elements on the Southeastern US continental shelf: influence of pore water advective transport and benthic microalgae. Cont Shelf Res 20:109-127

Johannes R (1967) Ecology of organic aggregates in the vicinity of a coral reef. Limnol Oceanogr 12:189-195

Johannes RE, Wiebe WJ, Crossland CJ (1983a) 3 patterns of nutrient flux in a coral-reef community. Mar Ecol Prog Ser 12:131-136

Johannes RE, Wiebe WJ, Crossland CJ, Rimmer DW, Smith SV (1983b) Latitudinal limits of coral reef growth. Mar Ecol Prog Ser 11:105-111

Jørgensen BB (1996) Material flux in the sediment. In: Jørgensen BB, Richardson K (eds) Eutrophication in coastal marine ecosystems. American Geophysical Union, p 115-135

Jørgensen BB, Sørensen J (1985) Seasonal cycles of O_2, NO_3 and SO_4 reduction in estuarine sediments - the significance of an NO_3 reduction maximum in spring. Mar Ecol Prog Ser 24:65-74

Kleypas JA, Buddemeier RW, Archer D, Gattuso JP, Langdon C, Opdyke BN (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. Science 284:118-120

Krupp DA (1984) Mucus production by corals exposed during an extreme low tide. Pac Sci 38:1-11

Kushmaro A, Rosenberg E, Fine M, Loya Y (1997) Bleaching of the coral *Oculina patagonica* by Vibrio AK-1. Mar Ecol Prog Ser 147:159-165

Lalli CM, Parsons TR (1997) Biological Oceanography-An introduction. Butterworth-Heinemann

Larkum AWD, Kennedy IR, Muller WJ (1988) Nitrogen fixation on a coral reef. Mar Biol 98:143-155

Lesser MP, Stochaj WR, Tapley DW, Shick JM (1990) Bleaching in coral-reef anthozoans - effects of irradiance, ultraviolet-radiation, and temperature on the activities of protective enzymens against active oxygen. Coral Reefs 8:225-232

Lewis JB (1977) Processes of organic production on coral reefs. Biol Rev Camb Philos Soc 52:305-347

Littler MM, Littler DS, Titlyanov EA (1991) Comparisons of N-limited and P-limited productivity between high granitic islands versus low carbonate atolls in the Seychelles archipelago - a test of the relative-dominance paradigm. Coral Reefs 10:199-209

Lough JM, Barnes DJ (2000) Environmental controls on growth of the massive coral Porites. J Exp Mar Biol Ecol 245:225-243

Markell DA, Trench RK, Iglesias-Prieto R (1992) Macromolecules associated with the cell-walls of symbiotic dinoflagellates. Symbiosis 12:19-31

Marshall M (1968) Observations on organic aggregates in the vicinity of coral reefs. Mar Biol 2:50-55

Marubini F, Atkinson MJ (1999) Effects of lowered pH and elevated nitrate on coral calcification. Mar Ecol Prog Ser 188:117-121

Marubini F, Thake B (1999) Bicarbonate addition promotes coral growth. Limnol. Oceanogr. 44:716-720

Mather P, Bennet I (1993) A coral reef handbook: a guide to the geology, flora and fauna of the Great Barrier Reef, 3rd edn. Australian Coral Reef Society. Surrey Beatty & Sons

Moran PJ (1986) The *Acanthaster* phenomenon. Oceanogr Mar Biol Ann Rev 24:379-480

Moriarty DJW, Pollard PC, Alongi DM, Wilkinson CR, Gray JS (1985) Bacterial productivity and trophic relationships with consumers on a coral reef (MECOR 1). In: Proceedings of the fifth international coral reef congress, Tahiti., p 457-462

Mortensen PB, Hovland MT, Fossa JH, Furevik DM (2001) Distribution, abundance and size of *Lophelia pertusa* coral reefs in mid-Norway in relation to seabed characteristics. J Mar Biol Assoc U.K. 81:581-597

Muscatine L (1980) Productivity of zooxanthellae. In: Falkowski PG (ed) Primary productivity in the sea. Plenum, New York, p 381-402

Muscatine L (1990) The role of symbiotic algae in carbon and energy flux in reef corals. 25:1-29

Muscatine L, D´Elia CF (1978) The uptake, retention, and release of ammonium by reef corals. Limnol Oceanogr 23:725-734

Muscatine L, Porter JW (1977) Reef corals - mutualistic symbioses adapted to nutrient-poor environments. Bioscience 27:454-460

Peters EC (1983) The role of environmental stress in the development of coral diseases and microparasite infestations. Am Zool 23:960-960

Pockley P (1999) Global warming 'could kill most coral reefs by 2100'. Nature 400:98-98

Precht E, Huettel M (2003) Advective pore-water exchange driven by surface gravity waves and its ecological implications. Limnol Oceanogr 48:1674-1684

Rasheed M, Badran M, Huettel M (2003a) Influence of sediment permeability and mineral composition on organic matter decomposition in three sediments from the Gulf of Aqaba, Red Sea. Estuar Coast Shelf Sci 57:369-384

Rasheed M, Badran M, Huettel M (2003b) Particulate matter filtration and seasonal nutrient dynamics in permeable carbonate and silicate sands of the Gulf of Aqaba, Red Sea. submitted to Coral Reefs

Rasheed M, Badran MI, Richter C, Huettel M (2002) Effect of reef framework and bottom sediment on nutrient enrichment in a coral reef of the Gulf of Aqaba, Red Sea. Mar Ecol Prog Ser 239:277-285

Richter C, Wunsch M, Rasheed M, Kotter I, Badran MI (2001) Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. Nature 413:726-730

Riebesell U, Zondervan I, Rost B, Tortell PD, Zeebe RE, Morel FMM (2000) Reduced calcification of marine plankton in response to increased atmospheric CO_2. Nature 407:364-367

Riedl RJ, Huang N, Machan R (1972) The subtidal pump: a mechanism of interstitial water exchange by wave action. Mar Biol 13:210-221

Rogers CS (1983) Sublethal and lethal effects of sediments applied to common Caribbean reef corals in the field. Mar Poll Bull 14:378-382

Rusch A, Forster S, Huettel M (2001) Bacteria, diatoms and detritus in an intertidal sandflat subject to advective transport across the water-sediment interface. Biogeochemistry 55:1-27

Rusch A, Huettel M (2000) Advective particle transport into permeable sediments - evidence from experiments in an intertidal sandflat. Limnol Oceanogr 45:525-533

Schlichter D, Liebezeit G (1991) The natural release of amino acids from the symbiotic coral *Heteroxenia fuscescens* as a function of photosynthesis. J Exp Mar Biol Ecol 150:83-90

Schlichter D, Svoboda A, Kremer BP (1983) Functional autotrophy of *Heteroxenia fuscescens* (Anthozoa: Alcyonaria): carbon assimilation and translocation of photosynthates from symbionts to host. Mar Biol 78:29-38

Schroeder JH, Purser BH (1986) Reef diagenesis. Springer, Berlin

Schuhmacher H (1976) Korallenriffe. BLV Verlagsgesellschaft, München

Schuhmacher H (1977) Ability of fungiid corals to overcome sedimentation. Proc. 3rd Int. Symp. Coral Reefs:503-509

Sebens KP (1994) Biodiversity of coral-reefs - what are we losing and why? Am Zool 34:115-133

Shum KT, Sundby B (1996) Organic matter processing in continental shelf sediments - The subtidal pump revisited. Mar Chem 53:81-87

Sier CJS, Olive PJW (1994) Reproduction and reproductive variability in the coral *Pocillopora verrucosa* from the Republic of Maldives. Mar Biol 118:713-722

Smith SV (1978) Coral-reef area and contributions of reefs to processes and resources of worlds oceans. Nature 273:225-226

Sommer U (1998) Biologische Meereskunde. Springer Verlag, Berlin, Heidelberg, New York

Soong K, Cho LC (1998) Synchronized release of medusae from three species of hydrozoan fire corals. Coral Reefs 17:145-154

Sorokin YI (1993) Coral reef ecology, ecological studies 102. Springer Verlag, Berlin

Sorokin YI (1994) Role of plankton in the turnover of organic-matter on the Great-Barrier-Reef, Australia. Hydrobiologia 308:35-44

Steiner SCC, Cortes J (1996) Spermatozoan ultrastructure of scleractinian corals from the eastern Pacific: Pocilloporidae and Agariciidae. Coral Reefs 15:143-147

Szmant AM (2002) Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? Estuaries 25:743-766

Szmant AM, Gassman NJ (1990) The Effects of prolonged bleaching on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. Coral Reefs 8:217-224

Tardent P (1979) Meeresbiologie. Georg Thieme Verlag, Stuttgart

Thunnel R, Anderson D, Gellar D, Miao Q (1994) Sea-surface temperature estimates for the tropical western Pacific during the last glaciation and their implications for the Pacific warm pool. Quaternary Research 41:255-264

Thurman HV (1993) Essentials of Oceanography, 4th edn. Macmillian Publisher, New York

Trench RK (1979) Cell biology of plant-animal symbiosis. Annu Rev Plant Physiol Plant Molec Biol 30:485-531

Veron JEN (1986) Corals of Australia and the Indo-Pacific. Anguc & Robertson, London/Sydney

Veron JEN (2000) Corals of the world. Australian Institue of Marine Science, Tonsville

Warner ME, Fitt WK, Schmidt GW (1996) The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae in hospite from four different species of reef coral: A novel approach. Plant Cell Environ 19:291-299

Wollast R (1991) The coastal organic carbon cycle: fluxes, sources, and sinks. In: Mantoura RFC, Martin JM, Wollast R (eds) Ocean margin processes in global change. John Wiley & Sons, p 365-381

Wollast R (2003) Continental margins - review of geochemical settings. In: Wefer G, Billet D, Hebbeln D, Jørgensen BB, Schlüter M, van Weering T (eds) Ocean margin systems. Springer-Verlag, Heidelberg, p 15-31

Yallop ML, Dewinder B, Paterson DM, Stal LJ (1994) Comparative structure, primary production and biogenic stabilization of cohesive and noncohesive marine sediments inhabited by microphytobenthos. Estuar Coast Shelf Sci 39:565-582

Ziebis W, Forster S, Huettel M, Jørgensen BB (1996a) Complex burrows of the mud shrimp *Callianassa truncata* and their geochemical impact in the sea-bed. Nature 382:619-622

Ziebis W, Huettel M, Forster S (1996b) Impact of biogenic sediment topography on oxygen fluxes in permeable seabeds. Mar Ecol Prog Ser 140:227-237

Chapter 2

The role of pelletization for mineralization in fine-grained coastal sediments

Christian Wild[1], Hans Røy[1], Markus Huettel[1,2]

[1]Max Planck Institute for Marine Microbiology, Celsiusstr. D-28359 Bremen, Germany
[2]Department of Oceanography, Florida State University, Tallahassee, FL 32306-4320, USA

This chapter has been submitted to Marine Ecology Progress Series.

ABSTRACT

Fecal pellet accumulations of the head-down deposit feeding polychaete *Heteromastus filiformis* can change key parameters of fine-grained Wadden Sea sediments. Permeability and porosity of the pelletized surface layer are increased by 2 orders of magnitude and 30% respectively relative to the surrounding sediment surface. Selective feeding of the polychaetes delivers organic-rich pellets to the sediment surface which initially consume approximately 10 times more O_2 than an equivalent volume of the ambient oxic surface sediment. Advective pore water transport is generated through the otherwise practically impermeable sediment surface layer as a consequence of the increase in permeability caused by deposition of the relatively large (400-500 µm) grain-like pellets and surface topography created by pellet mounds. This leads to deeper O_2 penetration in the pelletized accumulations as shown by O_2 microelectrode profiles. Flow velocity is one of the factors controlling the O_2 concentration and penetration depth in fecal pellet mounds. Incubation experiments in flow-through columns showed that the O_2 consumption in fecal pellets increases by approximately 24 µmol g^{-1} dry mass d^{-1} when the flow rate is increased by 2.8 mL h^{-1}. A faster (1.6 fold increased) degradation of reduced organic C and N contained in the fecal pellets was observed under the influence of flow (70% and 68% C and N degraded, respectively) compared to stagnancy (44% and 40% C and N degraded, respectively) in a 3-week flume incubation. Degradation of organic C and N in the surrounding surface sediment during the same time period was below the detection limit. We conclude that fecal pellets enhance organic matter turnover in fine-grained sediments due to generation of secondary sediment permeability that permits advective transport and thereby a faster mineralization of the deposited organic-rich pellets. Pelletization also may provide a mechanism for the breakup of refractory material derived from reduced sediment depths and thus leads to a more complete mineralization of sedimentary organic matter. Because pelletized sediment surface layers are a common phenomenon in shallow and deep marine environments, pellet deposition may play an important role for the cycling of matter in the ocean.

INTRODUCTION

Both, planktonic organisms like copepods (Haney & Trout 1990, Griffin 2000, Frangoulis et al. 2001), amphipods (Werner 2000), krill (Clarke et al. 1988, Perissinotto et al. 2000), dinoflagellates (Buck et al. 1990), salps (Raghukumar & Raghukumar 1999), chaetognaths (Dilling & Alldredge 1993) or appendicularians (Lopez-Urrutia & Acuna 1999) and benthic invertebrates (e.g. holothurians, oligochaetes, polychaetes and mollusks) process ingested food or sediment to fecal pellets. Fecal pellets can also be an important component of marine snow aggregates in the water column (Bochdansky & Herndl 1992). The size of fecal pellets ranges from <50 µm produced by meiofauna organism or small zooplankton like nauplii and protozoans (Pasternak et al. 2000, Wassmann et al. 2000) to several centimeters in length produced by holothurians (Conde et al. 1991). Planktonic fecal pellets have an important function for the vertical transport of organic matter, because pellet sinking rates can exceed those of their small constituents by far, so that this fine material may otherwise not be deposited (Haven & Morales-Alamo 1966, Gonzalez et al. 2000). Mussels like *Mytilus edulis* and *Cerastoderma edule* produce pseudofaeces (Barille & Cognie 2000, Urrutia et al. 2001), that is non-digested material released in the form of pellets.

In protected coastal zones and nutrient-rich shelf areas, fine-grained deposits can form that have a relatively high organic content. These muddy sediments can locally be of great ecological importance (e.g. upwelling areas, intertidal mudflats) and may also be important for the nutrient cycles in these areas. In such sediments, labile material is consumed immediately by fauna and bacteria. The more refractory material is slowly converted to microbial biomass that represents the main food source for head-down deposit feeders, e.g. the polychaetes *Abarenicola pacifica* (Marinelli 1992), *Clymenella torquata* (Craig & Lopez 1996) and *Heteromastus filiformis* (Clough & Lopez 1993).

H. filiformis (Capitellidae) inhabits intertidal muddy sandflats and produces typical cylindrical fecal pellets (400-500 µm long, 200 µm wide) that are deposited on the sediment surface in small mounds (3-5 mm in height). The pellets are usually black, because *Heteromastus* is ingesting sediment at 10 to 20 cm below the sediment-water interface, where the sediment is dyed black from iron sulfides (Clough & Lopez 1993, Neira & Hopner 1994). Pellet production by *Heteromastus* contributes substantially to the

recycling of detritus and nutrients in the Wadden Sea, especially in areas with high population densities (Neira & Hopner 1993). Fresh fecal pellets contain high amounts of organic carbon, and fine particles in the pellets are richer in organic carbon and protein than usually in fine particle of the deep sediments where *Heteromastus* feeds (Neira & Hopner 1994) suggesting selective uptake of organic-rich particulate matter. Fecal pellets have a relatively long persistence leading to pellet accumulation on the sediment surface. The first indications of these accumulations are the small but conspicuous fecal pellet mounds.

Once brought to the sediment surface, the reduced pellet material is subjected to chemical and biological oxidation. However, these compact fecal pellets have a size spectrum in the range of fine to coarse marine sands, and pellet accumulations or pellet layers may be characterised by permeabilities similar to those of such sands. A surface layer composed of pellets, thus may increase the surface layer permeability of an otherwise "impermeable" sediment .In this article, we term those sediments impermeable that are characterised by permeabilities of $k < 10^{-12}$ m^2.

An increased permeability permits advective transport of water and solutes through the porous layer. In addition, the development of pellet mounds also changes the sediment topography. This alters the small-scale flow regime and produces pressure differences that are the driving forces for advective pore water flows (Huettel & Gust 1992).

Ensuing pore water exchange has consequences for solute concentrations in the upper zone of permeable sediments, e.g. resulting in an increase of oxygen availability for aerobic respiration. Advective transport processes in pellet accumulations thus may cause faster decomposition of the pelletized material, because aerobic mineralization is significantly faster than anaerobic mineralization at low mineralization rates (Dauwe et al. 2001). Our working hypothesis was therefore that pellet formation increases organic matter mineralization in fine-grained sediment.

The deposition of pellet accumulations on the sediment also creates a porous surface that may act as a particle trap. Increased bacterial abundance associated with the pellets may convert this sediment trap into an efficient site for mineralization.

This study aims to quantify the degradation of *H. filiformis* fecal pellets in dependency of flow. For this purpose we conducted experiments in laboratory flumes and flow-through columns.

MATERIAL AND METHODS

Sample origin and collection

The sediment core for the flume experiments originated from an intertidal flat near the town Sahlenburg located on the German North Sea coast. *Heteromastus filiformis* pellets were collected at low tide in October 2002 for subsequent incubation in flow-trough columns and permeability measurements. In addition, all pellets of 40 randomly chosen pellet mounds were collected in separate vials for later determination of O_2 consumption, dry mass (DM), ash free dry mass (AFDM), and carbon and nitrogen content. Sediment samples from 0-2 cm (oxidised zone) and ≥ 10 cm (reduced zone) were taken as references for the measurements of all the parameters shown above.

Natural abundance and development of *H. filiformis* pellet mounds

Natural abundance of *H. filiformis* fecal pellet mounds was determined at Sahlenburg by counting the number of mounds within an area of 0.193 m², defined by a metal frame randomly placed on the sediment surface. In total, 16 frame areas were counted. We distinguished between fresh cone-shaped pellet mounds of black colour and older collapsed brownish/grey pellet mounds. The length and width of the base area of 8 fresh and 8 older mounds was measured to calculate the sediment surface area covered by fecal pellets. The new deposition of fecal pellet mounds during low tide was roughly estimated by counting the pellet mounds within the frame areas at 3 different times within 30 min.

Dry weight, porosity, carbon and nitrogen content of fecal pellets

The dry mass (DM) and porosity of fresh and older pellets was determined by drying the wet pellets at 60° C for 48 hours on pre-weighed filters and subsequent weighing. After determining the DM, C and N values in the pellets were measured by using an elemental analyser (Fisons AT1500).

Permeability measurement of fecal pellets and its dependence on flow

In order to assess the permeability of pellet accumulations, fecal pellets were filled in 2 glass tubes (inner diameter: 0.56 cm) to produce pellet columns of 16 cm length. Permeability (k) was then determined with a constant head permeameter (Klute & Dirksen 1986). One of the columns was left under stagnant conditions between measurements, whereas the other one was subjected to a slow flow trough the column ranging between 3 and 140 mL h^{-1}. Permeability was measured at regular intervals during the following 3 weeks in both columns.

Experimental set-up of the flume

The experiments were performed in a recirculating laboratory flume similar to that described by Ziebis et al. (1996). The open channel of the acrylic flume was 200 cm long, 30 cm wide and 20 cm deep. The drop box (60 cm long, 30 cm wide and 20 cm deep) holding the sediment core with a surface area of 0.3 m² exposed to flow was located 90 cm downstream from the entrance of the open channel. Sub-units of a large sediment block taken from the intertidal flat at low tide were reassembled in the flume to produce a sediment block with the original biochemical stratification. The remaining channel floor was covered with a 1 cm deep layer of natural surface sediment made flush with the core surface. The flume contained 160 L of seawater (salinity 34 PSU), which had been collected at the sampling site. Flow was produced by a propeller (driven by a DC motor) situated in the return conduit. Adjusting the voltage of the motor regulated the flow speed. Flow velocity was monitored by a mechanical flow-meter (Mini- Air-Water 2, Schiltknecht) located about 5 cm above the sediment. The flume was placed in a constant-temperature room in order to keep the water temperature at 10° C. Prior to the experiments, the sediment was allowed to equilibrate for 10 weeks at a flow velocity of 5 cm s^{-1}. After this equilibration period, the vertical stratification of the sediment core showed an oxic zone from the sediment surface down to 3 mm in depth as measured from oxygen profiles. The black FeS- zone was located at 8- 18cm sediment depth.

Oxygen profiles through fecal pellet mounds

The O_2-sensors used in the flume experiments were Clarke type microelectrodes with internal reference and guard cathode (Revsbech 1989). Tip diameters of our electrodes were 20-50 µm, stirring sensitivity less than 1 % and 90% response time about 1 s. The electrodes were calibrated between the O_2 concentration in the mixed water column determined by Winkler titration, and anoxic sediment, assuming a linear current response. When no zero value was available from the sediment, a zero signal was acquired in anoxic water with the same temperature and salinity as the flume water. The amplified signals from a pico-ampermeter were recorded on a strip-chart recorder. The sensors were moved along x, y and z axes by a micro-manipulator. Vertical profiles were measured at intervals of typically 200-250 µm. The position of the sediment-water interface was determined visually.

Impact of flow on O_2 profiles in fecal pellet mounds

We measured the O_2 concentration in the mounds of *H. filiformis* and the surrounding sediment at current speeds of 0 to 10 cm s^{-1} in 2 cm s^{-1} steps.

To test the influence of water flow on oxygen distribution in these mounds, the fecal pellets of one big mound were used to build two mounds arranged close to each other on the sediment surface. One of these artificial mounds was enclosed by an open acrylic tube (height 5 cm) preventing the effect of water flow but permitting access of oxygen-rich flume water. The other was exposed to the flume flow of 6 cm s^{-1}. Oxygen profiles were measured in both artificial mounds at 3 different time intervals (12, 24, 40 hours after the appearance of the original mound on the sediment surface).

Ageing of fecal pellet mounds in the flume

In this experiment, the tip of the electrode was lowered to a depth of 0.5 mm down in freshly produced (younger than 24 hours) fecal pellet mounds. At this position, the O_2 concentration changes in the pellet mounds were measured continuously for 16 hours. These measurements were conducted at two different current speeds (0 and 5 cm s^{-1}).

Flow measurements around fecal pellet mounds

We used 3 approaches to get information about the flow through and around fecal pellet mounds:

a) Dye trail method. Here a red dye (concentrated mallow tea) was adjusted to the seawater density and filled in a reservoir. This reservoir was connected to a small hypodermic needle. The opening of the needle was fixed in the flume about 1 cm upstream of an artifical pellet mound (height: 6 mm) at ca. 0.3 cm above the sediment surface. The dye then was slowly released from the needle and carried along by the unidirectional flow in the flume. We recorded the pathway of the flow patterns by using a digital camera connected to a stereo lens.

b) Potassium permanganate grain. We used a small (≤ 1mm) $KMnO_6$ grain and transferred it carefully to the sediment surface in the flume. Immediately afterwards a pellet mound was constructed above the $KmnO_6$ grain by allowing freshly collected *H. filiformis* pellets to sink down and accumulate around the crystal. Then the flow was started and the free stream velocity was adjusted to 10 cm s^{-1}. We recorded the movement of the purple dye plume coming out of the pellet mound on the downstream middle part of the mound by using time lapsed digital imaging.

c) LDA measurements. A Laser Doppler Anemometer (LDA) (DANTEC™) was used to quantify the horizontal flow velocity around the fecal pellet mound from b) at millimetre scale.

Oxygen consumption of fecal pellets as a function of flow

We used freshly collected pellets from Sahlenburg to fill 12 glass tubes with an inner diameter of 3 mm. A loose packing of the columns with pellets was achieved by allowing the pellets to sink down to the bottom of the tube. The pellet containing tubes were sealed free of air bubbles with glass fibre wool and connected to Tygon™ tubing at both openings. Then air-saturated seawater (same salinity and temperature as the water at the sampling station) was pumped through these columns by a peristaltic pump at a flow rate ranging from 4 to 21 mL h^{-1}. Oxygen was measured up- and downstream of the columns by inserting optic oxygen microsensors (Presens™, for the measuring principle see Klimant et al. 1995) into the flow just above and beneath each column. The maximum O_2

consumption of the pellets was calculated from the O_2 concentration differences between inflow and outflow measured 60 minutes after initiation of the flow. In total, 3 experiments, each with 3-4 pellet columns, were conducted. Table 1 shows an overview of these experiments, their duration and the flow rate applied to each column.

Table 1. Summary of all done flow-through column experiments with freshly collected fecal pellets.

Column Nr.	Pellet history	Column length (cm)	Incubation time (h)	Flow rate (cm/h)
1	20h in fridge	19.0	13	34
2	20h in fridge	18.0	13	37
3	20h in fridge	14.0	13	12
4	20h in fridge	14.5	13	17
5	+ 14 h stagnation at 19° C	13.2	not incubated	used as control
6	+ 14 h stagnation at 19° C	12.0	2	68
7	+ 14 h stagnation at 19° C	13.0	2	59
8	+ 14 h stagnation at 19° C	15.0	2	75
9	42h in fridge	14.8	18	28
10	42h in fridge	14.4	18	16
11	42h in fridge	15.3	18	15
12	42h in fridge	16.8	18	14

At the end of each experiment, the pellets from each column were collected and analysed for dry mass, carbon and nitrogen content.

In the experiment with stagnant conditions, freshly collected pellets of 15 mounds were incubated separately in 10 mL Winkler bottles with ambient seawater in the dark and calculated their O_2 consumption from the O_2 concentration in the bottles measured at regular time intervals. Likewise, replicate aliquots (n=5) of ambient seawater, oxidised surface sediment (0-2 cm sediment depth) and reduced black sediment (>10 cm sediment depth) were incubated and their O_2 consumption was measured. After the incubations, we determined the dry mass and ash free dry mass (AFDM) of the pellets and sediments by drying the material on pre-weight GF/F Filters (Whatman) and subsequent burning at 600° C for 6 hours. Oxygen consumption of the pellets was calculated as µmol O_2 h^{-1} g^{-1}.

Carbon and nitrogen content of fecal pellets as a function of flow

In order to quantify the degradation rate we measured the carbon and nitrogen content of fecal pellets and the surrounding sediment in dependency of flow. Pellets of 10 freshly produced fecal pellet mounds were combined and placed in the flume as 8 new mounds with a shape and height similar to naturally occurring mounds. Half of these mounds were isolated from the flume free flow velocity of 6 cm s^{-1} by enclosing the mounds within the centre of vertical acrylic tubes (height: 6 cm) pushed 1 cm into the sediment. In a second control experiment, 4 acrylic cylinders were also used to prevent water flow from the surrounding sediment. In regular intervals, we took samples of the surface sediment (< 0.5 cm depth) under flow and stagnant conditions. All samples were dried, their dry mass measured and subsequently analysed for C and N content (see above). All results were related to the pellet/sediment dry mass.

RESULTS

Natural abundance and production of *H. filiformis* fecal pellet mounds

Field observations

Natural abundances of *H. filiformis* pellet mounds were counted at low tide at Sahlenburg flat as 76 ± 20 (n=16) mounds per m^2 sediment surface. More than 80% of all mounds counted were collapsed to pellet accumulations on the sediment surface and had a grayish color (Fig. 1b). These pellet accumulations covered on average 150 mm² of the sediment surface, whereas the still cone-like shaped mounds (Fig. 1a) covered only about 40 mm² each. The total fecal pellet coverage of the sediment surface varied between 1-2%. The *H. filiformis* population at the study site produced 15 ± 9 new mounds per hour and m² sediment surface.

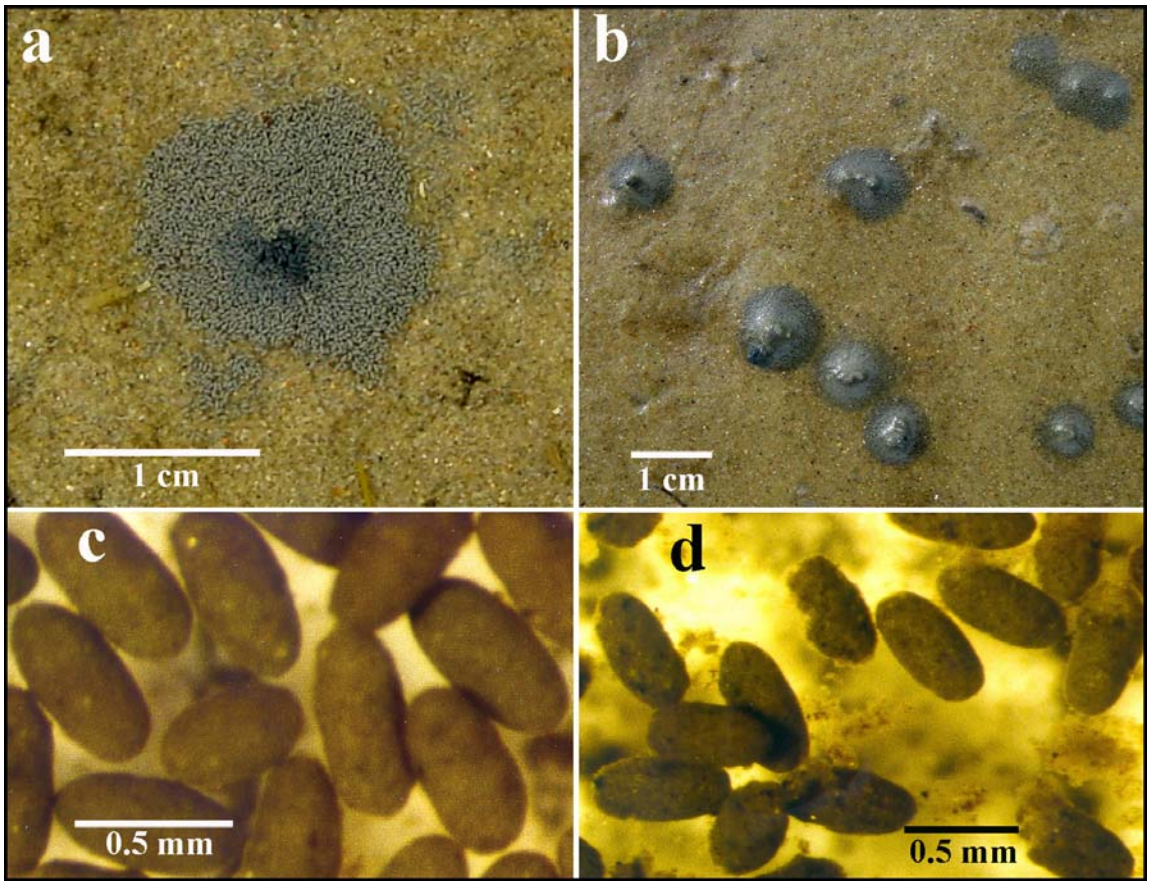

Figure 1. (a) A freshly produced fecal pellet mound with recently released black pellets on the mound top. **(b)** Pellet accumulations on the sediment surface at Sahlenburg. Detailed views on **(c)** fresh fecal pellets and **(d)** 2 week old fecal pellets incubated in the flume.

In general, the pellets were very loosely packed and even weak tidal currents were able to destroy the 3-dimensional shape of the freshly produced mounds converting these pellet mounds into flat pellet accumulations.

Laboratory observations

The sediment core in the flume contained one very active individual of *Heteromastus filiformis* that constructed 8 new mounds within a month. The average lifetime of those visible mounds was about 3 weeks. The deepest burrows of *H. filiformis* reached to a depth of 14 cm.

Permeability, porosity, carbon and nitrogen content of pellet accumulations

The process of pelletization causes a much higher permeability and porosity of the pelletized surface sediment compared to the surrounding sediment not covered with fecal pellets. Table 2 summarizes the characteristics of pellet accumulations and the bulk oxic/anoxic sediment.

Table 2. Characteristics of pellet accumulations in comparison to the bulk sediment. Values are averages ± standard deviation. Permeability value labelled with * is derived from (Ziebis et al. 1996).

	Porosity (%)	Permeability (*10^{-10} m²)	C content (mg/g DM)	N content (mg/g DM)	C:N ratio	O2 consumption (µmol/g DM/d)
Pellets	71.9 ± 2.5	1.22 ± 0.06	25.4 ± 2.6	2.0 ± 0.2	14.5	23.3 ± 8.5
Sediment (oxic)	41.9 ± 1.5	0.05*	2.0 ± 0.4	0.3 ± 0.1	7.0	2.7 ± 0.8
Sediment (anoxic)	34.3 ± 0.7	not measured	1.6 ± 0.6	0.18 ± 0.04	8.5	2.3 ± 0.6

The pellet accumulations on the sediment surface at Sahlenburg were characterised by a much higher porosity compared to the surrounding surface sediment. The permeability (k) of the sediment core in the flume, calculated from the sediments grain size, was in the range of 10^{-12} m^2. (Ziebis et al. 1996) measured similar values (5.4 x 10^{-12} m^2) in sediments from the same sampling site. The permeability in the columns of freshly collected fecal pellets was in the range of 10^{-10}, thus two orders of magnitude higher. Permeability measured in time series revealed that pellet accumulations stay permeable ($k > 10^{-11}$ m²) for at least 15 days under stagnant flow conditions and at least 22 days under the influence of flow. This shows a high temporal persistence of the compact *H. filiformis* fecal pellets. (see also Fig.1c and d in comparison).

The pelletized sediment surface layer is also enriched in organic material. *H. filiformis* fecal pellets contained a 16- and 7-fold increased amount of organic carbon and nitrogen, respectively, compared to the bulk surface sediment. The resulting C:N ratio of 14.5 indicates that the organic material enclosed in the pellets is mostly refractory or of higher plant origin (terrestrial plants or seagrasses) or has been stripped from its nitrogen containing components. An almost 10-fold increased O_2 consumption of pellet accumulations was measured under stagnant conditions relative to the surrounding sediment (Table 2).

Flow distribution through fecal pellet mounds

Due to the high permeability, boundary flows can penetrate into and through the mounds. We were able to observe flow into the pellet mounds via the flow visualization with dye (Fig.2b). Flow could penetrate the pellet mound on the upstream site of the mound. On the downstream site of the pellet mound steady countercurrents occur (Fig.2b), which also transport water into the pellet mound from the downstream site. The velocity of the countercurrent flow is about 60 mm s^{-1} (Figure 2a). The velocity of $KMnO_6$ dye trails leaving the fecal pellet mound was 1.3-2.3 mm s^{-1} at a flume free stream velocity of 100 mm s^{-1}.

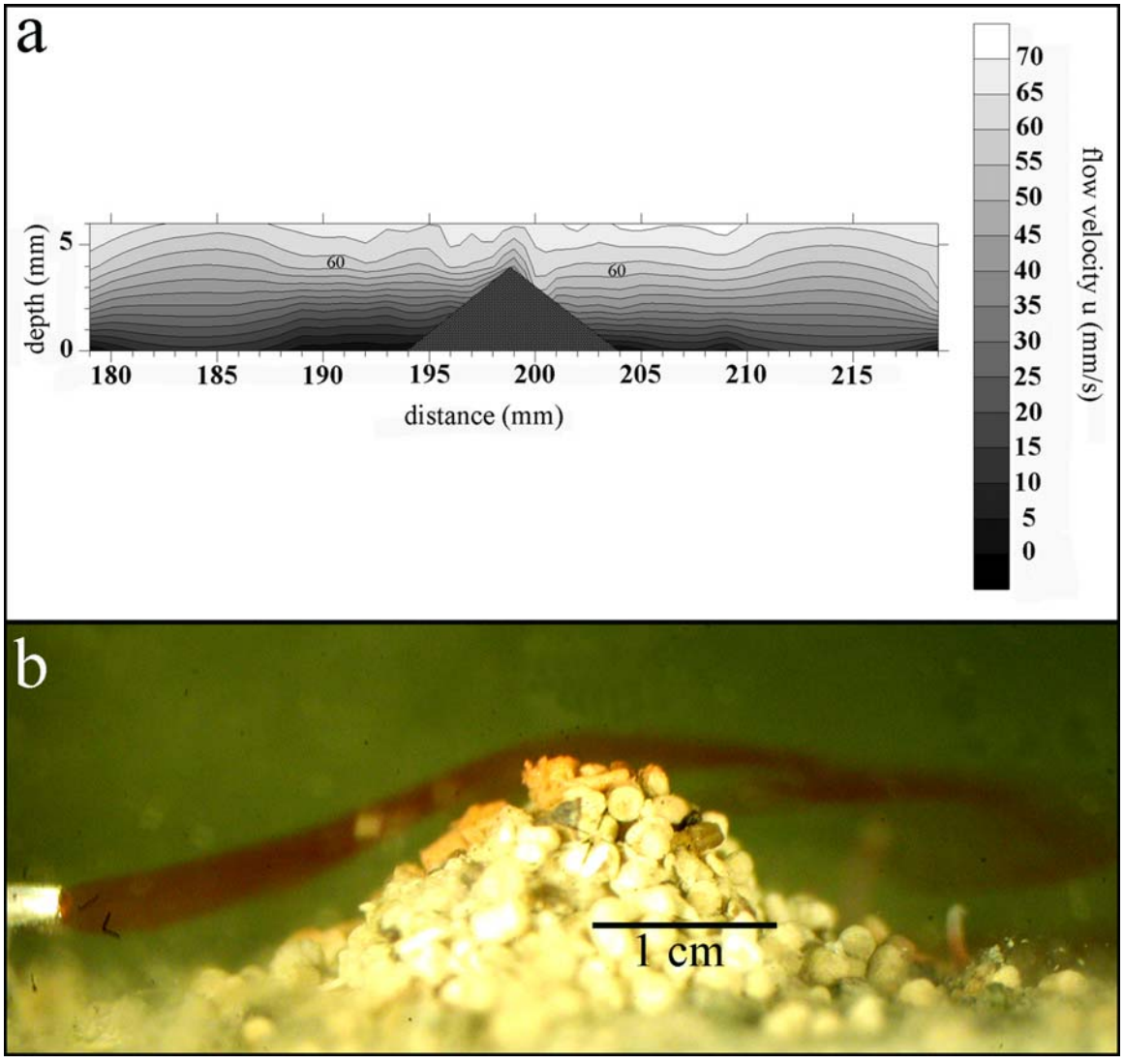

Figure 2. (a) Horizontal flow velocity (in mm s^{-1}) measured with LDA close to a *H. filiformis* fecal pellet mound. **(b)** Flow patterns around a fecal pellet mound visualised with a dye trail method. The bar indicates a length of 1 cm.

Distribution and penetration depth of O_2 in pellet mounds as a function of flow

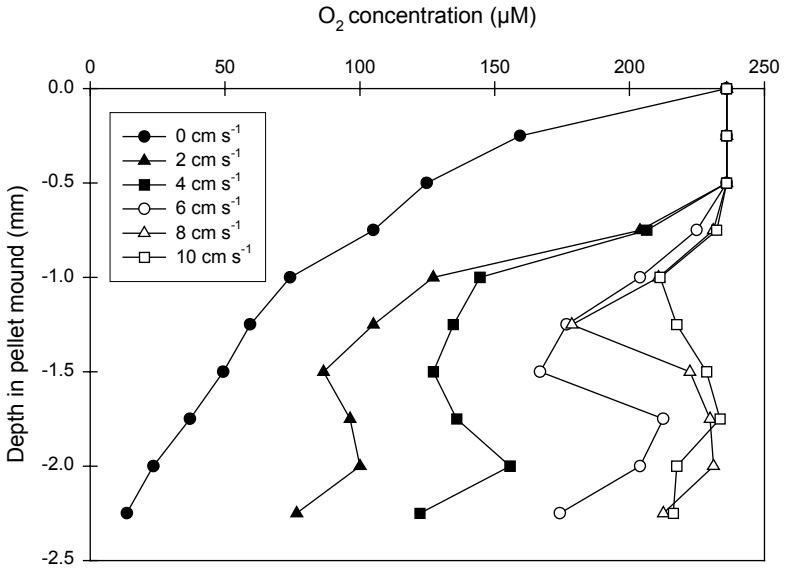

Figure 3. Oxygen profiles within a fresh fecal pellet mound of *Heteromastus filiformis* at different flow velocities.

Flow of water through pellet mounds enhances the O_2 availability and O_2 penetration depth in fecal pellet mounds. Water flow carried O_2 into the mounds even at a flow velocity of 2 cm^{-1}, visible as a distinct change in the oxygen concentration gradient in the upper 0.5 mm of the pellet mound (Fig.3). These advective transport processes lead to an increase of O_2 concentrations in the mounds with increasing flow velocities (Fig.3). Flow velocity, thus, is one of the factors controlling O_2 concentration within pellet mounds.

Under stagnant conditions, a steep O_2 concentration gradient through the pellet mound develops reflecting the effect of relatively slow diffusive transport of O_2 into the mound (Fig.3). The profiles did not reach a steady state, but showed considerable fluctuations over time, probably caused by worm activity.

The production of cone-shaped pellet mounds causes uneven O_2 distribution in the pellet accumulations that differ from the O_2 distribution in the surrounding sediment (Fig.4). At a flow velocity of 6 cm s^{-1}, the microelectrode measurements showed a gradual decrease of O_2 concentration in the pellet mound with depth to a minimum of 167 µM (29% lower than the O_2 concentration in the seawater) at 1.5 mm into the mound followed by an

increase to 213 µM at 1.75 mm mound depth. In contrast, the O_2 profiles in the surrounding sediment decreased continuously with increasing sediment depth. At 2.25mm depth O_2 concentration was 26 µM (71% decrease), whereas the O_2 concentration in the pellet mound at this depth was still 174 µM (26% decrease).

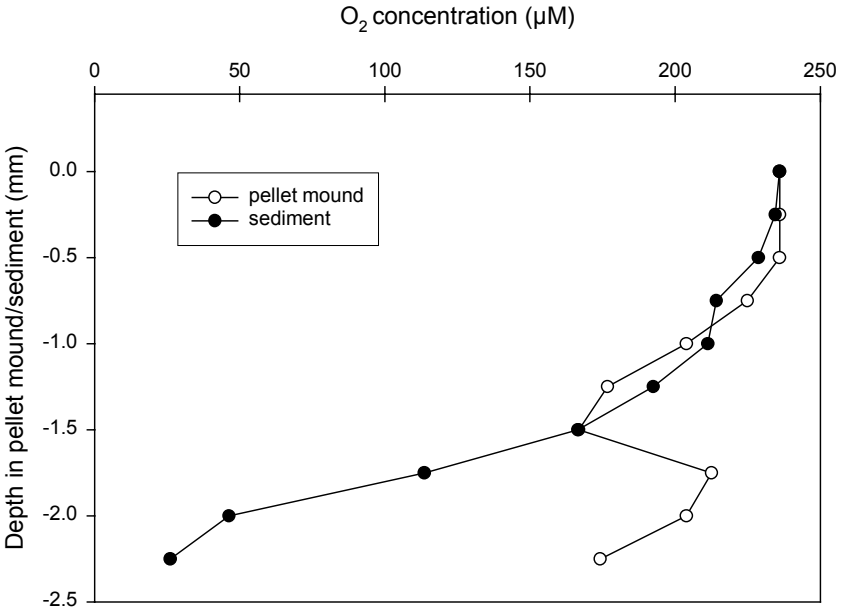

Figure 4. Oxygen profiles through a fresh fecal pellet mound and the surrounding sediment (distance < 5 cm) at a flow velocity of 6cm s^{-1}.

However, the shape of the O_2 profile measured in the sediment (Fig. 4) also indicates some advective transport in the uppermost layer (1-2 mm), because at this sediment depth no O_2 concentration gradient occurs. This is supported by the permeability calculations characterising the sediment permeability in the range of 10^{-12} m^2, thus slightly higher than the definition for impermeable sediments stated in the introduction.

O_2 distribution in fecal pellet mounds over the time

Figure 5 shows the O_2 concentration difference between flow and stagnant conditions in fecal pellet mounds over time. Under stagnant conditions, all O_2 was consumed within 8 hours and no free O_2 could be detected in the mound also after 16 hours. In contrast, at a moderate flow velocity (6 cm s^{-1}) the O_2 concentrations in the mound never reached less than 30% of the seawater O_2 concentration. Figure 4 also indicates that in fecal pellet

mounds, a higher O_2 concentration is maintained over time compared to the surrounding sediment.

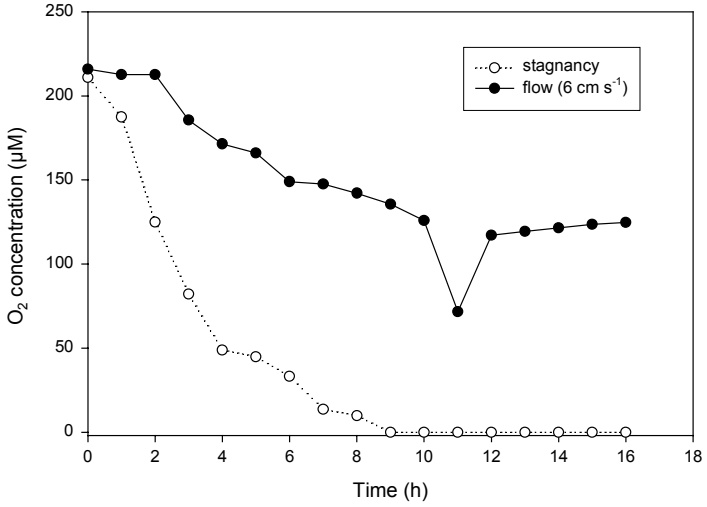

Figure 5. Ageing of fresh fecal pellets (4 hours old) at different flow velocities. O_2 concentrations were measured at 6 cm s^{-1} (solid line) and stagnant flow conditions (dotted line). Measurements were conducted at a depth of 0.5 mm within a faecal mound.

C and N degradation in fecal pellets and the surrounding sediment

A faster decrease in organic C and N content was measured in pellets that were subjected to flow than in those pellets left under stagnant flow conditions (Table 3). Under the influence of flow, 70% of the initial carbon and 68% of the initial nitrogen in the pellets were degraded and mineralised within 3 weeks, whereas under stagnancy only 44% and 40% of the initial C and N were degraded. This corresponds to a more than 1.6 fold increased degradation rate for organic matter under flow compared to stagnant conditions. The degradation rate in fecal pellets, thus, is strongly dependent on the advective water flow through the pellet accumulations.

Also, the carbon and nitrogen content in the surrounding sediment stayed relatively stable during the incubation time of 18 days (Table 3). C and N contents of the surface sediment were slightly but not significantly decreased under flow conditions, but did not decrease under stagnancy.

Table 3. Decrease in C and N content of *H. filiformis* fecal pellets and the surrounding sediment during the ageing process and under flow and stagnant conditions. Decrease in % per day is based on the difference between first and last measured value. Values are given as averages ± standard deviation and in mg (g pellet dry mass)$^{-1}$.

	n	flow (6 cm/s)		stagnancy	
pellet incubation (h)		**C**	**N**	**C**	**N**
2	2	43.4	2.8	43.4	3.0
168	6	20.4 ± 5.2	1.3 ± 0.3	27.4 ± 5.1	1.7 ± 0.4
504	6	13.0 ± 2.6	0.9 ± 0.2	24.2 ± 3.7	1.8 ± 0.3
decrease (% per day)		**3.3**	**3.2**	**2.1**	**1.9**
sediment incubation (h)					
0	4	1.7 ± 0.4	0.09 ± 0.02	1.7 ± 0.4	0.09 ± 0.02
430	3	1.5 ± 0.4	0.08 ± 0.02	1.8 ± 0.5	0.11 ± 0.02
decrease (% per day)		**no difference**	**no difference**	**no difference**	**no difference**

Impact of flow on pellet mound collapse

Pelletization alters the physical characteristics of the sediment. Oxygen micro-profiles measured at specific time intervals in pellet mounds that were exposed to stagnant water or flowing water reflected not only the effect of advective transport on O_2 penetration into the mounds but also the ageing and collapse of the mounds (Fig.6).

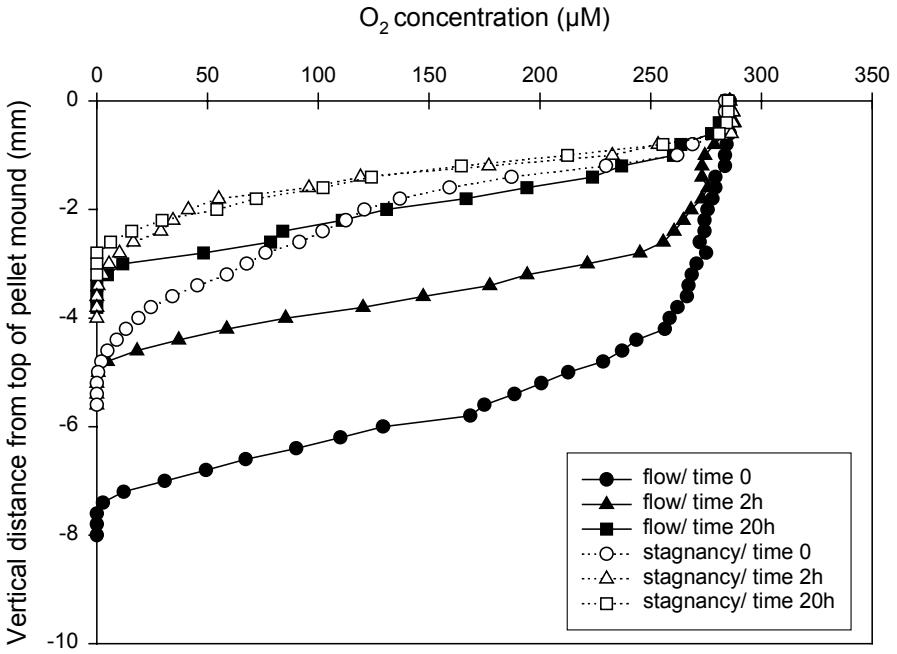

Figure 6. O_2 profiles in fecal pellet mounds with a flow velocity of 6cm s^{-1} (solid lines, closed symbols) and stagnant flow conditions (dotted lines, open symbols). Mound heights were 3 mm. Measurements were done after at the time points 0, 2 and 20 h relative to the occurrence of a fresh mound.

After deposition, O_2 penetration depth into the mounds under stagnant or flow conditions decreased within two hours by approximately 50%. This decrease continued in the mound exposed to flow, while in the mound in stagnant water, O_2 penetration depth remained more or less constant within the next 18 h.

The difference in shape between the oxygen concentration profiles in the mounds exposed to stagnant water or flowing water supports the finding that flow initiated advective pore water flow in the pellet mounds. The first O_2 profiles comparing no-flow and flow situation show this effect of advection on O_2 distribution most clearly. While under stagnant conditions the profile depicts a steep concentration gradient below the sediment surface, reaching zero O_2 at 5 mm depth, boundary flow caused relatively even O_2 distribution in the upper 4 mm in the mounds exposed to flow. Below that depth, a steep decline in O_2 concentration reveals the lack of advection.

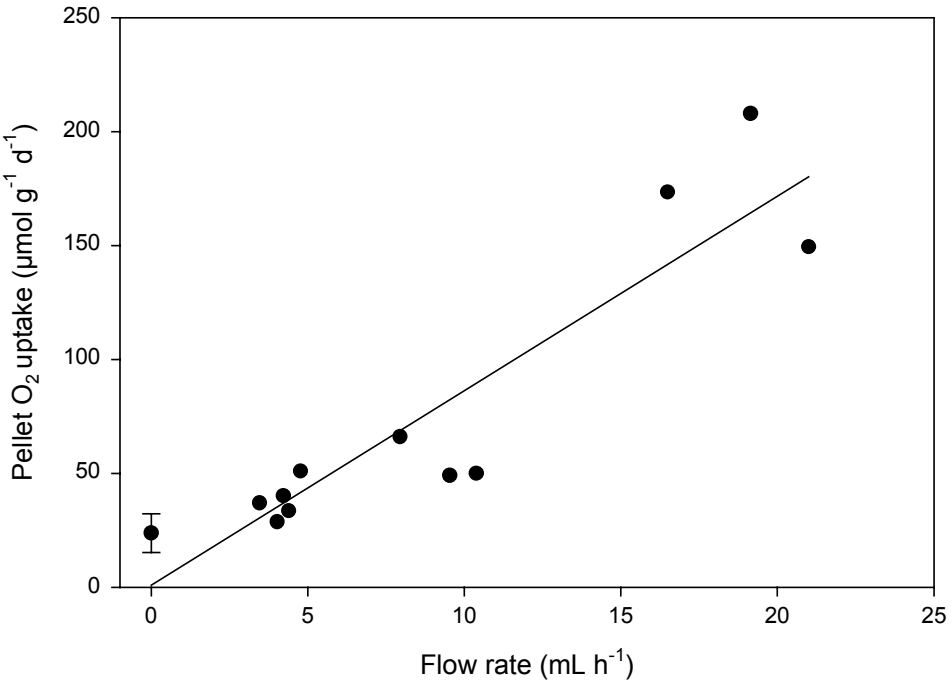

Figure 7. O_2 uptake of fecal pellets in dependence on the flow velocity through them applied in column experiments. The O_2 uptake under stagnant conditions was measured using pellet incubations in Winkler bottles, whereas the error bars are indicating the standard deviation of 15 replicates.

O_2 uptake of fecal pellets as a function of the flow rate

Figure 7 shows the results of all 11 column experiments and indicates that the O_2 uptake of incubated fecal pellets increases with increasing water flow through the columns. Compared to stagnant conditions we found a clear increase in O_2 uptake at flow velocities higher than 28 cm h^{-1} (corresponding to 8 mL h^{-1}, see figure 7). A linear fit ($R^2 = 0.84$) applied to the range of flow rates investigated indicates an increase of approximately 24 µmol g^{-1} d^{-1} when the flow rate is increased by 10 cm h^{-1} (equals 2.8 mL h^{-1}). The flow velocity applied in all column experiments was between 0.04 and 0.20 mm s^{-1}. We assume that the flow velocities applied in our column experiments are similar to those naturally occurring in and downstream of pellet mounds, because of our measurements of 1.3-2.3 mm s^{-1} derived from measuring the velocity of a $KMnO_6$ dye trail leaving a pellet mound (see above).

Table 4. Physico-chemical and biological properties of pellet accumulations on the sediment surface and un-pelletized sediment surface in relative comparison.

	pelletized sediment surface	non-pelletized sediment surface
permeability/grain size/porosity	high	low
main transport mechanism	advection	diffusion
boundary roughness	yes	no
viscous sublayer	no	yes
surface area for exchange processes	large	small
sediment flushing	extensive	almost none
release of reduced substances	yes	no
oxygen penetration	deep	plain
oxygen availability	high	small
organic content	high	low
organic quality	refractory	reactive
organic matter decomposition	fast	slow
meiofauna	abundant	few

DISCUSSION

Effects of pellet production on characteristics of the sediment surface

Our results show that fecal pellets produced by the head-down deposit feeder *Heteromastus filiformis* influence some physical parameters of the fine-grained Wadden Sea surface sediment that are important for the sedimentary mineralization processes. Due to the pelletization, both the porosity and permeability of the sediment surface layer are increased. Neira & Hopner (1993) discovered in their study area Jadebusen Bay an uncompacted fluffy mud layer of pelletal origin building the uppermost sediment layer with a high water content. We found that permeability was about 2 orders of magnitude higher and porosity increased by 30% compared to the fine-grained not pelletized sediment surface. Pellet accumulations on the sediment surface stay permeable for weeks due to the relative stability of the pellets, in contrast to pellets of holothurians, which are disintegrated within hours (Conde et al. 1991). The permeability values of the pellet accumulations were typical for medium to coarse sands, in contrast to the surrounding surface sediment that was characterized by a relatively low permeability. This means that pellet production and deposition at the sediment surface can convert a practically impermeable to a permeable sediment surface. Surface layers of pellet accumulations thus create a "secondary permeability" like mentioned in Huettel & Gust (1992). Our permeability measurements also showed that pellet accumulations stay permeable ($k > 10^{-11}$ m²) for at least 15 days under stagnant flow conditions and at least 22 days under the influence of flow. This is probably caused by the removal of fine sedimentary material by the flow. These measurements indicate the temporal stability of a pelletized and permeable surface layer.

Consequences for transport of water and O_2 into the surface sediment

Impermeable sediments are usually dominated by diffusive transport, whereas permeable sediments are dominated by advective transport of water and solutes through them (Huettel & Webster 2001). In addition, a surface topography created by fecal pellet mounds can also increase advective transport into the permeable sediment (Huettel & Gust 1992, Ziebis et al. 1996).

Our flow visualization around pellet mounds indicates that water flow can penetrate the pellet accumulations and also leads to eddy formation at the downstream edge of pellet mounds (Fig.2). The O_2 profiles through fecal pellet mounds showed a minimum in O_2 concentration in the central part of pellet mounds (Fig.3), which is caused by the largest distance to the surrounding sea water and reduced advective transport due to reversed flow at the downstream site of the mound. This reversed flow weakens the horizontal flow through the mounds entering at the upstream side.

Oxygen penetrated deeper in fecal pellet mounds under the influence of flow than under stagnant conditions (Fig.5 and 6). Both, the absolute penetration depth and the penetration depth difference between flow and stagnant condition decreased with increasing age of the pellet mounds. The decrease in absolute penetration depth may be also caused by a decrease in permeability over the time.

We could show that advective transport of O_2 into the sediment is enhanced by the pelletization process due to the high permeability and turbulent flow patterns caused by the micro-topography of the mounds. The O_2 concentration in pellet mounds directly depends on the flow rate (Fig. 3). This hints to the induction of advective flow by the pellet mounds. Both, O_2 concentration and O_2 penetration depth were increased in pellet mounds compared to the surrounding surface sediment (Fig.4) as a result of the generated advective processes. In summary, O_2 availability over space and time is higher in pellet accumulations compared to the usual smooth and fine-grained sediment surface of our study area. In case of a high density of pellet producing macrofauna, the sediment reworking and fecal pellet formation can fluidize the upper layer of muddy sediments (Rhoads & Young 1970).

Consequences for organic matter degradation

Assuming that the mineralization process is fastest with O_2 as electron acceptor (Dauwe et al. 2001) the pattern of the flow profiles with a central O_2 minimum (Fig. 3) indicates that the degradation of fecal pellet mounds may be most rapid in the top and close to the bottom, whereas the central layer degrades slowest. This results in the highest degradation efficiency at the top of the pellet mounds, because here the freshest fecal pellet material accumulates.

Carbon and nitrogen components are much more rapidly degraded in pellet accumulations compared to the surrounding sediment. In addition, degradation in pellet accumulations was fastest under the influence of flow (Table 3). These findings can be explained by the increased O_2 supply caused by advective transport and a fast removal of metabolic end products via water flow through the permeable pelletized layer. The transport of O_2 into the sediment enhances organic matter decomposition and nitrification (Jørgensen & Sørensen 1985, Enoksson & Samuelsson 1987, Dauwe et al. 2001).

O_2 concentration in fecal pellets over time increased after 12 hours under flow conditions (Fig.5) indicating that chemical and biological oxidation processes in the fecal pellets had passed their maximum and the O_2 supply then was higher than the concurrent uptake. Oxidation and remineralization of the reduced fecal pellet material therefore strongly depends on the flow velocity. These measurements also confirm that boundary flows over fecal pellet mounds produce advective transport of O_2 in the mound and thus increase the O_2 supply.

In addition, the column experiments presented in Figure 7 show that the O_2 consumption of fecal pellets depends on the flow rate, explaining the higher degradation efficiency of organic matter with increased flow through the pelletized layer. Flow induced higher O_2 consumption indicates higher decomposition efficiency. Large microbial populations, detected on the surface of fecal pellets (Reimers 1982, Mattingly 1988), are responsible for the aerobic degradation of organic matter enclosed in fecal pellets.

What kind of organic matter is degraded?

We found a high organic content in the pellets of *H. filiformis* compared to the bulk sediment and also in comparison to sediment from the feeding zone exceeding 10 cm in depth. This is caused by selective feeding on fine particles (Neira & Hopner 1994). Neira & Hopner (1994) also found an increased content of organic C in fresh *H. filiformis* pellets compared to the feeding zone, but their organic C values were only 2.4 fold increased, whereas our results even showed a 16-fold increase in C and a 11-fold increase in N. However, we found 2.5 % C in fecal pellets, a very similar value to the 2% measured by Neira & Hopner (1994). We assume that the C content of Wadden Sea sediment at Sahlenburg was much less than in the Jadebusen Bay, the study area of Neira

& Hopner (1993). Our results confirm a selective feeding behaviour of *H. filiformis*. Clough & Lopez (1993) summarized that *H. filiformis* uses detritus, benthic algae and bacteria as food source, but its C retention efficiencies were very low, i.e. only 4% for detritus. This explains the still high organic content in the pellets and also indicates the refractory character of the ingested food as indicated by the high C:N ratios of between 14 and 15 which we found for the pellets. *H. filiformis* seems to exclusively feed on C sources stored in anoxic and sulfidic sediments that are not utilized by other deposit feeding organisms (Clough & Lopez 1993).

The advective supply of O_2 to this refractory material deposited in fecal pellets at the sediment surface provides a mechanism for the breakup of this relatively inert material and thus accomplishes a more thorough mineralization of sedimentary organic matter (see Table 4). Sulfurization in reduced sediment layers for example can lead to a preservation of organic matter (Damste et al. 1998).

Importance of pelletization for the recycling of matter

We can calculate an annual mean pellet production for Sahlenburg of 0.2 - 2.1 kg m^{-2} (dry mass) based on our pellet production data and the dry mass of 0.033 - 0.383 g for 15 randomly chosen and collected pellet mounds. This corresponds to an annual carbon transport rate of 5-53 g m^{-2} by *H. filiformis* from the anoxic and sulfidic sediment layer to the sediment surface. These estimates are based on October data and, thus, could be overestimates because during winter and early spring the *Heteromastus* population is much less dense. However, Neira & Hopner (1994) reported values of up to 730 g C m^{-2} $year^{-1}$ for the German Jadebusen Bay, Wadden Sea, suggesting that our estimates are not too high. Different population densities at both study sites very likely cause these large differences, but it is also known that pellet production is lowest during the ebbing tide (Neira & Hopner 1993). Because our measurements of pellet production rates took place at low tide, these rates and calculated C transport rates can be seen as the lower limits for October production rates at Sahlenburg. For the Jadebusen Bay, an area at the German North Sea coast which shows a similar tidal periodicity to our study area, it was found that *H.filiformis* is reworking a sediment volume per year corresponding to a sediment layer of 6 cm thickness (Neira & Hopner 1993). These findings in combination with our

study underline the importance of *H. filiformis* activity and pellet formation for the recycling of C and N. Pelletization and ensuing advection can promote a more efficient recycling of material deposited at the seafloor, because of increased degradation rates and the degradation of refractory material. The transport of this material from deeper sediment layers to the sediment surface by *H. filiformis* thus prevents a final burial of organic matter in fine-grained Wadden sea sediments. Sediment reworking by *H. filiformis* may especially important, because of the selective transport of reactive material to the sediment surface. Sand and inorganic particles are not included in the 6 cm sediment layer reworked per year.

The trapping of particles or the resuspension of fecal pellets can additionally increase the recycling of matter caused by a pelletized surface layer. Under high pellet production rates (high animal abundance), rapid accumulation of pellets may produce a thick pellet layer that traps particles from the water column due to advective filtering and thus act as catalyst for the degradation of this matter. This catalytic filtration is enhanced by high enzymatic activity like found for copepod fecal pellets (Bochdansky et al. 1995). Neira & Hopner (1994) discovered that in the presence of meiofauna 15% of the initial pellets and in absence of meiofauna about 96% were intact after 20 days. Meiofauna seem to be specialized on the life within and from fecal pellets. The pelletized surface layer may thus create appropriate microenvironments for organisms like nematodes, ciliates, harpacticoid copepeods and ostracods typical living into the micro-space between sand grains. The pelletization of the surface layer of fine-grained Wadden sea sediments therefore may alter the sedimentary community. We observed at Sahlenburg that *Heteromastus* fecal pellets are easily resuspended because of their small size. Resuspension and transport of polychaete pellets was also observed by Taghon et al. (1984). This further leads to an increased O_2 availability and a resulting faster degradation. Neira & Hopner (1993) estimated that in the Jadebusen Bay, Wadden Sea, the quantity of sediment transported by *H. filiformis* is about 64 L m^{-2} y^{-1} (equals 6 cm y^{-1}). For the Loire estuary, France, Gillet & Gorman (2002) even reported that a dense community of *H. filiformis* transports a sediment layer of 12 cm each year to the surface. Pelletization of the sediment surface by *H. filiformis* therefore seems to be a common situation in coastal areas and may be an important process for the oxidation of reduced

compounds like iron (2+) or manganese (2+). Via pellets, these compounds reach the sediment surface without being oxidized or precipitated. At the sediment surface, these and other reduced compounds are oxidized and regenerated when again transported deeper into the bed. Our O_2 consumption rates of fecal pellets may therefore also reflect the re-oxidation of reduced inorganic compounds.

In many estuarine, coastal and shelf areas, even in the deep sea, there are areas where the surface sediment is composed of pellets (Risk & Moffat 1977, Minoura & Osaka 1992, Bode et al. 1998). This may be most pronounced in upwelling areas where the pelagic pellet production is extreme (Reimers 1982, Brodie & Kemp 1995). The results of this study signify that in such areas the mineralization of organic matter can be enhanced due to the pelletization of the sediment surface.

ACKNOWLEDGEMENTS

We thank M. Alisch, S. Menger and L. Hönemann for assistance concerning sample collection, experimental set-up and subsequent analyses. P. Cook is acknowledged for improving the manuscript. This work was funded by the Max Planck Society (MPG), Germany.

LITERATURE CITED

Barille L, Cognie B (2000) Revival capacity of diatoms in bivalve pseudofaeces and faeces. Diatom Res 15:11-17

Bochdansky AB, Herndl GJ (1992) Ecology of amorphous aggregations (marine snow) in the northern Adriatic Sea .5. role of fecal pellets in marine snow. Mar Ecol Prog Ser 89:297-303

Bochdansky AB, Puskaric S, Herndl GJ (1995) Influence of zooplankton grazing on free dissolved enzymes in the sea. Mar Ecol Prog Ser 121:53-63

Bode A, Varela M, Barquero S, Alvarez-Ossorio T, Gonzalez N (1998) Preliminary studies on the export of organic matter during phytoplankton blooms off La Coruna (north-western Spain). J Mar Biol Assoc U.K. 78:1-15

Brodie I, Kemp AES (1995) Pelletal structures in Peruvian upwelling sediments. J Geol Soc 152:141-150

Buck KR, Bolt PA, Garrison DL (1990) Phagotrophy and fecal pellet production by an athecate dinoflagellate in Antarctic sea ice. Mar Ecol Prog Ser 60:75-84

Clarke A, Quetin LB, Ross RM (1988) Laboratory and field estimates of the rate of fecal pellet production by Antarctic krill, *Euphausia superba*. Mar Biol 98:557-563

Clough LM, Lopez GR (1993) Potential carbon sources for the head-down deposit feeding polychaete *Heteromastus filiformis*. J Mar Res 51:595-616

Conde JE, Diaz H, Sambrano A (1991) Disintegration of holothurian fecal pellets in beds of the seagrass *Thalassia testudinum*. J Coast Res 7:853-862

Craig NI, Lopez GR (1996) Reactive and nonreactive particle dynamics in dense assemblages of the head down deposit feeder *Clymenella torquata*. In: Twenty-fourth annual benthic Ecology Meeting, held in Columbia, South Carolina, March 7-10, p 30

Damste JSS, Kok MD, Köster J, Schouten S (1998) Sulfurized carbohydrates: an important sedimentary sink for organic carbon? Earth Planet Sci Let 164:7-13

Dauwe B, Middelburg J, Herman P (2001) The effect of oxygen on the degradability of organic matter in subtidal and intertidal sediments of the North Sea area. Mar Ecol Prog Ser 215:13-22

Dilling L, Alldredge AL (1993) Can chaetognath fecal pellets contribute significantly to carbon flux. Mar Ecol Prog Ser 92:51-58

Enoksson V, Samuelsson MO (1987) Nitrification and dissimilatory ammonium production and their effects on nitrogen flux over the sediment-water interface in bioturbated coastal sediments. Mar Ecol Prog Ser 36:181-189

Frangoulis C, Belkhiria S, Goffart A, Hecq JH (2001) Dynamics of copepod faecal pellets in relation to a *Phaeocystis*dominated phytoplankton bloom: characteristics, production and flux. J Plankton Res 23:75-88

Gillet P, Gorman E (2002) Population structure and secondary production of *Heteromastus filiformis* (Polychaeta : Capitellidae) in the Loire estuary, France. J Mar Biol Assoc U.K. 82:395-402

Gonzalez HE, Ortiz VC, Sobarzo M (2000) The role of faecal material in the particulate organic carbon flux in the northern Humboldt Current, Chile (23 degrees S), before and during the 1997-1998 El Nino. J. Plankton Res. 22:499-529

Griffin SL (2000) Influence of food type on the production and settling rate of faecal pellets produced by an estuarine copepod. Mar Freshw Res 51:371-378

Haney JF, Trout MA (1990) Relationships between fecal pellet production and feeding in the Calanoid copepod *Boeckella*. J Plankton Res 12:701-716

Haven DS, Morales-Alamo R (1966) Occurence and transport of fecal pellets in suspension in a tidal estuary. Sediment Geol:141-151

Huettel M, Gust G (1992) Impact of bioroughness on interfacial solute exchange in permeable sediments. Mar Ecol Prog Ser 89:253-267

Huettel M, Webster IT (2001) Porewater flow in permeable sediments. In: Boudreau BP, Jørgensen BB (eds) The benthic boundary layer. Oxyford University Press

Jørgensen BB, Sørensen J (1985) Seasonal cycles of O_2, NO_3 and SO_4 reduction in estuarine sediments - the significance of an NO_3 reduction maximum in spring. Mar Ecol Prog Ser 24:65-74

Klimant I, Meyer V, Kühl M (1995) Fiber-optic oxygen microsensors, a new tool in aquatic biology. Limnol Oceanogr 40:1159-1165

Klute A, Dirksen C (1986) Hydraulic conductivity and diffusivity: laboratory methods. In: Klute A (ed) Methods of soil analysis -part 1- physical and mineralogical methods, 2nd edn. American Society of Agronomy

Lopez-Urrutia A, Acuna JL (1999) Gut throughput dynamics in the appendicularian Oikopleura dioica. Mar Ecol Prog Ser 191:195-205

Marinelli RL (1992) Effects of polychaetes on silicate dynamics and fluxes in sediments - importance of species, animal activity and polychaete effects on benthic diatoms. J Mar Res 50:745-779

Mattingly RL (1988) Pelletization of sediment by the deposit-feeding invertebrate *Ptychoptera townesi* (Diptera, Ptychopteridae). Arch Hydrobiol 112:421-431

Minoura K, Osaka Y (1992) Sediments and sedimentary processes in Mutsu Bay, Japan - pelletization as the most important mode in pepositing argillaceous sediments. Mar Geol 103:487-502

Neira C, Hopner T (1993) Fecal pellet production and sediment reworking potential of the polychaete *Heteromastus filiformis* show a tide dependent periodicity. Ophelia 37:175-185

Neira C, Hopner T (1994) The role of *Heteromastus filiformis*(Capitellidae, Polychaeta) in organic carbon cycling. Ophelia 39:55-73

Pasternak A, Arashkevich E, Riser CW, Ratkova T, Wassmann P (2000) Seasonal variation in zooplankton and suspended faecal pellets in the subarctic Norwegian Balsfjorden, in 1996. Sarsia 85:439-452

Perissinotto R, Gurney L, Pakhomov EA (2000) Contribution of heterotrophic material to diet and energy budget of Antarctic krill, Euphausia superba. Mar Biol 136:129-135

Raghukumar S, Raghukumar C (1999) Thraustochytrid fungoid protists in faecal pellets of the tunicate *Pegea confoederata*, their tolerance to deep-sea conditions and implication in degradation processes. Mar Ecol Prog Ser 190:133-140

Reimers CE (1982) Organic-matter in anoxic sediments off central Peru - relations of porosity, microbial decomposition and deformation properties. Mar Geol 46:175-197

Revsbech NP (1989) An oxygen microsensor with a guard cathode. Limnol Oceanogr 34:472-276

Rhoads DC, Young DK (1970) Influence of deposit-feeding organisms on sediment stability and community trophic structure. J Mar Res 28:150-162

Risk MJ, Moffat JS (1977) Sedimentological significance of fecal pellets of *Macoma balthica* in Minas Basin, Bay of Fundy. J Sedim Petrol 47:1425-1436

Taghon GL, Nowell ARM, Jumars PA (1984) Transport and breakdown of fecal pellets: Biological and sedimentological consequences. Limnol Oceanogr 29:64-72

Urrutia MB, Navarro E, Ibarrola I, Iglesias JIP (2001) Preingestive selection processes in the cockle *Cerastoderma edule*: mucus production related to rejection of pseudofaeces. Mar Ecol Prog Ser 209:177-187

Wassmann P, Ypma JE, Tselepides A (2000) Vertical flux of faecal pellets and microplankton on the shelf of the oligotrophic Cretan Sea (NE Mediterranean Sea). Prog Oceanogr 46:241-258

Werner I (2000) Faecal pellet production by Arctic under-ice amphipods-transfer of organic matter through the ice/water interface. Hydrobiologia 426:89-96

Ziebis W, Huettel M, Forster S (1996) Impact of biogenic sediment topography on oxygen fluxes in permeable seabeds. Mar Ecol Prog Ser 140:227-237

Chapter 3

In-situ measurements of advective solute transport in permeable shelf sands

Clare E. Reimers[1], Hilmar A. Stecher III[1], Gary L. Taghon[2], Charlotte M. Fuller[2], Markus Huettel[3,4], Antje Rusch[3,5], Natacha Ryckelynck[1] and Christian Wild[3]

[1]College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis OR 97331 USA

[2]Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick NJ 08901 USA

[3]Max Planck Institute for Marine Microbiology, Celsiusstr. 1, D-28359 Bremen, Germany

[4]Department of Oceanography, Florida State University, Tallahassee, FL 32306-4320, USA

[5]Department of Earth and Planetary Science, Washington University, St. Louis, MO 63130, USA

This chapter has been accepted by Continental Shelf Research.
Only the abstract of the manuscript is displayed. The full-version can be provided upon request.

ABSTRACT

Solute transport rates within the uppermost 2 cm of the sediment column of a continental shelf sand deposit, with a mean grain size of 400-500 μm and permeabilities of 2.0-2.4 x 10^{-11} m^2, have been measured *in situ* by detecting the breakthrough of a pulse of iodide after its injection into the bottom water. These tracer experiments were conducted on the New Jersey USA shelf at a water depth of ~13 m from a small tethered tripod that carried a microprofiling system for positioning and operating a solid-state voltammetric microelectrode, close-up video camera, acoustic current meter and a motorized 1.5-liter "syringe". When triggered on shipboard, the syringe delivered a 0.21M solution of KI and red dye through five nozzles positioned around and above the buried tip of the voltammetric sensor for 0.65 to 5 minutes. Mixing by bottom turbulence and flow quickly dispersed the tracer, and a timed sequence of repetitive voltammetric scans was used to monitor its subsequent migration into the sand. The average one-dimensional vertical velocity, expressed as the depth of the sensor tip in the sand divided by the time to iodide breakthrough, was found to vary from 6 to 53 cm hr^{-1} and to decrease generally with sediment depth. Because of dispersion and episodic pumping associated with the greatest 5% of wave heights and current speeds recorded, some concentration versus time responses showed evidence of uneven solute migration. For reasons of mass balance, the advective flow field in the surface layers of permeable beds includes regions of water intrusion, horizontal pore water flow and upwelling which also may explain some of the observed uneven migration. Pore water advection was also evident in oxygen profiles measured before and after tracer injection with the voltammetric sensor. These profiles showed irregular distributions and oxygen penetration depths of 4- 4.5 cm.

Sand cores from the study site subjected to continuous pore fluid pumping showed that oxygen consumption was positively correlated with rates of flow. The effect was calculated to be equivalent to increasing the benthic oxygen flux by 0.036 mmol m^{-2} d^{-1} for every 1 L m^{-2} d^{-1} flushed through a 5 cm thick oxic zone. Thus, it is concluded that *in situ* oxygen consumption rates must be highly variable and dependent on the prevalent wave and current conditions.

Chapter 4

Benthic O_2 consumption and organic matter turnover in organic-poor, permeable shelf sands

Antje Rusch[1,2], Markus Huettel[1,3], Christian Wild[1] and Clare Reimers[4]

[1]Max Planck Institute for Marine Microbiology, Celsiusstr. 1, D-28359 Bremen, Germany

[2]Department of Earth and Planetary Science, Washington University, St. Louis, MO 63130, USA

[3]Department of Oceanography, Florida State University, Tallahassee, FL 32306-4320, USA

[4]College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis OR 97331 USA

This chapter will be submitted to Aquatic Geochemistry.
Only the abstract of the manuscript is displayed. The full-version can be provided upon request.

ABSTRACT

Boundary currents and high hydraulic conductivity of sandy shelf sediments of the South Atlantic Bight (SAB) cause filtration of water through the surface layers of these beds. In shipboard experiments, sediment cores retrieved from 15 m water depth were flushed at realistic pore water velocities with filtered seawater containing either acetate or 4-methylumbelliferyl-ß-D-glucoside (MUF-Glu) in order to assess the response to addition of dissolved organic matter and to quantify the potential activity of extracellular ß-glucosidases. In a second set of column experiments, the effect of different flushing rates on the oxygen consumption in natural sand cores was assessed. The flushing experiments revealed that the microbial community living in the permeable sands of the SAB shelf reacts promptly on degradable DOC carried into and though the sediment with the water forced into the bed by boundary layer currents. At natural pore water flow velocities, the bacteria growing on the sand grains could decompose added DOC within the sediment before the pore water was released from the bed. The column experiments showed that within the natural range of pore water velocities recorded in these shelf sediments in-situ, the oxygen consumption rate of the sediment increased with pore water velocity. Results suggest that these sands can have oxygen consumption rates exceeding those of fine-grained, organic-rich deposits because they are not limited by diffusional transport. The advective supply with degradable matter and electron acceptors causes that the consumption rate of the bed can change dramatically within time scales of hours to minutes. We conclude that highly permeable sand beds of the South Atlantic Bight are efficient biocatalytical filters that can rapidly react on dissolved organic matter carried into these sediments by the strong boundary layer flows.

Chapter 5

Benthic photosynthesis and oxygen consumption in permeable carbonate sediments at Heron Island, Great Barrier Reef, Australia

Mohammed Rasheed [1], Christian Wild[2], Ulrich Franke[2], Markus Huettel[3]

[1]Marine Science Station, University of Jordan and Yarmouk University, P O Box 195, Aqaba, Jordan

[2]Max Planck Institute for Marine Microbiology, Celsiusstr. D-28359 Bremen, Germany

[3]Department of Oceanography, Florida State University, Tallahassee, FL 32306-4320, USA

This chapter has been accepted for publication in Estuarine Coastal Shelf Science.

ABSTRACT

In order to investigate benthic photosynthesis and oxygen demand in permeable carbonate sands and the impact of benthic boundary layer flow on sedimentary oxygen consumption, in-situ and laboratory chamber experiments were carried out in Heron Island, Great Barrier Reef. Total photosynthesis, net primary production and respiration were estimated to be 162.9 ± 43.4, 98.0 ± 40.7, and of 64.9 ± 15.0 mmol C m^{-2} d^{-1} respectively. DIN and DIP fluxes for these sands reached 0.34 and 0.06 mmol m^{-2} d^{-1}, respectively. Advective pore water exchange had a strong impact on oxygen consumption in the permeable sands. Consumption rates in the chamber with larger pressure gradient (20 rpm, 1.2 Pa between centre and rim) simulating a friction velocity of 0.6 cm s^{-1} were approximately 2-fold higher than in the chambers with slow stirring (10 rpm, 0.2 Pa between centre and rim, friction velocity of 0.3 cm s^{-1}). In the lab chamber experiments with stagnant water column, oxygen consumption was 8 times lower than in the chamber with fast stirring. Lab chamber experiments with Br^- tracer revealed solute exchange rates of 2.6, 2.2, 0.7 ml cm^{-2} d^{-1} at stirring rates of 20, 10, and 0 rpm, respectively. In a laboratory experiment investigating the effect of sediment permeability on oxygen and DIC fluxes, a 3-fold higher permeability resulted in 2 to 3-fold higher oxygen consumption and DIC release rates. Our experiments demonstrate the importance of boundary flow induced flushing of the upper layer of permeable carbonate sediment on oxygen uptake in the coral sands. The high filtration and oxidation rates in the sup-tropical permeable carbonate sediments and the subsequent release of nutrients and DIC reveals the importance of these sands for the recycling of matter in this oligotrophic environment.

INTRODUCTION

In shallow shelf environments, a large fraction of the pelagic organic matter production is deposited at the sea floor, and light reaching the bed permits high benthic primary production (Gibbs, 1981; Jahnke *et al.,* 2000). The sediments in these environments, thus, are expected to have high biogeochemical activity, and the production process in the water column is tightly linked to mineralization in these beds (Walsh, 1988; Jørgensen, 1996). Most of the sediments in the shallow nearshore zone are relatively coarse and permeable because strong bottom currents and waves prevent the deposition of fine particles (Emery, 1968). In such permeable beds, pore water flow is an important transport process (Huettel & Gust, 1992). These advective pore water flows are driven by pressure gradients at the sediment water interface caused by the interaction of boundary currents and seafloor topography or by wave pumping (Huettel & Gust, 1992; Riedl *et al.,* 1972). Such advective transport can enhance the rate of organic matter mineralization (e.g. Forster *et al.,* 1996; Shum & Sundby, 1996), and may make sandy sediments more reactive than cohesive sediments (Reay *et al.,* 1995). Hence, this transport mechanism may be an important process for the cycling of matter in the nearshore environment (Rutgers Van Der Loeff, 1981; Huettel & Gust, 1992; Rhoads & Hecker, 1994).

In subtropical and tropical climates, biogenic sands that consist of carbonates produced mainly by corals, foraminifera, algae, molluscs and echinoderms frequently dominate the sediments in the coastal zone. Due to the high permeability and porosity of carbonate sands, advective transport in carbonate sediments can be very effective (Rasheed *et al.,* 2002). Through their porous grains, these sands have a relatively high specific surface area available for microorganism colonization (Schroeder & Purser, 1986). Dissolution and precipitation reactions of calcium carbonate may enhance the buffer capacity of the sediment, which may enhance organic matter mineralization and nutrient recycling (Sansone, 1985; Tribble *et al.,* 1990, Sansone *et al.,* 1993; Charpy-Roubaud *et al.,* 1996).

In contrast to the terrigenic silicate shelf sediment of colder climes, relatively little is known about the reactivity and organic matter mineralization in carbonate sands. Although coral sands occur wherever corals grow and, thus, are common sediments in subtropical and tropical shallow waters, their role for the cycling of matter in these environments is not well understood. Hardly any information is available on the metabolism in permeable carbonate sands that are flushed by bottom currents and waves. The coarse carbonates can filter organic particles from the water column (Rasheed *et al.,* 2003) and, thus, may be important for the recycling of nutrients in the oligotrophic reef environment.

In this contribution, oxygen consumption and nutrient release were investigated in permeable carbonate sands from an oligotrophic reef environment at Heron Island in the Great Barrier Reef. Solute fluxes from sediments have been studied extensively in order to estimate rates of organic matter mineralization and benthic respiration. Oxygen is energetically the most favorable electron acceptor for microbial aerobic respiration (Fenchel *et al.,* 1998), and the oxygen consumption, thus, is commonly used as an indicator for organic matter mineralization in marine sediments (e.g. Aller, 1980; Smith & Hinga, 1983). A common method for the assessment of benthic fluxes is the laboratory or in-situ chamber incubation of sediment and subsequent monitoring of the solute concentrations changes over time in the enclosed water volume (e.g. Kristensen, 1993; De Master *et al.,* 1996; Nicholson *et al.,* 1999). In-situ incubations have been widely used (see Tengberg *et al.,* 1996 for a review) and may produce more realistic results than the laboratory incubations. The latter suffer from artifacts caused by the removal of the sediment core from its natural environment and the transport to the lab, which may seriously disturb the sediment core. In this study, O_2, dissolved inorganic carbon (DIC), inorganic nutrients and NaBr tracer fluxes were measured in carbonate sands of different permeabilities using laboratory and in-situ chamber incubations. The goals of this study were to assess benthic oxygen uptake and nutrient and DIC production in permeable carbonate sediments and to investigate the effect of advective transport on fluxes of material from these sediments.

MATERIAL AND METHODS

Study site

This study was conducted at Heron Island (23° 27' S, 151° 55' E). The Island (ca. 800 × 200 m) is a true coral cay, situated on the Western end of a platform reef. The reef lies on the Tropic of Capricorn, at the southern end of the Great Barrier Reef, 70 km off the coast of Gladstone (Fig. 1). Heron Island hosts a research station of the University of Queensland with laboratory facilities. In-situ sediment incubations were carried out at Shark Bay, a shallow water site (at ca. 0.2–2.5 m water depth depending on the tide) at the eastern end of the Island. Most of the sediments used for laboratory experiments were also collected from Shark bay. The finer sands were sampled at a site (ca. 3 m deep) in the central area of the reef lagoon.

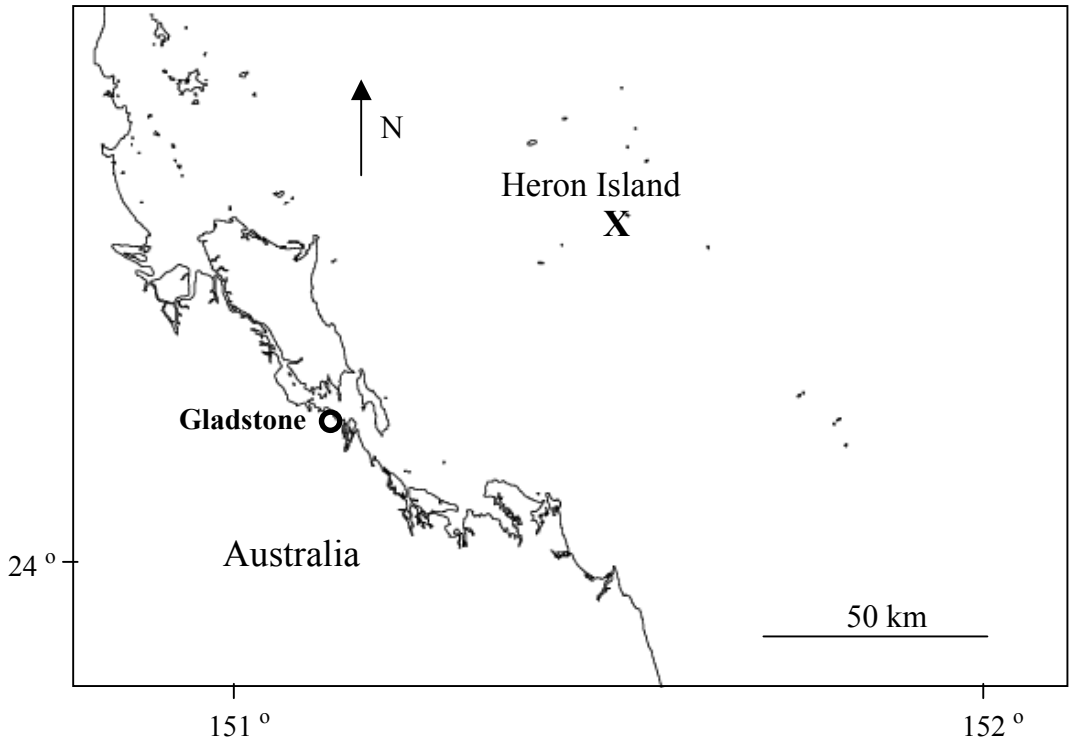

Figure 1. Map showing the location of Heron Island and the town of Gladstone.

Sediment characteristics

Shark Bay (SB) sediments for lab incubations were sieved into two size fractions; coarse (larger than 500 μm) and medium sands (smaller than 500 μm). The finer lagoon sediments had a median grain size of ca 220 μm. Some physical and chemical properties of the sediments that were measured in this study are listed in Table 1. The permeabilities of the sediments were measured using a constant head permeameter as described by Klute and Dirksen (1986). All sediments were highly permeable (> 1×10^{-11} m^2). Sediment porosities were calculated from weight loss of wet sediment after drying at 60°C for 24 h. Specific surface areas of the sediments were determined by measuring nitrogen adsorption to the grain surfaces using a Quantachrome Quantasorb instrument. Particulate organic carbon (POC) and nitrogen (PON) content were measured using an Heraeus CHNO-rapid elemental analyser (Muller *et al.,* 1994) with sulphanilamide as a calibration standard. The samples were pre-treated with 6N HCL till gas development ceased, and then washed twice with distilled water and dried at 60°C.

Table 1. Physical and chemical properties of the sediments used for the different experiments

Sediment	*Surface area ($m^2 g^{-1}$)*	*Permeability (m^2)*	*Porosity % (vol/vol)*	*Median grain size (μm)*	*POC (%)*	*PON (%)*
SB	0.29	1.22×10^{-10}	41.3	838	0.24	0.042
coarse	0.18	3.75×10^{-10}	42.0	829	0.18	0.038
medium	0.31	1.17×10^{-10}	42.7	536	0.21	0.040
fine	0.74	1.37×10^{-11}	42.2	221	0.37	0.048

Incubation experiments

Oxygen, DIC, NaBr and nutrient fluxes were assessed with in-situ and laboratory chamber incubations of natural and sieved sediments (Table 2). The influences of advective pore water exchange and benthic primary production were investigated by applying different stirring and light conditions.

Table 2. Summary of the incubation experiments and measurements carried out in these incubations. u_* is the friction velocity. ΔP & u_* were calculated according to Huettel and Gust (1992).

Experiment	*Sediment used for incubation*	*Light*	*Stirring, pressure gradient & u_**	*No. of incubated cores*	*Measured parameters*
In-situ incubation #1	SB sediments	dark and light	fast (20 rpm, ΔP = 1.2 Pa , $\boldsymbol{u_*}$ = 0.6 cm s^{-1}) slow (10rpm, ΔP = 0.2 Pa , $\boldsymbol{u_*}$ = 0.3 cm s^{-1})	4 (2 dark and 2 light)	O_2, DIC
In-situ incubation # 2	SB	dark and light	fast	6 (4 dark and 2 light)	O_2, DIC , DIN, DIP
Lab incubation # 1	SB	dark	no stirring	6	O_2, DIC
Lab incubation # 2	SB (coarse and medium sediments)	dark	fast	6 (3 coarse and 3 midium)	O_2, DIC
Lab incubation # 3	SB	light	fast, slow and no stirring	6	NaBr

In-situ incubations

Two in-situ incubations were carried out in Shark Bay to estimate O_2, DIC and nutrient fluxes from the natural permeable sediments under different light and stirring conditions. The incubation chambers were transparent cylindrical acrylic containers (19 cm inner diameter, 32 cm high). Flat plastic lids covered the chambers and were fixed by 4 stainless steel clips. The lid contained a sampling port with a syringe holder for water samples and a second port to replace the sampled water. An oxygen optode (Presens) in the lid monitored oxygen concentrations in the chamber water. The water inside the chambers was stirred by a flat rotating disk (15 cm diameter) connected to a DC motor with gear box. The rpm of the stirring disk were adjusted and controlled electronically. The rotating water column generates a radial pressure gradient in the chamber that forces water into permeable sediment close to the chamber wall and out of the sediment in the central area and, thus, can simulate sediment percolation as generated by boundary flow-topography interaction (Huettel & Rusch, 2000). Chambers for all in-situ incubations were deployed during low tide when the height of the water was approximately 0.5 m. The chambers were inserted gently into the sediments to a depth of about 10 cm and thus, included a water column of approximately 22 cm height. The lids then were closed and fixed by the clips. Chambers used for dark incubations were covered with tough opaque black plastic foils secured with rubber bands at the top and the bottom. The waters inside the chambers were stirred either at 20 rpm producing a pressure gradient of 1.2 Pa between center and rim and a friction velocity u_* of 0.6 cm s^{-1} (henceforth termed "fast stirring") or 10 rpm, producing a gradient of 0.2 Pa between center and rim and a u* of 0.3 cm s^{-1} ("slow stirring"). At defined time intervals, dissolved oxygen was measured in the chamber water using the optodes and 100 ml water were removed for DIC, nutrient and bromide analyses and replaced by ambient sea water. The total duration of the incubations was about 8h for the first in-situ incubation and 5h for the second incubation. The volume of water in the chambers was determined after removing the lid of the chambers by measurement of water height with a ruler at 4 different positions in the chamber. Fluxes of solutes were calculated from linear regressions of solute concentrations over time.

Laboratory chamber incubations

Three laboratory chamber incubations were carried out to assess O_2, DIC and bromide fluxes from permeable carbonate sediments (Table 2). The first lab incubation was done with cores from Shark Bay immediately after collection. The chambers were placed in a big container flushed by natural sea water, which kept the temperature of the incubations at the in-situ temperature. For these incubations, small chambers were used (10 cm diameter and 40 cm height). The lengths of the sediment cores were approximately 10 cm and the heights of the water column above the sediments approximately 30 cm. The chambers were sealed by plastic lids with two sampling ports for O_2 measurement and DIC samples. The water column was not stirred during the incubation, except 1 minute before each O_2 measurement and the water sampling to ensure a homogenous water column . Dissolved oxygen was measured in each chamber at different time intervals using a Clark type microelectrode (Revsbech, 1989). For DIC analysis, 10 ml of the water was withdrawn at different time intervals using a syringe and replaced by 10 ml of sea water. The duration of the incubation was approximately 17 h.

The second incubation was done using two sediments of different grain size (coarse and medium, 829 and 536 μm median, respectively) in order to assess the effect of sediment permeability on solute fluxes. The incubation was done using the same chambers that were used for the in-situ incubations. For temperature control, the chambers were placed in the large container as described for the first lab incubation. The height of the sediment columns in the chambers was 16 cm and the chamber water was stirred at 20 rpm. Dissolved O_2 was measured at different time intervals, and water samples were withdrawn for DIC and nutrients (DIP and DIN) analysis during the incubation. The duration of the experiment was 6 hours.

The third incubation was carried out to investigate fluid exchange rates between overlaying water and permeable carbonate sediments under different flow conditions. In this experiment, permeable sediment (ca. 800 µm median) was incubated using the same chambers that were used for the in-situ incubations with three different stirring speeds (20 and 10 rpm and without stirring). Bromide was added to the water overlaying sediments as a solute tracer (~2.05 mM final concentration) in order to facilitate quantification of the water exchange between water column and sediment. Water samples (5ml) were withdrawn at different time intervals for bromide analysis. The duration of the experiment was 6 h.

Oxygen consumption test

This experiment was done to estimate the oxygen consumption rates in four different sediments with different grain sizes and organic matter contents (Table 2); Shark Bay sediments, sieved coarse and medium sediments originating from Shark Bay, and the fine sediments from the lagoon site. 15 cm^3 of each sediment were incubated separately in a gas tight bottle (60 ml) with filtered (0.2 µm) sea water (ca. 45 ml). 3 bottles were used for each sediment type. Oxygen concentrations were measured initially by microelectrode in each bottle. The bottles were then closed tightly, and oxygen concentrations were measured for each sediment type after 2, 12, and 20 h of incubation.

Advective transport in permeable carbonate sediments

The magnitude of sediment-water advective exchange depends mainly on the pressure gradients caused by the interaction of boundary layer flow and sediment topography (Forster *et al.,* 1996) and on sediment permeability (Huettel & Gust, 1992). In this study, the effect of different pressure gradients (generated by the central stirring in the chambers) was investigated in in-situ incubation #1, lab incubation # 1, lab incubation # 3 and the oxygen consumption test (bottle experiment = stagnant conditions). The effect of sediment permeability was investigated in lab incubation # 2.

Benthic photosynthesis measurements

The light and dark chamber incubation technique was used to assess gross and net benthic photosynthesis in-situ. Oxygen output or uptake in light and dark incubations with fast stirring were used for these assessments. Gross primary production (GPP) was calculated from the increase in O_2 concentration in the light chambers. Net primary production (NPP) was calculated by subtracting the sedimentary O_2 consumption (SOC) measured in the dark incubations from Pg.

Oxygen penetration measurement

A new optode technique was used to measure oxygen penetration depth in Shark bay sediment, which produced two-dimensional pictures of oxygen distribution at the sediment water interface (Klimant et al. 1995, Holst and Grunwald 2001). The sediment was transported into open cylindrical chamber (30cm height; 18,5cm inner diameter; 19cm outer diameter) contained an opening of the size of 5 x 2cm to place a planar O_2 optode at the inner side of the chamber. The sediment was left for at least 4 h to settle while the overlaying water was bubbled with air. The chamber was then closed with a lid (air-bubble free), and the overlaying water was stirred during the whole measurement period with the rotating disc at 40 rpm. Images were taken automatically every 2 minutes until the oxygen in the overlaying water was totally consumed

Chemical analysis

Inorganic nutrients (DIP and DIN) were analysed spectrophotometrically following the methods of Grasshoff *et al.* (1999). Bromide concentrations were determined by ion chromatography using a Waters™ cation column (flow rate 1ml min^{-1}, injection volume 100 µl) and NaBr as standard for calibration. Dissolved inorganic carbon (DIC) concentrations in the water samples were measured 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.

RESULTS

In-situ incubations

In-situ incubation #1

Light influenced oxygen and DIC concentrations in the in-situ chambers that were not covered by black foil. O_2 increased gradually, especially in the first 400 minutes of incubation, while DIC concentrations decreased (Fig. 2).

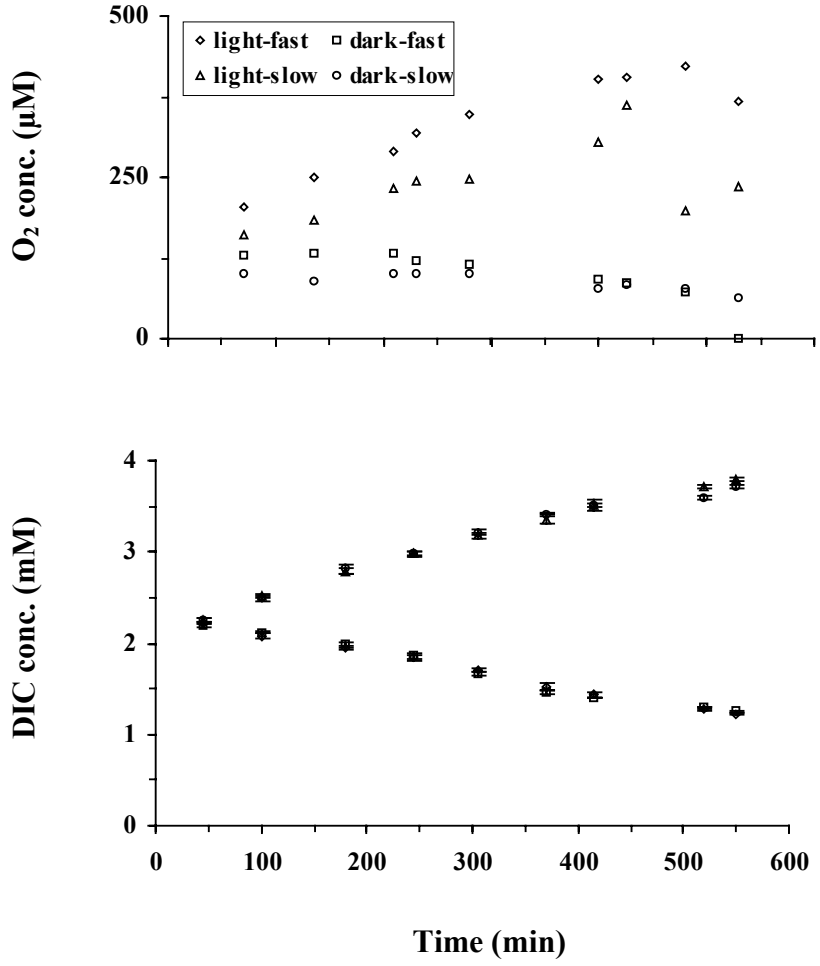

Figure 2. Time course of oxygen (µM) and DIC (mM) during the in-situ chamber incubation 1 with different light and stirring conditions for light-fast (diamond), dark-fast (squares),light-slow (triangles), and dark-slow (circles). Error bars of the DIC concentrations represent the standard deviations of three samples.

In dark chambers, the situation was reversed. Oxygen concentrations decreased to almost zero in one of the dark chambers (Fig. 2), while the DIC concentrations increased. The fluxes of O_2 and DIC calculated from these incubations are shown in Table 3. DIC fluxes were always higher than the oxygen fluxes, irrespective of the direction of the fluxes. The production or consumption rates of O_2 with fast stirring (20 rpm) were higher than with slow stirring (10rpm) (2.25, 2.20 fold respectively, Table 3). The differences in DIC fluxes between slow and fast stirring, however, were not that pronounced (Fig. 2 and Table 3).

Table 3. Benthic fluxes of O_2, DIC, NH_4^+, NO_2^-+NO_3^-, PO_4^{-3}, and Br^- (mmol m^{-2} d^{-1}) in the different chamber incubation experiments. Positive values are efflux out of the sediment and negative values are influx into the sediment.

Experiment	Description	O_2	DIC	NH_4^+	NO_2^- & NO_3^-	PO_4^{-3}	Br^-
In-situ 1	light fast	136.9	-649.0				
	light slow	60.8	-593.2				
	dark fast	-55.8	958.3				
	dark slow	-25.4	912.7				
In-situ 2	light fast	78.6 ± 32.3	-410.7 ± 7.2	0.007	-0.013	-0.115	
	dark fast	-67.2 ± 16.2	444.2 ± 77.0	0.384	-0.041	0.062	
Lab 1	dark, no stirring	-6.8 ± 3.1	28.8 ± 8.0				
Lab 2	medium sand	-5.4 ± 4.1	94.6 ± 15.5				
	coarse sand	-14.9 ± 9.4	206.2 ± 23.9				
Lab 3	fast						-54.0 ± 6.8
	slow						-43.9 ± 4.6
	no stirring						-14.3 ± 4.5

In-situ incubation #2

The second incubation experiment carried out with 6 chambers (4 dark and 2 light) confirmed the results of the first in-situ incubation, and fluxes of O_2 and DIC calculated from these incubations were similar (Table 3). Like in the first in-situ incubation, oxygen was consumed in dark and produced in light in contrast to CO_2 (Table 3). In this incubation, DIN and DIP concentrations were measured, and fluxes of these solutes were calculated (Table 3). NH_4^+ was released both in the dark and in the light with higher flux in the dark (384 vs 7 μmol m^{-2} d^{-1}, respectively). NO_2^-+NO_3^- was higher in the dark (13 μ mol m^{-2} d^{-1}). PO_4^{3-} fluxes, on the other hand, indicated release in dark and uptake in the light chambers (62 vs -11.5 respectively).

Total photosynthesis, net primary production and respiration were calculated using the oxygen fluxes in the dark and light in-situ 1 and 2 incubations with fast stirring. The estimated values were 163 ± 43, 98 ± 41, and 65 ± 15 mmol C m^{-2} d^{-1}, respectively.

Lab incubations

Lab incubation #1

The time course of O_2 and DIC concentrations in the water of the dark laboratory chambers showed the same trend as in the dark in-situ incubations. However, in the lab chambers, which were not stirred, the rates of production and consumption of DIC and O_2 were lower than the rates recorded in the stirred in-situ dark incubation although the same sediments were incubated (Table 3). This shows the impact of stirring on the fluxes of solutes in permeable sediments.

Lab incubation #2

This incubation was done using coarse and medium sands of different permeability (coarse sands had 3-fold higher permeability, Table 1). O_2 consumption and CO_2 production during the incubation (Fig. 3) differed between medium and coarse sediments (Table 3). Oxygen consumption was 5.4 and 15.2 mmol m^{-2} d^{-1} for medium and coarse sediment respectively.

DIC increased gradually with rates of 94.6 and 206.2 mmol m^{-2} d^{-1}. Oxygen consumption and CO_2 production rates were higher in the coarse than in the medium sediment (factor of 3 and 2 respectively, Table 3).

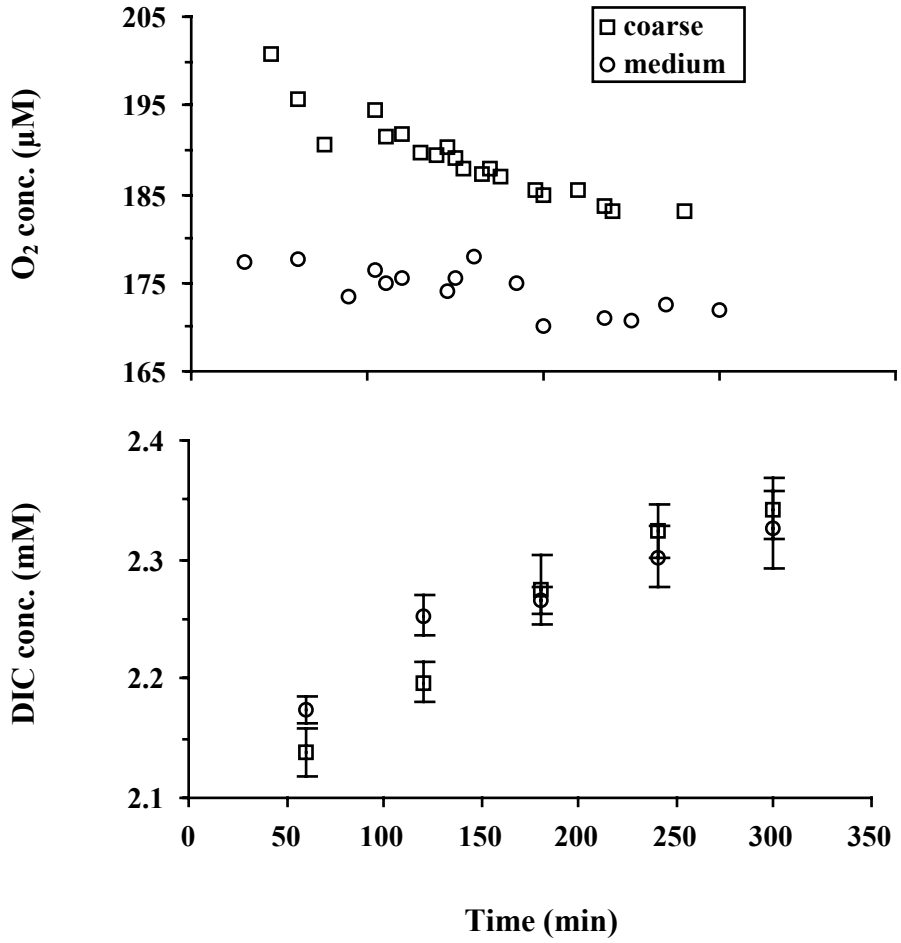

Figure 3. Time course of oxygen (µM) and DIC (mM) during the lab incubation for coarse (squares) and medium sediments (circles). Error bars of the DIC concentrations represent the mean standard deviations of three samples from each chamber.

Lab incubation #3

The sediment used in this experiment was highly permeable (in the range of 10^{-10} m^2) and allowed advective pore water exchange. The concentrations of the Br^- solute tracer decreased faster in the chambers with stirring than in those without stirring (Fig. 4). Calculated exchange rates were 2.6, 2.2, 0.7 ml cm^{-2} d^{-1} for 20, 10, and 0 rpm stirring speeds, respectively.

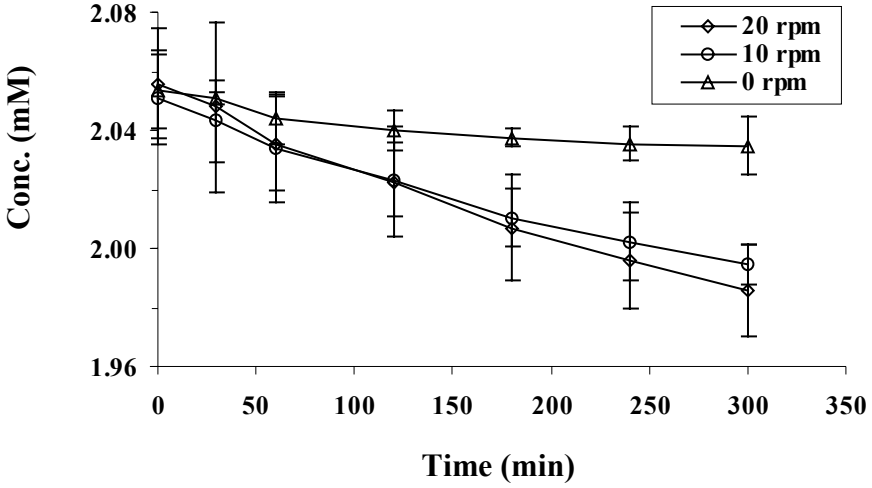

Figure 4. Time course of Br^- concentrations (mM) during lab incubation with a stirring velocity of 20 rpm (diamonds), 10 rpm (circles) and without stirring (triangles). Error bars represent the standard deviations of three incubated chambers for each stirring speed.

Oxygen penetration measurement

The average oxygen penetration depth with 1-2 mm was fairly small and resulted in steep oxygen gradients, although the overlaying water was stirred with relatively high speed (40 rpm). Areas of increased oxygen penetration depth (4-5 mm) were caused locally by bioturbation, indicated at Fig.5 with white arrows. Within the experiments the oxygen penetration depth did not increase (data not shown).

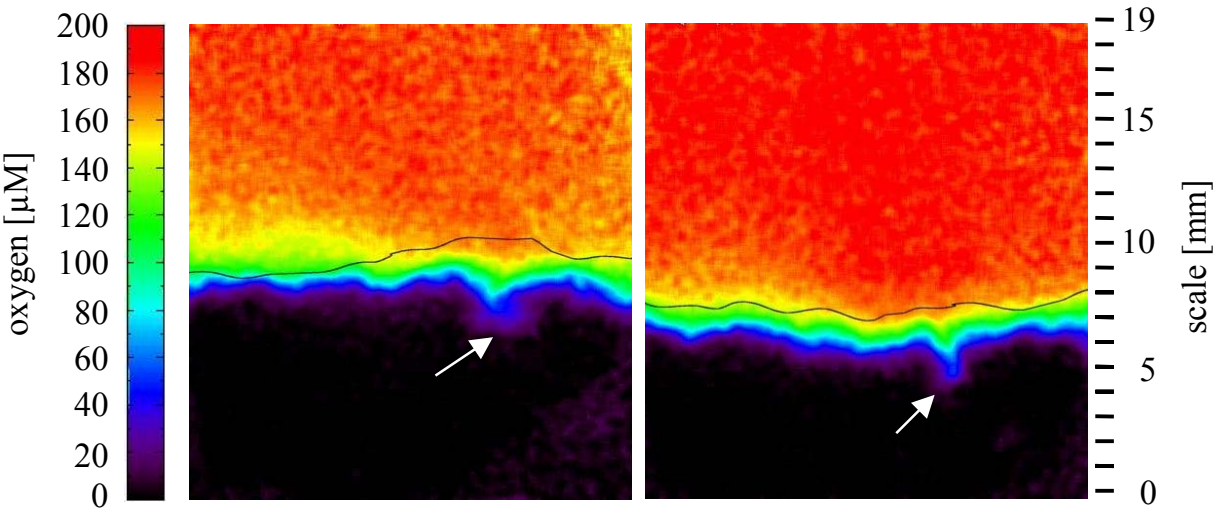

Figure 5. Smoothed (boxcar filter, smoothing value = 4) 2-dimensional oxygen distributions of two different sediment samples from Shark Bay from the start of the experiments. The black line indicates the sediment surface. White arrows indicate locally bioturbation with increased oxygen penetration depth.

Oxygen consumption test

Oxygen consumption in the fine lagoon sediment was approximately 2-fold higher than in medium and coarse Shark Bay sediments (Fig. 6, Table 4). Final oxygen concentrations in the bottles were 36.8, 95.7, and 105.5 µM for fine, medium and coarse sediment, respectively, revealing that consumption rates in coarse and medium sands were comparable (3.37 vs 2.88 mmol m^{-2} d^{-1}). In this bottle incubation, the O_2 consumption rate for the permeable Shark Bay sediments was almost similar to that recorded in the laboratory chamber incubation 1 without stirring (5.12 vs 6.18 mmol m^{-2} d^{-1} respectively).

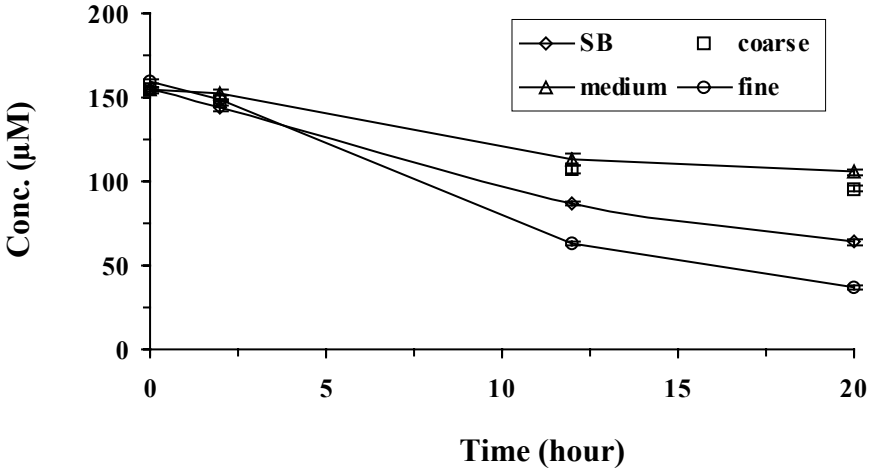

Figure 6. Time course of oxygen concentrations (µM) during the bottle incubation experiment with Shark Bay (diamond), coarse (squares), medium (triangles) and fine (circles) sediments. Error bars represent the standard deviations of three oxygen measurements.

Table 4. O_2 consumption rate (mmol m^{-2} d^{-1}) for different sediments measured in the small bottle incubation.

Sediment	O_2 consumption
SB	5.12
coarse	3.37
medium	2.88
fine	6.90

DISCUSSION

Our study addresses benthic photosynthesis, oxygen consumption and nutrient fluxes in coarse carbonate sands. As demonstrated by the flux of Br^- tracer into the sands, advective pore water exchange is an important mechanism for the transport of metabolites into and out of these permeable sediments. This enhanced transport accelerates the decomposition of sedimentary organic matter (Huettel & Rusch, 2000), and may partly explain the high productivity reported for tropical and subtropical coastal carbonate sediments (e.g. Sorokin, 1995; Charpy-Roubaud *et al.,* 1996; Alongi, 1998).

Benthic flux

The sedimentary consumption of oxygen measured in the in-situ dark incubations with stirring was higher than the consumption measured in other tropical and subtropical coastal sites (Table 5). However, ammonium and phosphate fluxes fell in the range of fluxes measured elsewhere in similar environments (Table 5). With respect to Hines (1985) and Erftemeijer and Middelburg (1993) (Table 5), these authors calculated diffusive fluxes from pore water concentration gradients suggesting that advective pore water exchange (Huettel *et al.,* 1996; Huettel & Rusch, 2000) was not of important, which may explain the smaller fluxes. All our measured fluxes were relatively high. This may be attributed to the high permeability (1.22×10^{-10} m^2) of the investigated sediments and the associated strong advective pore water exchange. Huettel and Gust (1992) and Jahnke *et al.* (2000) have shown the impact of advective pore water flows that enhance solute and particle transport into and out of the sediment. However, solute fluxes between marine sediments and the overlying water can be highly variable. This may be explained by the variability of factors that regulate the sediment water exchange rates, such as temperature (e.g. Alongi, 1998; Clavero *et al.,* 2000), quantity and quality of organic matter supply (e.g. Sloth *et al.,* 1995; Pedersen *et al.,* 1999), physical and chemical properties of the sediment (e.g. Shum & Sundby, 1996; Lopez *et al.,* 1995) and methods of flux estimation (e.g. Bertuzzi *et al.,* 1996).

Organic matter in sediments is mineralized aerobically and anaerobically. Aerobic mineralization uses oxygen as electron acceptor and produces CO_2. The ratio of O_2 : DIC fluxes under these conditions should be 1 (Kristensen, 2000). However, DIC is also

produced by anaerobic processes using electron acceptors such as NO_3^-. HS^- can be produced by sulfate reduction which increases DIC. This can cause the ratio between O_2 consumption and CO_2 production to be smaller than 1. In our incubation experiments, the O_2 : DIC fluxes were always less than 1 (0.03-0.22) suggesting that oxygen consumption accounted only for 3 to 22% of the recorded CO_2 production. O_2 profiles in Shark Bay sediments (fig. 5) indicated a low O_2 penetration depth (1-2 mm) and a highly active anaerobic metabolism with sulfate as the electron acceptor, which could explain the observed small ratios between O_2 consumption and CO_2 production. This is not an unusual phenomenon. In some temperate coastal sediment, oxygen consumption has been estimated to account for only 4-17% of total organic carbon oxidation (Canfield *et al.*, 1993 a, b). Some of the consumed oxygen may be used for the geochemical reoxidation of reduced compounds, which consumes oxygen without producing CO_2. Likewise, in carbonate sediments, like the ones investigated in this study (Table 1), precipitation and dissolution of carbonate minerals may effect the DIC production (Green *et al.,* 1993; Heip *et al.,* 1995). In sediments from the Albufera of Majorca Lopez *et al.* (1995) found a total CO_2 flux of 732 mmol m^{-2} d^{-1} where 336 mmol m^{-2} d^{-1} were due to carbonate re-dissolution.

Flux stoichiometries can give important insights into the processes that govern the sedimentary mineralization of organic matter and the related solute fluxes. The theoretical ratios of O:N and O:P for aerobic mineralization can be calculated from the Redfield ratio (C:N:P = 106:16:1, Froelich *et al.,* 1979) assuming a ratio of 1 for CO_2:O_2 (Berelson *et al.,* 1998). The ratios of O:N and O:P calculated from our flux measurements were 196 and 1084, i.e. much higher than the expected ratios (6.6 and 106 respectively), which indicates that oxygen was consumed by geochemical oxidation processes in the sediment and that our measured nutrient fluxes were low. Denitrification may have reduced the DIN flux (Cowan & Boynton, 1996; Berlson *et al.,* 1998) at the end of incubations when oxygen concentrations were low. Another interpretation of the low N fluxes is the partial conversion of PON into DON that was not measured in our case (Berelson *et al.,* 1998). With respect to DIP, the low flux may be attributed to the high removal of phosphate at the oxic sediment water interface, where it can be bound to the

surface of the carbonate grains (Atkinson, 1987; Ingall & Jahnke, 1993; Bertuzzi *et al.,* 1996, Spagnoli & Bergamini, 1997).

Table 5. Benthic fluxes of Heron Island compared with fluxes measured in other coastal sediments. Positive values are efflux out of the sediment and negative values are influx into the sediment.

Location	NH_4^+ (µmol m^{-2} d^{-1})	PO_4^{-3} (µmol m^{-2} d^{-1})	Oxygen (mmol m^{-2} d^{-1})	References
Araruama Lagoon Brazil	170-1080	(-30)-30	-50.7 ± 12.1	Knoppers et al. (1996)
Kanoeohe Bay, reef flat, Hawaii	490	35		Stimson and Larned (2000)
Ishigaki Island lagoon	67± 60			Miyajima et al. (2001)
South Sulawesi Indonesia	104-306	38-112		Erftemeijer and Middelburg (1993)
Tikehau lagoon Ploynesia	50-704			Capone et al. (1992)
Hiroshima Bay			–12.5 to –38.1	Seiki et al. (1989)
South Atlantic Bight	6 ± 7		-34.8 ± 32.9	Marinelli et al. (1998)
Bermuda	115-312	1-7		Hines (1985)
Gulf of Aqaba, Red sea	338 ± 30	30 ± 2	-5.9 ± 0.5	Rasheed et al. In press.
Heron Island	340	60	-67.2 ± 16.2	This study

Effect of advective exchange

Oxygen consumption and production rates in the chambers with larger pressure gradient (1.2 Pa between center and rim) were ca. 2-fold higher than in those chambers with lower pressure gradient (0.2 Pa between center and rim). The pressure gradients generated by these different stirring velocities compared well with those that are generated by the natural boundary flows interacting with small seabed topography (Huettel & Gust, 1992). The lab experiment #1 and bottle incubation with stagnant water columns support the results of in-situ incubation #1. Oxygen consumption rates in these lab experiments,

where the flux was mainly diffusive, was 9 times lower than in the in-situ chambers with fast stirring where advective transport was active in addition to diffusion. Lab incubation # 3 that compared Br^- solute tracer flux at three stirring speeds (0. 10, 20 rpm), revealed the presence of advective pore water exchange in the SB sediments and confirm the contribution of advection for the results of in-situ incubation #1. Br^- flux in the chamber with fast stirring was significantly higher than in the incubations with slow stirring or without stirring. The exchange rates of 2.6, 2.2, 0.7ml cm^{-2} d^{-1} calculated for 20, 10, and 0 rpm stirring speed suggest that the solute fluxes could be enhanced by factor 3 (10 rpm chamber) and 4 (20 rpm chamber) by advection. We recorded enhancements in oxygen consumption by factor 2 (in-situ exp # 1), which fall in the range suggested by the bromide flux calculations. The larger enhancements of the oxygen fluxes relative to the bromide fluxes by advection may be related to the release of reduced substances from the sediment due to the advective transport. These reduced compounds consume oxygen in the water column and thereby affect the flux.

The additional circulation of the water through the sediment caused by advection carries more oxygen and other electron acceptors (NO_3, SO_4) deeper into the sediment enhancing the mineralization rate of dissolved and particulate organic matter and the oxidation reduced substances as sulfide, ferrous iron (Huettel et al. 1998). The increased decomposition activity causes an enhancement of the release of DIC and DIN.

Berninger and Huettel (1997) investigated oxygen concentrations and photosynthetic oxygen production in intertidal permeable sediments under different flow velocities, and concluded that advective transport in addition to diffusion became effective at boundary layer flow velocities > 2 cm s^{-1}. In flume experiments, applying different boundary flow velocities above incubated sediments, Forster *et al.* (1996) proved that the sedimentary oxygen consumption rate is a function of flow velocity. The authors found that oxygen consumption rate increased by 91 ± 23% in coarse sand when flow velocity increased from 3 to 14 cm s^{-1}. Even in sediments with lower permeabilities an increase in interfacial solute flux of up to 43% has been found for stirred chambers relative to unstirred ones (Callender & Hammond, 1982). Likewise Glud *et al.* (1995) found in stirred flux chambers, a 31% increase of total oxygen uptake when the stirring velocity was changed from 12 to 25 rpm. In fine grained, impermeable sediments, flow velocity affects the

penetration depth and consumption of oxygen in the sediment by controlling the thickness of the diffusive boundary layer (Kristensen, 2000). With increasing flow velocity, the boundary layer is reduced in thickness, which also can enhance solute flux across the sediment-water interface (Jørgensen & Revsbech, 1985, Glud *et al.,* 1994)

Effect of permeability

In lab incubation # 2, oxygen and DIC fluxes were investigated for medium and coarse sands. The permeability of the coarse sand was 3-fold higher than that of the medium sands (Table 1), and 3-fold and 2-fold higher oxygen consumption and DIC production were found in the coarse sand, respectively (Table 3). This confirms the importance of permeability permitting pore water flushing. The latter enhances organic matter mineralization in the sediment and increases oxygen uptake and DIC output. Rasheed *et al.,* (unpubl. data) found 1.5-fold higher organic matter mineralization rates in sediment when permeability increased by a factor of 2. In flume and field experiments comparing degradation of algal material in sediments with different permeabilities, Huettel & Rusch (2000) found a 2.7-fold higher degradation rate in sediment with a permeability of 4.6×10^{-10} m^2 than in sediment with a permeability of 2.8×10^{-11} m^2. Increased oxygen consumption and organic matter mineralization rates with increasing sediment permeability were also reported in other studies (e.g. Marinelli *et al.,* 1998; Dauwe *et al.*, 2001). Increasing sediment permeability increases the circulation of water through the pores of the sediment and thus, enhances the mineralization rates of organic materials (Shum & Sundby, 1996; Huettel & Rusch, 2000). However, without water flow above the sediment, different sediment permeabilities would not affect the mineralization rate as shown in our bottle incubations (Table 4). However, the fine sediments that had a lower permeability (Table 1), had a higher oxygen consumption rate than the coarse and medium sands. This can be attributed to the higher organic content in this sediment (0.42%) compared to the coarse and medium sediments (0.22, and 0.25%) and the higher specific surface area of the fine sediment. In this experiment, which was carried out without stirring, only diffusion controlled the transport of electron acceptors for the mineralization of organic matter. In this case, permeability can be neglected, and the

main factor, which controls the mineralization rates is organic matter content and reactive surface area (e.g. Kelly & Nixon, 1984).

Conclusions

Carbonate sands of the Heron Island lagoon have relatively high oxygen consumption rates. This can be attributed to the relatively high permeabilities of these sediments, which permits high advective solute exchange and deep penetration of metabolites in the sediment as a result of the current, wind and wave action above the permeable sea bed (Riedl *et al.,* 1972; Vanderborght *et al.,* 1977; Webster & Taylor, 1992). The enhanced solute exchange increases organic matter mineralization rates and the oxidation of reduced compounds in the sediment. In the shallow lagoon, benthic photosynthesis is very active and contributes significantly to the oxygen dynamics at the sea floor. Carbonate sands found mainly in tropical and subtropical reef regions cover approximately 10% of the continental shelves. These regions have been reported to exhibit high productivity (Sorkin, 1995), although reef waters usually have very low nutrient concentrations (D'Elia & Wiebe, 1990). Cloren (1996) suggested that productivity in shallow coastal ecosystems is closely associated with sea floor biogeochemical processes. High permeability, porous grains, and the mineralogy of carbonate sands may be important factors that make these sands suitable for organic matter degradation. Carbonate sands may act as a buffer in regulating the pH of interstitial waters (Tribble, 1993), which may affect mineralization of organic material in these sands. We propose that permeable carbonate sands play an important role for the nitrogen, phosphate and carbon cycling in tropical and subtropical regions.

ACKNOWLEDGEMENTS

The Max Planck Society (MPG) has funded this work. Thanks are due to Martina Alisch for her help in the field and the lab. We wish to thank the staff and member of the research station in Heron Island for providing the lab facilities for this work. We would like also to thank Hella Buschhoff and Dr. Peter Müller from the Geology Department, Bremen University for their assistance in the determination of POC and PON. Thanks are due to Dr. Martin Kölling from Geology Department, Bremen University for his

assistance in the determination of sediment surface area. We thank Ingo Klimant and Gregor Liebsch for the preparation of the O_2 planar optodes. Gerhard Holst and Björn Grunwald are thanked for the help with the electronics and the maintenance of the MOLLI system, the Image acquisition and Image processing software. Georg Herz is thanked for the building of the stirring chambers.

LITERATURE CITED

Aller, R. C. 1980 Diagenetic processes near the sediment-water interface of Long Island Sound: II. Fe and Mn. *Advances in Geophysics* **22**, 351-415.

Alongi, D. M. 1998 *Coastal Ecosystem Processes*, CRC Press, Boca Raton, FL, 419 pp.

Atkinson, M. J. 1987 Low phosphorus sediments in a hypersaline marine bay. *Estuarine Coastal and Shelf Science* **24**, 335-347.

Berelson, W. M., Heggie, D., Longmore, A., Kilgore, T., Nicholson, G. & Skyring, G. 1998 Benthic nutrient recycling in Port Phillip Bay, Australia. *Estuarine Coastal and Shelf Science* **46**, 917-934.

Berninger, U. G. & Huettel, M. 1997 Impact of flow on oxygen dynamics in photosynthetically active sediments. *Aquatic Microbial Ecology* **12**, 291-302.

Bertuzzi, A., Faganeli, J. & Brambati, A. 1996 Annual variation of benthic nutrient fluxes in shallow coastal waters (Gulf of Trieste, Northern Adriatic Sea). *Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I* **17**, 261-278.

Callender, E. & Hammond, D. E. 1982 Nutrient exchange across the sediment-water interface in the Potomac river estuary. *Estuarine Coastal and Shelf Science* **15**, 395-413.

Canfield, D. E., Jørgensen, B. B., Fossing, H., Glud, R., Gundersen, J., Ramsing, N. B., Thamdrup, B., Hansen, J. W., Nielsen, L. P. & Hall, P. O. J. 1993 Pathways of organic carbon oxidation in three continental margin sediments. *Marine Geology.* **113**, 27-40.

Canfield, D. E., Thamdrup, B. & Hansen, J. W. 1993 The anaerobic degradation of organic matter in Danish coastal sediments: Iron reduction, manganese reduction, and sulfate reduction. *Geochimica et Cosmochimica Acta* **57**, 3867-3883.

Capone, D. G., Dunham, S. E., Horrigan, S. G. & Duguay, L. E. 1992 Microbial nitrogen transformations in unconsolidated coral-reef sediments. *Marine Ecology Progress Series* **80**, 75-88.

Charpy-Roubaud, C., Charpy, L. & Sarazin, G. 1996 Diffusional nutrient fluxes at the sediment-water interface and organic matter mineralization in an atoll lagoon (Tikehau, Tuamotu Archipelago, French Polynesia). *Marine Ecology Progress Series* **132**, 181-190.

Clavero, V., Izquierdo, J. J., Fernandez, J. A. & Niell, F. X. 2000 Seasonal fluxes of phosphate and ammonium across the sediment- water interface in a shallow small estuary (Palmones River, southern Spain). *Marine Ecology Progress Series* **198**, 51-60.

Cloern, J. E. 1996 Phytoplankton bloom dynamics in coastal ecosystems: A review with some general lessons from sustained investigation of San Francisco Bay, California. *Reviews of Geophysics* **34**, 127-168.

Cowan, J. L. W. & Boynton, W. R. 1996 Sediment-water oxygen and nutrient exchanges along the longitudinal axis of Chesapeake Bay: Seasonal patterns, controlling factors and ecological significance. *Estuaries* **19**, 562-580.

D'Elia, C. F., Wiebe, W.J. 1990 Biogeochemical nutrient cycles in coral reef ecosystem. In *Ecosystems of the World. Coral Reef* (Dubinsky, Z., ed.). Elsevier, Amsterdam, vol. 25, pp. 49-74.

Dauwe, B., Middelburg, J. J. & Herman, P. M. J. 2001 Effect of oxygen on the degradability of organic matter in subtidal and intertidal sediments of the North Sea area. *Marine Ecology Progress Series* **215**, 13-22.

DeMaster, D. J., Ragueneau, O. & Nittrouer, C. A. 1996 Preservation efficiencies and accumulation rates for biogenic silica and organic C, N, and P in high-latitude sediments: The Ross Sea. *Journal of Geophysical Research Oceans* **101**, 18501-18518.

Emery, K. O. 1968 Relict sediments on continental shelves of the world. *American Association Petroleum Geologists* **52**, 445-464

Erftemeijer, P. L. A. & Middelburg, J. J. 1993 Sediment-nutrient interactions in tropical seagrass beds - a comparison between a terrigenous and a carbonate sedimentary environment in South Sulawesi (Indonesia). *Marine Ecology Progress Series* **102**, 187-198.

Fenchel, T., King, G. M. & Blackburn, T. H. 1998 *Bacterial Biogeochemistry: the Ecophysiology of Mineral Cycling*, Academic Press, San Diego, 307 pp.

Forster, S., Huettel, M. & Ziebis, W. 1996 Impact of boundary layer flow velocity on oxygen utilisation in coastal sediments. *Marine Ecology Progress Series* **143**, 173-185.

Froelich, P. N., Klinkhammer, G. P., Bender, M. L., Luedtke, N. A., Heath, G. R., Cullen, D., Dauphin, P., Hammond, D., Hartman, B. & Maynard, V. 1979 Early oxidation of organic matter in pelagic sediments of the eastern equatorial Atlantic suboxic diagenesis. *Geochimica et Cosmochimica Acta* **43**, 1075-1090.

Gibbs, R. J. 1981 Sites of river derived sedimentation in the ocean. *Geology* **9**, 77-80.

Glud, R. N., Gundersen, J. K., Revsbech, N. P. & Jørgensen, B. B. 1994 Effects on the benthic diffusive boundary layer imposed by microelectrodes. *Limnology & Oceanography* **39**, 462-467.

Glud, R. N., Gundersen, J. K., Revsbech, N. P., Jørgensen, B. B. & Huettel, M. 1995 Calibration and Performance of the Stirred Flux Chamber From the Benthic Lander Elinor. *Deep Sea Research Part I-Oceanographic Research Papers* **42**, 1029-1042.

Grasshoff, K., Kremling, K. & Ehrhardt, M. 1999 *Methods of Seawater Analysis*, Wiley-Vch, Weinheim, 600 pp.

Green, M. A., Aller, R. C. & Aller, J. Y. 1993 Carbonate dissolution and temporal abundances of foraminifera in Long-Island Sound sediments. *Limnology and Oceanography* **38**, 331-345.

Hall, P. O. J. & Aller, R. C. 1992 Rapid, small-volume, flow injection analysis for $\sum CO_2$ and NH_4^+ in marine and freshwaters. *Limnology and Oceanography* **37**, 1113-1119.

Heip, C. H. R., Goosen, N. K., Herman, P. M. J., Kromkamp, J., Middelburg, J. J. & Soetaert, K. 1995 Production and consumption of biological particles in temperate tidal estuaries. In *Oceanography and Marine Biology - an Annual Review*, vol. 33, pp. 1-149.

Hines, M. E. 1985 Microbial biogeochemistry in shallow water sediments of Bermuda. *5th international Coral Reefs Congress* **31**, 427-432.

Holst, G. & Grunwald B. 2001 Luminescence lifetime imaging with transparent oxygen optodes. *Sensors & Actuators B-Chemical* **74**, 78-90.

Huettel, M. & Gust, G. 1992 Impact of bioroughness on interfacial solute exchange in permeable sediments. *Marine Ecology Progress Series* **89**, 253-267.

Huettel, M., Ziebis, W. & Forster, S. 1996 Flow-induced uptake of particulate matter in permeable sediments. *Limnology and Oceanography* **41**, 309-322.

Huettel, M., Ziebis, W., Forster, S. & Luther, G. W. 1998 Advective transport affecting metal and nutrient distributions and interfacial fluxes in permeable sediments. *Geochimica et Cosmochimica Acta* **62**, 613-631.

Huettel, M. & Rusch, A. 2000 Transport and degradation of phytoplankton in permeable sediment. *Limnology and Oceanography* **45**, 534-549.

Ingall, E. & Jahnke, R. 1993 Evidence for enhanced phosphorus regeneration from marine- sediments overlain by oxygen depleted waters. *Geochimica et Cosmochimica Acta* **58**, 2571-2575.

Jahnke, R. A., Nelson, J. R., Marinelli, R. L. & Eckman, J. E. 2000 Benthic flux of biogenic elements on the Southeastern US continental shelf: influence of pore water advective transport and benthic microalgae. *Continental Shelf Research* **20**, 109-127.

Jørgensen, B. B. & Revsbech, N. P. 1985 Diffusive boundary layers and the oxygen uptake of sediments and detritus. *Limnology and Oceanography* **30**, 111-122.

Jørgensen, B. B. 1996 Material flux in the sediment. In *Eutrophication in Coastal Marine Ecosystems* (Jørgensen, B. B. & Richardson, K., eds.). American Geophysical Union, vol. 52, pp. 115-135.

Kelly, J. R. & Nixon, S. W. 1984 Experimental studies of the effect of organic deposition on the metabolism of a coastal marine bottom community. *Marine Ecology Progress Series* **17**, 157-169.

Klimant, I., Meyer, V. & Kuhl, M.1995 Fiberoptic Oxygen Microsensors, a New Tool in Aquatic Biology. *Limnology and Oceanography* **40**, 1159-1165.

Klute, A. & Dirksen, C. 1986 Hydraulic conductivity and diffusivity: laboratory methods. In *Methods of Soil Analysis - Part 1 - Physical and Mineralogical Methods* (Klute, A., ed.). American Society of Agronomy, Madison, pp 687-700.

Knoppers, B., Landim De Souza Weber, F., Landim De Souza Marcelo, F., Rodriquez Eliane, G., Landim Elisa De Fatima Da Cunha, V. & Vieira Antonio, R. 1996 In situ measurements of benthic primary production, respiration and nutrient fluxes in a hypersaline coastal lagoon of SE Brazil. *Revista Brasileira de Oceanografia* **44**, 155-165.

Kristensen, E. 1993 Seasonal variations in benthic community metabolism and nitrogen dynamics in a shallow, organic-poor Danish lagoon. *Estuarine Coastal and Shelf Science* **36**, 565-586.

Kristensen, E. 2000 Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. *Hydrobiologia* **426**, 1-24.

Lopez, P., Vidal, M., Lluch, X. & Morgui, J. A. 1995 Sediment metabolism in a transitional continental marine area - the Albufera-Fo-Majorca (Balearic-Islands, Spain). *Marine and Freshwater Research* **46**, 45-53.

Marinelli, R. L., Jahnke, R. A., Craven, D. B., Nelson, J. R. & Eckman, J. E. 1998 Sediment nutrient dynamics on the South Atlantic Bight continental shelf. *Limnology and Oceanography* **43**, 1305-1320.

Miyajima, T., Suzumura, M., Umezawa, Y., Koike, I. 2001 Microbiological nitrogen transformation in carbonate sediments of a coral-reef lagoon and associated seagrass beds. *Marine Ecology Progress Series* **217**, 273-286

Muller, P. J., Schneider, R. R. & Ruhland, G. 1994 Late quaternary pCO_2 variations in the Angola current: evidence from organic carbon $\Delta^{13}C$ and alkenon temperatures. In *Carbon Cycling in the Glacial Ocean: Constraints on the Ocean's Role in Global Climate Change* (Zahn, R., Kaminski, M. & Pedersen, T. F., eds.). Springer, Berlin, vol. 17, pp. 343-366.

Nicholson, G. J., Longmore, A. R. & Berelson, W. M. 1999 Nutrient fluxes measured by two types of benthic chamber. *Marine and Freshwater Research* **50**, 567-572.

Pedersen, A. G. U., Berntsen, J. & Lomstein, B. A. 1999 The effect of eelgrass decomposition on sediment carbon and nitrogen cycling: A controlled laboratory experiment. *Limnology and Oceanography* **44**, 1978-1992.

Rasheed, M., Badran, M. I., Richter, C. & Huettel, M. 2002 Effect of reef framework and bottom sediment on nutrient enrichment in a coral reef of the Gulf of Aqaba, Red Sea. *Marine Ecology Progress Series* **239**, 277-285.

Rasheed, M., Badran, M. I. & Huettel, M. 2003 Particulate matter filtration and seasonal nutrient dynamics in permeable carbonate and silicate sands of the Gulf of Aqaba, Red Sea. *Coral Reefs* **22(2)**.

Reay, W. G., Gallagher, D. L. & Simmons, G. M. 1995 Sediment-water column oxygen and nutrient fluxes in nearshore environments of the lower Delmarva Peninsula, USA. *Marine Ecology Progress Series* **118**, 215-227.

Revsbech, N. P. 1989 An oxygen microsensor with a guard cathode. *Limnology and Oceanography* **34**, 474-478.

Rhoads, D. C. & Hecker, B. 1994 Processes on the continental slope off North Carolina with special reference to the Cape Hatteras region. *Deep Sea Research Pt II-Top St Oce* **41**, 965-980.

Riedl, R. J., Huang, N. & R., M. 1972 The subtidal pump, a mechanism of intertidal water exchange by wave action. *Marine Biology* **13**, 210-221.

Rutgers Van Der Loeff, M. M. 1981 Wave effects on sediment water exchange in a submerged sand bed. *Netherlands Journal of Sea Research* **15**, 100-112.

Sansone, F. J. 1985 Methane in the reef flat porewaters of Davies Reef, Great Barrier Reef, Australia. *Proc. Fifth Int. Coral Reef Congress.* **3**, 415-419.

Sansone, F. J., Chanton, J. P., Haberstroh, P. R. & Bozeat., R. 1993 Methane cycling in coral reef frameworks. *In: Trends in Microbial Ecology* (Guerrero, R. and Pedros-Alio, C., eds.). *Spanish Social. Microbioogyl.* pp. 157-162.

Schroeder, J. H. & Purser, B. H. 1986 *Reef Diagenesis*, Springer, Berlin, pp. 1-131.

Seike, T., Izawa, H., Date, E. 1989. Benthic nutrient remineralization and oxygen consumption in the coastal area of Hiroshima Bay Japan. *Water Research* **23**, 219-228.

Shum, K. T. & Sundby, B. 1996 Organic matter processing in continental shelf sediments - the subtidal pump revisited. *Marine Chemistry* **53**, 81-87.

Sloth, N. P., Blackburn, H., Hansen, L. S., Risgaardpetersen, N. & Lomstein, B. A. 1995 Nitrogen cycling in sediments with different organic loading. *Marine Ecology Progress Series* **116**, 163-170.

Smith, K. L. & Hinga, K. R. 1983 Sediment community respiration in the deep sea. In *The Sea* (Rowe, G. T., ed.). Wiley, New York, vol. 8, pp. 331-370.

Sorkin, Y. I. 1995 Coral reef ecology. Ecological studies (Heldmaier, G., Lange, O.L, Mooney, H.A., Sommer U., Ed.), 192, Springer-Verlag, Berlin, 464 pp.

Spagnoli, F. & Bergamini, M. C. 1997 Water-sediment exchange of nutrients during early diagenesis and resuspension of anoxic sediments from the Northern Adriatic Sea shelf. *Water Air and Soil Pollution* **99**, 541-556.

Stimson, J. & Larned, S. T. 2000 Nitrogen efflux from the sediments of a subtropical bay and the potential contribution to macroalgal nutrient requirements. *Journal of Experimental Marine Biology and Ecology* **252**, 159-180.

Tengberg, A., Hall, P. & Hulth, S. 1996 Free vehicle modular bottom-lander technology for biogeochemical in situ studies. *Progress in Oceanography* **118**, 125-126.

Tribble, G. W., Sansone, F. J. & Smith, S. V. 1990 Stoichiometric modeling of carbon diagenesis within a coral- reef framework. *Geochimica et Cosmochimica Acta* **54**, 2439-2449.

Tribble, G. W. 1993 Organic matter oxidation and aragonite diagenesis in a coral reef. *Journal of Sedimentary Petrology* **63**, 523-527.

Vanderborght, J. P., Wollast, R. & Billen, G. 1977 Kinetic-models of diagenesis in disturbed sediments .1. Mass- transfer properties and silica diagenesis. *Limnology and Oceanography* **22**, 787-793.

Walsh, J. J. 1988 *On the Nature of Continental Shelves*, Academic Press, New York, 520 pp.

Webster, I. T. & Taylor, J. H. 1992 Rotational dispersion in porous media due to fluctuating flow. *Water Resources Research* **28**, 109-119.

Chapter 6

Effects of transparent exopolymer particles and muddy terrigenous sediments on the survival of hard coral recruits

Katharina E. Fabricius[1], Christian Wild[2], E. Wolanski[1] and D. Abele[3]

[1]Australian Institute of Marine Science, PMB No.3, Townsville MC, Qld 4810, Australia
[2]Max Planck Institute for Marine Microbiology, Celsiusstr.1, D-28359 Bremen, Germany
[3]Alfred Wegener Institute for Polar and Marine Research, Columbusstr., D-27568 Bremerhaven, Germany

This chapter has been published in Estuarine Coastal Shelf Science 57 (2003): 613-621

ABSTRACT

Sedimentation is a major cause of mortality in scleractinian coral recruits. In this study, we compared the effects of muddy coastal sediments, with and without enrichment by marine snow, on the survivorship of recruits of the hard coral *Acropora willisae*. Transparent exopolymer particles (TEP) were measured as characteristic components of marine snow using a staining method.

(Passow & Alldredge 1995). Four-week-old recruits were exposed to: (1) muddy coastal sediments; (2) TEP; (3) TEP-enriched muddy coastal sediments; and (4) unfiltered sea water, for 43 h in aerated flow chambers. Thirty-three percent (± 5 SE) of coral recruits died after 43-h exposure to TEP-enriched muddy coastal sediments (≅14 mg cm^{-2} sediment enriched with 3.8 ± 0.2 µg cm^{-2} gum xanthan (GX) equivalent TEP). In contrast no or minimal mortality was observed in the other three treatments. Mortality increased to >80% when the amount of deposited TEP was almost tripled (10.9 ± 1.3 µg GX cm^{-2}) and sediment increased by 50%. Thus, coral recruits survived short-term exposure to low levels of TEP and low levels of muddy sediments, but sediments enriched with TEP at concentrations recorded at some of the inshore stations proved to be detrimental. Concentrations of TEP were measured in the central Great Barrier Reef (latitude 16–18° S) in summer, the season of coral spawning and recruitment. Within <10km of the coast, TEP concentrations were high (mean=291 ± 49 SE µg GX L^{-1}, range=152–791 µg GX L^{-1}). Concentrations declined with increasing distance from the coast, and averaged 83 (±26 SE) µg GX L^{-1} around oceanic reefs >40km of the coast. Our study suggests that both sediment composition and short-term (43 h) sediment deposition affect survival of coral juveniles, which has implications for the capacity of inshore reefs to be recolonised by corals to recover from acute disturbance events.

INTRODUCTION

Sedimentation is a major cause of mortality in the initial life stages of hard corals (Cnidaria: Scleractinia). It can locally reduce recruitment rates (Sato 1985; Gilmour 1999; Babcock and Smith, in press), and at higher concentrations affect a range of life history parameters in adult corals (Rogers 1990). However, with the exception of grain sizes (Fisk 1981, Stafford-Smith and Ormond 1992), not much is known about differences in sediment characteristics that may influence the survival of corals exposed to sedimentation. A pilot study indicated that low-level sedimentation of sticky muddy "marine snow" aggregates affects small reef organisms, such as coral-inhabiting barnacles, more than intermediate amounts of clean sediment (Fabricius and Wolanski 2000). It is likely that sediment characteristics such as tendencies to form sticky marine snow aggregates, and differences in organic and microbial concentrations, may also alter the effect of sedimentation on coral recruits.

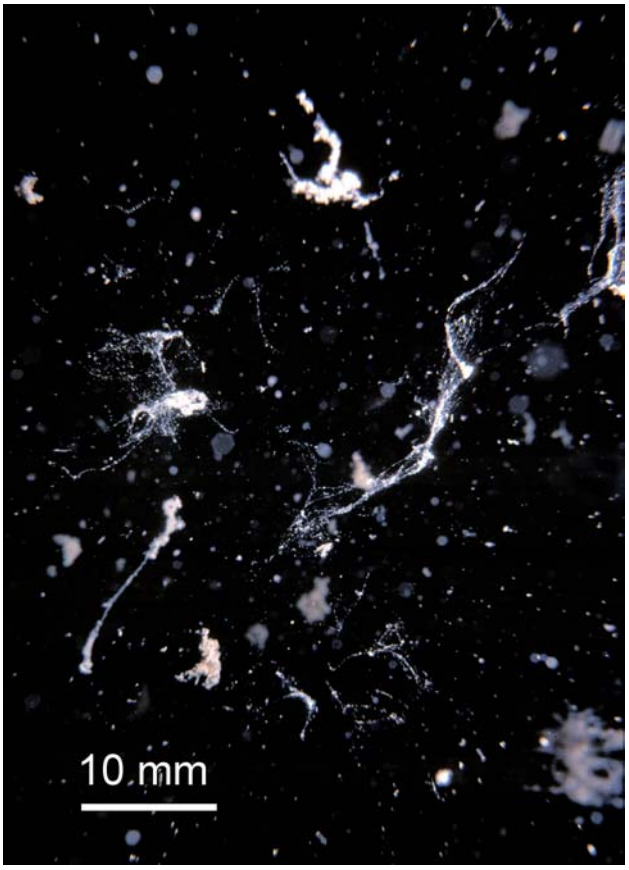

Figure 1. Suspended sediment colliding with large, transparent exopolymer particles (TEP) to form "marine snow" aggregates.

Microbes, diatoms and metazoans such as appendicularians exude dissolved mucopolysaccharides that may become particulate through the formation of cation bridges (Alldredge *et al.* 1986; Logan *et al*. 1995; Hansen *et al*. 1996). Such particles are known as

transparent exopolymer particles (TEP) (Passow and Alldredge 1994). Microbes and diatoms that bloom in the water column, or colonise suspended and sedimented particles, can promote the biological formation of TEP (Kiørboe *et al.* 1990; Passow *et al.*, 1994, Wolanski *et al.* 1997; Ayukai and Wolanski 1997). At moderate turbulence, TEP collide with other suspended particulate matter, and their stickiness facilitates the development of composite marine snow aggregates which can grow to considerable size (Fig. 1; Eisma 1986; Passow and Alldredge 1994; Wolanski and Gibbs 1995). During calm periods the aggregates settle out from the water column and are deposited on benthic organisms and the surrounding sea floor (Wolanski *et al.* 1998). Thus TEP plays an important role in the formation of macroaggregates and in sedimentation processes (Logan *et al.* 1995). They also serve as substrate for microbes involved in nutrient recycling and as particulate food for grazers (Alldredge *et al*. 1986).

Riverine flood plumes originating from wet tropical agricultural lands in Queensland (East Australia, latitude 16° -18° S) discharge high concentrations of dissolved and particulate nutrients and sediments into the Great Barrier Reef (Wolanski 1994; Devlin *et al*. 2001). Such flood plumes are the largest external source of nutrients for the GBR lagoon (Furnas *et al.* 1997, Furnas and Mitchell 2001). Although a link between nutrient availability and TEP formation has not been established, it is conceivable that nutrients injected by riverine flood waters may promote the growth of TEP-producing diatoms and bacteria. Periods of high concentrations of TEP can coincide with high concentrations of suspended particulate matter – either newly imported with the flood plume, or resuspended from the shallow sea floor. In inshore areas of the Great Barrier Reef, such co-occurrences are particularly likely during monsoonal summer rain. Early summer (November to December) is also the time of mass spawning of many reef invertebrates including the reef-building hard corals. Within a few days or weeks of the mass spawning event, coral larvae settle on suitable substratum. They metamorphose to primary polyps, which soon start depositing their calcium carbonate skeleton, and add new polyps by budding. After 4 to 6 weeks, these recruits measure up to 2 mm in diameter and 1 mm in height, and consist of 1 to 6 polyps (K. Fabricius, personal observation). This early post-settlement time is likely to be the most vulnerable stage in the benthic life phase of a coral. The ability of young coral recruits to survive local exposure to sedimentation or other adverse environmental conditions has large-scale consequences for the capacity of coral reef communities to recover from disturbance events.

In this study, we tested the short-term effects of deposition of TEP-enriched muddy marine snow and sediments on the survival of recruits of hard corals (Cnidaria: Scleractinia), by exposing them to sediments with and without TEP-enrichment. We also present data on summer concentrations of TEP in the central Great Barrier Reef off the wet tropical agricultural lands in Queensland, in order to determine what levels of TEP are likely to be encountered by coral recruits in inshore waters of the central Great Barrier Reef.

MATERIAL AND METHODS

Experimental study of the survival of coral recruits

The effects of TEP, muddy sediment, and a combination of both, on the survival of 4 to 6 weeks old coral recruits was determined experimentally. Recruits were obtained following the protocol of Heyward and Negri (1999): The egg-sperm bundles from ten colonies of *Acropora willisae* (collected from an inshore reef off Townsville a few days before the predicted mass spawning), were mixed for cross-fertilisation, and distributed over 12 10-L buckets in a water bath. Gentle aeration and water flow-through was applied 12 h later to each bucket (plankton mesh was glued over the outflow). After 2 days, 96 unglazed 5.5 x 5.5 cm^2 terracotta tiles, pre-conditioned by immersion in the coastal sea for 3 weeks, were added to the buckets as settlement substrata, and the larvae settled and metamorphosed on the recruitment tiles within 3-5 days. Eight days after the spawning, the recruitment tiles were vertically suspended on ropes in a 3 m^3 flow-through outdoor tank under 70% shade cloth, in which a circular current of about 3 cm sec^{-1} was created by pumps. When the recruits were 26 days old, the experiments commenced. From the forty tiles with the highest recruit numbers, eight tiles were randomly selected. The position, number of polyps, and state (alive, i.e., healthy tissue visible; and dead, i.e., bare skeleton without tissue) of each recruit was mapped on the upper side of each tile using a dissecting microscope. The number of live recruits per upper tile surface averaged 9.75 ± 6.9 (SD) at the beginning of the experiment.

Fine, muddy subtidal sediment was collected from behind a breakwater protecting the mouth of a small creek off Magnetic Island. Coarse material was removed with a set of sieves, and the <125 μm sediment fraction was kept in aerated sea water until further use. Water rich in TEP was collected from the outflow of a ~5000 L prawn holding tank at the AIMS mariculture facility. Flow-through was stopped overnight after the prawns were fed in the afternoon. The next morning, water from the mid-water column of the prawn tank was collected in a 150-L container. Water samples were taken to analyse TEP, nutrient and chlorophyll contents: these were similar to those of natural inshore seawater, except for elevated nitrogen and phosphorus concentrations in the prawn tank water (Table 2). Aggregates were allowed to settle for 30 min, then most of the nutrient-rich surface water was siphoned off and discarded, and 10 litres from the bottom of the container were used for the experiment.

Four treatments were established (Sediment, TEP, Sediment & TEP, and unfiltered sea water without particle addition as Control) as follows. Four 12-L flow chambers were set up in a controlled temperature room at 26° C (9.5 h light / 14.5 h dark) and filled with unfiltered sea water. The TEP-enriched water was mixed, subdivided into 2 equal lots, and each lot was added to 2 of the flow chambers containing 7 l of unfiltered sea water. Fifty ml of the wet sediment was suspended in 1 L of seawater, stirred vigorously, and divided into 2 aliquots. One aliquot was added to a chamber with only unfiltered seawater (Sediment), the other to a chamber containing TEP-enriched sea water (Sediment & TEP). Neither sediment nor TEP was added to the fourth tank (Control). Propellers provided gentle unidirectional flow of 2 cm s^{-1} (imitating conditions on back reef slopes at calm days), and an aquarium air pump was used to aerate the chamber water through air stones. Two tiles were placed horizontally, with the mapped recruits on the upper side, in each chamber. Duplicate water samples from each flow chamber were analysed for TEP concentrations at the beginning of each run (Table 1). The recruits were exposed to the treatments for 43 h; most of the particulate material settled on the chamber floor and on the tiles within <4 h.

Table 1. TEP concentration suspended in the water of the flow chambers at the beginning of the runs, and amount of TEP and sediments deposited on the recruitment tiles at the end of the runs (8 tiles per run, 2 tiles per treatment).

Treatment	TEP suspended (µg GX L^{-1})		TEP deposited (µg GX cm^{-2})		Sediment deposited (mg cm^{-2})	
	Runs 1,2,4,5	Run 3	Runs 1,2,4,5	Run 3	Runs 1,2,4,5	Run 3
Sediment	292 ± 143	429	2.40± 0.40	6.62 ± 3.09	13.8 ± 3.42	14.4 ± 3.06
TEP	566 ± 119	1626	4.67± 0.30	13.9 ± 2.64	3.95 ± 0.73	9.27 ± 1.50
Sediment & TEP	465 ± 80	1201	3.83± 0.15	10.9 ± 1.28	13.7 ± 3.51	20.3 ± 1.73
Control	76 ± 44	48	0.65± 0.15	2.03 ± 0.25	1.04 ± 0.23	2.21 ± 0.31

After 43 h, the tiles were carefully removed from the flow chambers, and deposited material was rinsed off each tile with filtered seawater into separate jars. All previously mapped coral recruits were again allocated to the categories alive and dead. The water from the jars was mixed vigorously and subdivided into four subsamples, which were filtered at low vacuum

(15 mg kPa) onto polycarbonate membrane filters (47 mm diameter) with nominal pore size of 0.4 μm. Two of the subsamples were dried and weighed to determine the weight of particulate matter deposited per unit area of tile surface (Table 1), the other two subsamples were used for TEP determination, as described below.

The recruits survival experiment was run five times, each time using eight new tiles, TEP newly obtained from the prawn tank, and a new subsample of the sediment batch. Each time the allocation of treatments to the four flow chambers was systematically varied.

Logistic regression, which is able to deal with proportional data and binomially distributed error terms (Collett 1991), was used to assess the dependence of survival of the coral recruits on the four treatments (TEP, Sediment, Sediment & TEP, Control). In Run 3, TEP concentration was increased three-fold and sediment increased 1.5-fold (Table 1); this run was treated separately in the analyses. All statistical analyses used S-Plus Version 2000 (Statistical Sciences 1999).

Water sampling and analytical methods

Water samples were collected on the shallow continental shelf of the Great Barrier Reef between 16° and 18° latitude S on two field trips, to determine *in situ* levels of TEP. During Voyage 1 (December 1999), stations were positioned both along the shore in the inshore region (9 samples from 5 stations <10 km off the coast) and across the shelf (6 samples from 3 midshelf stations 10 - 25 km off the coast, and 4 samples from 2 outer shelf stations ≥40 km off the coast, Table 2). At each station of Voyage 1, a sample was collected from 5 m depth with a 20-L Niskin bottle lowered from the deck of the research vessel while the ship was anchored ~200 m behind a reef. A second water sample was collected by a snorkeler, who brought three lots of water from 5 m depth and 1 m above the coral reef in a 5-L Niskin bottle to the surface, where the three Niskin bottle contents were combined in a rinsed bucket. Two reefs were visited twice, with a 5-day interval between the visits (Double Island and Alexandra Reef, Table 3). The results, as expected, identified the inshore area as region of highest TEP concentrations. During Voyage 2 (January 2000), the sampling therefore focused predominantly on inshore waters. At each of the 18 stations of Voyage 2, one sample was collected from 5 m depth with the 20-L Niskin bottle lowered from the deck of the vessel.

Table 2. Summary water column properties of inshore, midshelf and outer shelf reefs of the central Great Barrier Reef during Voyage 1 (December 1999) and Voyage 2 (January 2000), and from the outflow of the prawn tanks, as used in the experiments. The data represent untransformed means ± SE. N = number of samples. SS = suspended solids, Chl = chlorophyll, Phae = phaeopigments, PN = particulate nitrogen, TN total nitrogen, PP = particulate phosphorus, TP = total phosphorus.

Source		N	Distance to coast (km)	TEP (µg GX L^{-1})	Salinity (PSU)	SS (mg L^{-1})	Chl (µg L^{-1})	Phae (µg L^{-1})	PN (µmol L^{-1})	TN (µmol L^{-1})	PP (µmol L^{-1})	TP (µmol L^{-1})
Voyage 1	Inshore	9	1.4 ± 0.3	176 ± 23	34.5 ± 0.1	3.22 ± 0.46	0.49 ± 0.04	0.22 ± 0.02	2.62 ± 0.31	8.44 ± 0.56	0.109 ± 0.008	0.19 ± 0.001
	Midshelf	6	18 ± 2	139 ± 60	35.0 ± 0.1	2.27 ± 0.53	0.35 ± 0.03	0.16 ± 0.02	2.41 ± 0.29	8.25 ± 0.66	0.079 ± 0.008	0.18 ± 0.02
	Outer-shelf	4	45 ± 3	83 ± 26	35.1 ± 0.01	1.67 ± 0.21	0.26 ± 0.04	0.12 ± 0.02	2.02 ± 0.16	6.35 ± 0.39	0.066 ± 0.008	0.13 ± 0.01
Voyage 2	Inshore	15	1.6 ± 0.2	388 ± 46	34.0 ± 0.1	1.90 ± 0.16	0.40 ± 0.06	0.20 ± 0.03	1.83 ± 0.20	11.71 ± 0.79	0.078 ± 0.007	0.14 ± 0.01
	Midshelf	3	15 ± 0.3	205 ± 42	34.4 ± 0.2	1.68 ± 0.55	0.21 ± 0.09	0.11 ± 0.04	2.14 ± 0.63	9.96 ± 0.05	0.045 ± 0.003	0.09 ± 0.01
Mean Inshore		24	1.5 ± 0.2	308 ± 37	34.2 ± 0.1	2.40 ± 0.24	0.44 ± 0.04	0.21 ± 0.02	2.06 ± 0.19	10.45 ± 0.61	0.095 ± 0.01	0.16 ± 0.01
Prawn tank		4	N/A	320 ± 15	30.8 ± 0.03	3.42 ± 0.16	0.50 ± 0.02	0.33 ± 0.03	6.58 ± 1.98	24.18 ± 0.36	1.15 ± 0.21	2.06 ± 0.05

During this Voyage, 11 of 18 stations were located away from coral reefs, and Double Island was again visited twice.

The water samples were subsampled as follows. For the determination of dissolved silicate, ammonium, nitrite, nitrate and phosphate, ten subsamples (10 ml each) were filtered through 0.45 µm Sartorius Minisart Cellulose acetate filters, and frozen at – 20° C. For the determination of salinity, a 500 ml subsample was stored in a tightly closed bottle at room temperature. For the determination of chlorophyll *a*, particulate nitrogen and phosphorus, six subsamples (100 – 250 ml) were filtered onto pre-combusted 0.2 µm Whatman GF/F 25 mm filters, and frozen at – 20° C. For the determination of suspended solids, duplicate subsamples (500 or 1000 ml) were filtered onto pre-weighed polycarbonate filters of 0.4 µm pore width, which were later dried at 80° C for 24 h, and re-weighed. All samples were later processed at the Australian Institute of Marine Science using standard procedures (described in detail in Furnas and Mitchell 1996).

To determine TEP concentrations, generally two to four (Table 3) subsamples of the seawater (100-1000 ml, depending on observed the aggregate density) were filled into separate jars, preserved with formalin (final concentration: 2%), and stored at 4° C. For further analyses, the subsamples were filtered at low vacuum (15 kPa) onto polycarbonate membrane filters (47 mm diameter) with 0.4 µm nominal pore size, and the filters transferred to a petri dish. Concentrations of TEP were determined following Passow and Alldredge (1995) as follows. The material on the filters was stained for 2–5 sec with 500 µl of a freshly filtered (0.2 µm) 0.02% aqueous solution of Alcian Blue (8 GX, ICN Biomedicals, Aurora, USA) in 0.06% acetic acid (pH 2.5). They were then gently rinsed twice with distilled water to remove excessive dye, and transferred to 30 ml beakers containing 6 ml of 80% sulphuric acid. After 2 h extraction, during which the beakers were gently shaken 4 to 6 times, the concentration of pigment in the sulphuric acid was spectrophotometrically determined at 787 nm. A calibration factor for each newly mixed staining solution was established following Passow and Alldredge (1995), using gum xanthan (practical grade, ICN Biomedicals) as standard. Based on these calibrations, TEP concentrations are presented as gum xanthan equivalents per liter (GX L^{-1}).

Table 3. Mean TEP concentrations, and number of subsamples analysed (N). In Voyage 1 (Stations 1 – 11), samples marked with "Ship" were taken 200 m away from coral reefs, samples marked with "Reef" were taken 1 m above coral reefs. In Voyage 2 (Stations 12–29), all samples were taken from the ship. Stations <10 km off the coast are classified as inshore, 10 – 25 km are midshelf, and ≥40 km are outer shelf.

Station Number	Date	Reef	Distance to Coast (km)	N	TEP Concentration (µg GX L^{-1} ± SE) Ship	N	TEP Concentration (µg GX L^{-1} ± SE) Reef
1	14.12.1999	Double Is.	1	2	334 ± 33	2	564 ± 23
2	15.12.1999	Alexandra Rf.	1	2	531 ± 14		
3		Low Is.	15	2	201 ± 18	1	276
4	16.12.1999	Snapper Is.	3	2	125 ± 67	1	185
5		Cape Tribulation	1	2	210 ± 53	2	94 ± 67
6	17.12.1999	Norman Rf.	50	2	45 ± 3	1	157
7		Hastings Rf.	40	2	80 ± 20	2	51 ± 8
8	18.12.1999	Upolu Rf.	25	2	130 ± 59	2	44 ± 37
9		Alexandra Rf.	1	2	180 ± 42	2	132 ± 42
10	19.12.1999	Double Is.	1	2	158 ± 37	2	162 ± 49
11		Green Is.	15	2	23 ± 1	2	29 ± 3
12	4.1.2000	Dunk Is.	3	2	247 ± 83		
13		Mourilyan Inlet	<1	3	791 ± 58		
14		Russell River	<1	4	300 ± 27		
15		Fitzroy Is.	12	5	270 ± 55		
16	5.1.2000	Trinity Inlet	<1	4	339 ± 37		
17		Double Is.	1	4	279 ± 44		
18		Garioch Rf.	2	3	445 ± 132		
19		Port Douglas	<1	4	374 ± 81		
20		Daintree River	<1	3	377 ± 64		
21		Cape Tribulation	2	2	748 ± 50		
22		Snapper Is.	3	3	430 ± 27		
23		Daintree River	2	3	193 ± 29		
24		Low Is.	15	3	222 ± 29		
25	6.1.2000	Double Is.	3	3	498 ± 14		
26		Yorkey's Knob	1	7	337 ± 37		
27		Cairns Fairleader	1	4	252 ± 52		
28		Mission Bay	1	2	197 ± 48		
29		Green Is.	15	4	125 ± 26		

Linear regression models were used to test for relationships between concentrations of TEP and sediment, chlorophyll, or nutrients. The concentration of TEP (double-square-root transformed) was the response variable, and sediment, chlorophyll, or nutrients, and voyage number, were used as explanatory variables.

RESULTS

Survival of coral recruits exposed to TEP and muddy sediment

In the four experimental runs with low TEP and sediment exposure (Table 1), the mortality in coral recruits differed among the 4 treatments ($\chi^2_{(3)}$ = 55.2, P <0.0001, Fig. 2a). Mortality in the Sediment & TEP treatment (TEP: 570 µg GX L^{-1} suspended (3.8 µg GX cm^{-2} deposited), sediment: 14 mg cm^{-2}) averaged 33.2%. No recruits died in the control or the Sediment treatment, and only one from a total of 74 recruits (3.3%) died in the TEP treatment. The Sediment & TEP treatment thus contrasted strongly to the remaining treatments ($\chi^2_{(1)}$ = 53.65, P <0.0001), but there were no differences among the latter three ($\chi^2_{(2)}$ =1.55, P=0.461).

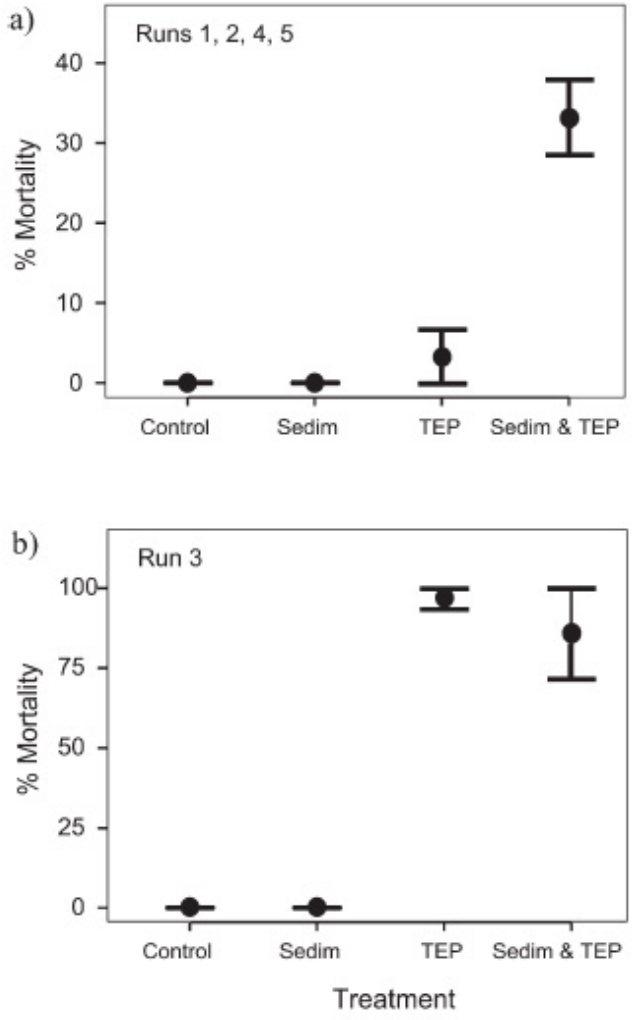

Figure 2. Percent mortality of young recruits of the coral *Acropora willisae* exposed to a 43-hrs deposition of muddy coastal sediment ("Sedim"), TEP-aggregates ("TEP"), TEP adhering to muddy sediment ("Sedim & TEP"), and unfiltered seawater without particle addition ("Control"). Data are mean mortality per run and treatment, ± one standard error. Each run included eight tiles carring live recruits (two per treatment). Concentrations of sediment and TEP applied in the experiments are listed in Table 1.

In Run 3, deposited TEP was tripled and sediments increased by ~50% (TEP: 1200 µg GX L^{-1} suspended (11 µg GX cm^{-2} deposited), sediment: 20 mg cm^{-2}; Table 1) resulted in mortality rates of 81.8% in the Sediment & TEP treatment, 98.4% in the TEP treatment, and 3.8% in the Sediment treatment (Fig. 2b). None of the recruits died in the controls.

TEP concentrations in the field

During Voyage 1, highest values of TEP, suspended solids, chlorophyll *a*, phaeopigments, and particulate phosphorus occurred on the inshore reefs (<10 km from the coast). Concentrations decreased towards the midshelf, and were lowest on the outer shelf reefs (>40 km offshore, Tables 2 and 3). TEP concentrations averaged 176 µg GX L^{-1} (range = 94 - 531) on inshore reefs, 139 µg GX L^{-1} (range = 24 - 276) on the midshelf, and 83 µg GX L^{-1} (range = 45 - 157) on the outer shelf. Concentrations of suspended solids and chlorophyll were also about twice as high inshore compared with outer shelf waters, and salinity increased from 34.47 ± 0.11 PSU (± SE) inshore to 35.12 ± 0.005 PSU around the outer shelf reefs (Table 2). Particulate and total nitrogen showed only weak cross-shelf patterns, possibly because of the presence of some nitrogen-fixing *Trichodesmium*. There was no difference between samples taken 1 m above the reef, to those taken from the ship about 200 m away from the reef (paired t-test: $t_{(9)} = -0.642$, P = 0.537).

On the second, mostly inshore voyage, no long-shore pattern was found in TEP (Table 3). TEP concentrations in the inshore samples averaged 388 ± 46 µg GX L^{-1}. They were particularly high in several coastal areas, with the highest concentration of 791 ± 101 µg GX L^{-1} recorded in Mourilyan River estuary south of Cairns. The lowest mean value of Voyage 2 was recorded off the Daintree River (Station 23: 193 ± 51 µg GX L^{-1}). Concentrations of TEP, chlorophyll *a*, phaeopigments, and phosphorus again tended to be higher, and salinity was lower, in the 15 inshore samples compared to the 3 midshelf samples (Table 2).

Concentrations of TEP increased with concentrations of suspended solids in the water (data from both voyages combined: $t_{(34)} = 4.41$, P= 0.0001, Fig. 3); the rate of increase being independent of voyage ($t_{(33)} = -0.59$, P = 0.560). TEP concentrations

were higher during Voyage 2 than Voyage 1 ($t_{(34)}$=7.42, P <0.0001) for a given concentration of suspended solids. In contrast, concentrations of TEP were unrelated to concentrations of chlorophyll, phaeopigments, particulate nitrogen, particulate phosphorus, salinity, and all of the dissolved nutrients during the two observation periods (P > 0.05). TEP concentrations varied greatly between samples and days (e.g., Double Island that was visited four times: (mean = 333 µg GX L^{-1}, range = 158-564 µg GX L^{-1}).

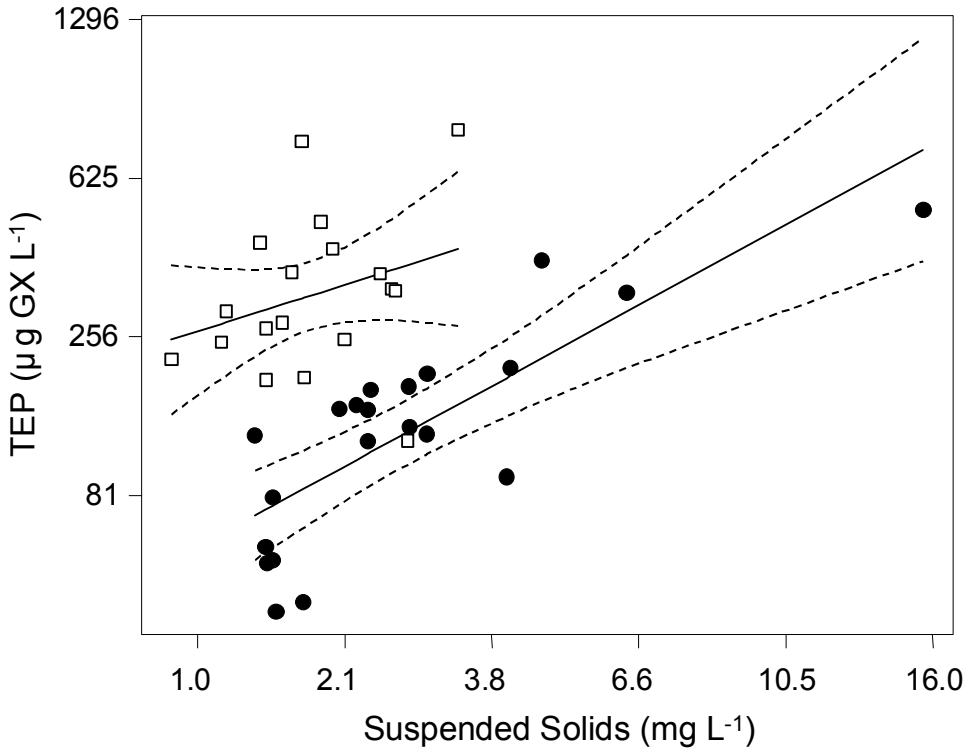

Figure 3. Relationships between concentrations of TEP (in µg GX L^{-1}), and suspended solids (mg L^{-1}) in the Cairns area. Black filled circles indicate samples from Voyage 1, open squares are from Voyage 2. Values are back-transformed from double-square root transformation for ease of interpretation. Dashed lines indicate 90% confidence limits.

DISCUSSION

Our study demonstrated that sediments rich in TEP can damage recruits of the inshore coral *Acropora willisae* within less than two days of deposition, well within the time frames of natural sediment deposition events. Mortality of *A. willisae* recruits was 0% below 400 µg GX L^{-1} TEP concentration, and high when TEP concentrations exceeded 1000 µg GX L^{-1} (~10 µg GX cm^{-2} after deposition). The mechanisms of damage are still unknown, however anoxia under the sediment, and toxic metabolites of microbes associated with the TEP aggregates may contribute to the synergistic damaging effects. In the northern Adriatic Sea, large marine snow aggregates have been shown to contain a number of types of toxins, some of which inhibit the P-glycoprotein (Pgp) extrusion pump responsible for mediating the outward transport of toxins in aquatic organisms (Müller *et al*. 1998). Mass killings of benthic organisms exposed to marine snow in the Adriatic Sea have been linked to the presence of these toxins (Müller *et al*. 1998), and to anoxia (Stachowitsch 1984, Herndl 1988).

Tolerance for sediment exposure varies widely among coral species, but experimental studies which applied 200 – 800 mg cm^{-2} of sediments to adult corals have commonly reported physiologically impaired performance or death of underlying tissue (reviewed in Rogers 1990; Stafford-Smith 1993). Survival threshold levels have been found to be a product of the amount and duration of sedimentation (Philipp and Fabricius, in review). Our present study showed that recruits of *Acropora willisae* were able to survive sedimentation levels of <14 mg cm^{-2} for 43 h if the sediment contained little TEP, whereas the same amount of sediment induced mortality when it was enriched with TEP. A reatively low sediment tolerance in coral recruits has been previously documented: for example, clay sediment deposition rates of 2 – 12 mg cm^{-2} d^{-1} reduced the number of larvae of *Acropora millepora* settling and surviving for 8 months in the field (Babcock and Smith 2001), and sedimentation rates of 3 – 7 mg cm^{-2} d^{-1} decreased the number of larvae of *Acropora millepora* settling on upper surfaces of tiles in tanks (Babcock and Davies 1991). Thus evidence is increasing that the threshold level for young coral recruits to survive sedimentation is up to two orders of magnitude lower than that of adult corals.

A survival threshold value of TEP (i.e., a concentration below which no mortality occurs in a given period of exposure time) is not easily found. It needs to incorporate sedimentation levels, as TEP and sediments affected the corals in a synergistic fashion, and both variables were strongly correlated in the field. The estimate of a threshold value is further compromised by the fact that TEP concentrations appear to be systematically underestimated in the presence of sediments. This artefact may be caused by a blockage of actively binding molecular groups by mud aggregates, preventing Alcian Blue to bind to the TEP molecules (U. Passow, personal communication). This may also explain why in this study, TEP concentrations appeared to be consistently lower in the Sediment & TEP treatment than those in the TEP treatment. In addition, comparisons of experimental and field data to derive a threshold value must account for differences in the depths of the water columns in flow chambers and reef (0.15 m, and up to 10 m, respectively): If we simplistically assume that TEP deposition per unit substratum area underneath a water column is proportional to the length of the water column, it becomes obvious that rates of aggregate deposition on reefs may be many fold greater than those simulated in the laboratory.

Nitrogen and phosphorus concentrations in the TEP treatment were higher than those in the other treatments, even after dilution of the water from the prawn tank with unfiltered sea water. Elevated nutrient levels can alter the photophysiology and calcification rates of adult scleractinian corals (Muscatine et al. 1989, Marubini and Davies 1996). However, the 97% survival of recruits in the "TEP only" treatment in the experimental runs 1, 2, 4 and 5 indicates that the water quality of the water from the prawn farm were unlikely to have caused mortality in the TEP & Sediment treatment, and the TEP treatment in Run 3.

To our knowledge, TEP has not been quantified in tropical marine systems prior to this study. TEP concentrations exceeded 400 µg GX L^{-1} at several inshore stations during our surveys (Table 3: Mourilyan Inlet, Double Island, Alexandra Reef, Garioch Reef, and Cape Tribulation Reef). In contrast, TEP values remained well below 400 µg GX L^{-1} at all mid- and outer shelf stations (maximum: 276 µg GX L^{-1}). Concentrations in inshore waters of the central Great Barrier Reef in summer (mean = 291, range = 152 - 791 µg GX L^{-1}) were on the higher end of the range of those

recorded from shallow inshore areas in other (temperate climate) regions. For example, TEP values in the Monterey Bay of California ranged between 50 and 310 μg GX L^{-1} in summer (Passow and Alldredge 1995), and in the Kieler Bucht of the Baltic Sea between 50 and 200 μg GX L^{-1} (Kraus 1997), whereas other parts of the Baltic Sea contained 241 μg GX L^{-1} ± 66 SE (Engel and Passow, in press). Our TEP concentrations in the oceanic waters around the outer shelf reefs (mean = 83, range = 29 - 157 μg GX L^{-1}) were however comparable to those recorded from the open Atlantic Ocean near Bermuda (mean = 53, range = 27 - 294 μg GX L^{-1}; Engel *et al*. 1997), despite the fact that our samples were collected near coral reefs. The values were also similar to those recorded from the reef flat of Heron Islands, a midshelf reef in the Southern Great Barrier Reef, where TEP concentrations averaged 44 μg GX L^{-1} (range = 29 - 73 μg GX L^{-1}; C. Wild, unpublished data).

Patterns of TEP distribution and causes of TEP production are likely to be complex and multi-causal around tropical coral reefs, and more measurements are needed to adequately determine spatial and temporal patterns and the origin of TEP in the region. Extensive microscopy of live, unpreserved subsamples from each station of Voyage 1 revealed that marine snow aggregates were predominantly composed of mixed amorphic and decomposed detrital material complemented by transparent particles, and a diverse array of fecal pellets, diatom cells and chains, and ciliates (Wild 2000). There was no difference between TEP concentrations in samples taken by divers just one meter above corals compared to those taken 200 m away from reefs, instead TEP concentrations above and around coral reefs strongly decreased with increasing distance from the coast. These data suggest that TEP values were probably little affected by the mucus production of scleractinian corals, octocorals and other benthic organisms. The correlation between TEP concentrations and suspended solids (Fig. 3) indicated that TEP was predominantly attached to, or derived from, non-fluorescent particles, and thus possibly predominantly resuspended from the shallow sea floor. This parallels findings from the Lake Kineret, where a large proportion of TEP was derived from previously particulate, detrital material (Berman and Viner-Mozzini 2001).

Marine snow aggregates reached large sizes in some inshore areas, however the variability in size and density was high. Video records and observations on SCUBA showed individual aggregates >100 mm long at the back reef of Double Island off Cairns, together with numerous aggregates 20-40 mm in length, during Voyage 1 (described in detail in Wild 2000). Double Island and Alexandra Reef were visited for the first time just after persistent 25 - 40 km h^{-1} winds subsided. During these calming conditions, slow but continuous sinking of the large aggregates was clearly visible for the divers. When these reef sites were re-visited 5 days later, TEP concentrations had dropped by 47% and 30% respectively (from 449 to 160 µg GX L^{-1} at Double Island, and from 531 to 156 µg GX L^{-1} at Alexandra Reef). Furthermore, the large transparent aggregates had disappeared from view, possibly having settled out onto the reef and surrounding sea floor. This is consistent with previous observations of marine snow sinking at ~5 cm min^{-1} during calm periods (i.e., at currents <10 cm s^{-1}), with the sinking speed depending on the type, density, and size of the aggregates (Eisma 1986, Alldredge and Gotschalk 1988, Wolanski *et al.* 1998).

Coral recruit densities on terracotta tiles are two orders of magnitude higher than juvenile densities in four of the nearshore reefs where we measured marine snow (990 $m^{-2} \pm 83$ SE, versus 2.2 ± 0.2 m^{-2}, Fabricius, Harrington and Smith, unpublished data), indicating a high mortality in the early life stages of scleractinian corals. If our experimental results are indicative of ecological processes occuring in the field, the deposition of sediments enriched with marine snow may increase the mortality rates of coral recruits in coastal areas that are prone to forming marine snow.

ACKNOWLEDGEMENTS

Many thanks to Kealan Doyle, Michael Browne, and Simon Spagnol for assistance in TEP and aggregate size analyses, and to Andrew Negri, Andrew Heyward, and Paul Hough for their help during coral spawning and with rearing the coral larvae at the Reef HQ in Townsville. We are very greatful to Glenn De'ath for conducting some of the statistical analyses, Uta Passow for sharing her expertise in dealing with TEP, and Sue Ghonim, Michelle Skuza, and Margaret Wright for analysing the chlorophyll- and nutrient samples. Many thanks also to Luke Smith, Glenn De'ath, Uta Passow and Jon Brodie for comments on an earlier draft of the manuscript. This study was funded by

the Cooperative Research Centre for the Great Barrier Reef World Heritage Area (CRC Reef), and the Australian Institute of Marine Science (AIMS).

LITERATURE CITED

Alldredge, A. L., Cole, J. J. & Caron, D. A. 1986 Production of heterotrophic bacteria inhabiting organic aggregates (marine snow) from surface waters. *Limnology and Oceanography* **31,** 68-78.

Alldredge, A. L. & Gotschalk, C. 1988 In situ settling behavior of marine snow. *Limnology and Oceanography* **33,** 339-351.

Ayukai, T. & Wolanski, E. 1997 Importance of biologically mediated removal of fine sediments from the Fly River plume, Papua New Guinea, *Estuarine, Coastal and Shelf Science* **44,** 629-639.

Babcock, R. & Davies, P. 1991 Effects of sedimentation on settlement of *Acropora millepora*. *Coral Reefs* **9,** 205 – 208.

Babcock, R. & Smith, L. (in press) Effects of sedimentation on coral settlement and survivorship. Proceedings of the ninth International Symposium for Reef Studies, Bali, Oct. 2000

Berman, T. & Viner-Mozzini, Y. 2001 Abundance and characteristics of polysaccharide and proteinaceous particles in lake Kinneret. *Aquatic Microbiol Ecology* **24,** 255-264.

Collett, D. 1991 Modelling binary data. Chapman & Hall, London: 369 pp.

Devlin, M. J., Waterhouse, J., Taylor, J. & Brodie, J. 2001 Flood plumes in the Great Barrier Reef: Spatial and temporal patterns in composition and distribution. *Great Barrier Reef Marine Park Research Publication* No 68, Townsville.

Eisma, D. 1986 Flocculation and de-flocculation of suspended matter in estuaries. *Netherlands Journal of Sea Research* **20,** 183-199.

Engel, A., Koeve, W. & Zeitzschel, B. 1997 Verteilung Transparenter Exopolymer Partikel (TEP) im Nordostatlantik. Untersuchungen entlang eines 20 W Schnittes (Meteor 36/2). Berichte Fachbereich Geowissenschaften Universität Bremen **109**, 23 pp.

Engel, A.,& Passow, U. (in press) The carbon and nitrogen content of transparent exopolymer particles (TEP) in relation to their Alcian Blue adsorption. *Marine Ecology Progress Series*

Fabricius, K. E. & Wolanski, E. 2000 Rapid smothering of coral reef organisms by muddy marine snow. *Estuarine, Coastal and Shelf Sciece* **50,** 115-120.

Fisk, D. A.. 1981 Sediment shedding and particulate feeding in two free-living, sediment-dwelling corals (*Heteropsammia cochlea* and *Heterocyanthus aequicostatus*) at Wistari Reef, Great Barrier Reef. Proceedings of the Fourth International Coral Reef Symposium, Manila **2,** 21-26.

Furnas, M. J. & Mitchell, A. W. 1996 Nutrient inputs into the central Great Barrier Reef (Australia) from subsurface intrusions of Coral Sea waters: a two-dimensional displacement model. *Continental Shelf Research* **16,** 1127-1148.

Furnas, M. J. & Mitchell, A. W. 2001 Runoff of Terrestrial Sediment and Nutrients into the Great Barrier Reef World Heritage Area. In: E. Wolanski (ed.) *Oceanographic Processes of Coral Reefs*, pp. 37-49. CRC Press, Boca Raton, USA.

Furnas, M. J., Mitchell, A. W. & Skuza, M. 1997 Shelf-scale nitrogen and phosphorus budgets for the central Great Barrier Reef. *Proceedings of the eighth International Coral Reef Symposium,* Panama **2,** 809-814.

Gilmour, J. 1999 Experimental investigation into the effects of suspended sediment on fertilisation, larval survival & settlement in a scleractinian coral. *Marine Biology* **135,** 451-462.

Hansen, J. L. S., Kiørboe, T. & Alldredge, A. L. 1996 Marine snow derived from abandoned larvacean houses: sinking rates, particle content and mechanisms of aggregate formation. *Marine Ecology Progress Series* **141,** 205-215.

Herndl, G. J. 1988 Ecology of amorphous aggregations (marine snow) in the Northern Adriatic Sea. II. Microbial activity in marine snow and its implications to overall pelagic processes. *Marine Ecology Progress Series* **48,** 265-275.

Heyward, A. J. & Negri, A. P. 1999 Natural inducers for coral larval metamorphosis. *Coral Reefs* **18,** 273-279.

Kiørboe, T., Andersen, K. P. & Dam, H. G. 1990 Coagulation efficiency and aggregate formation in marine phytoplankton. *Marine Biology* **107,** 235-245.

Kraus, M. 1997 Zur Bildung von TEP (transparent exopolymer particles) in der Kieler Bucht. Unpublished Diplom Thesis, Christian-Albrechts-Universität Kiel

Logan, B. E., Passow, U., Alldredge, A. L., Grossart, H. & Simon, M. 1995 Rapid formation and sedimentation of large aggregates is predictable from coagulation rates (half-lives) or transparent exopolymer particles (TEP). *Deep Sea Research* **42,** 203-214.

Marubini, F., and P. Davies. 1996. Nitrate increases zooxanthellae population density and reduces skeletogenesis in corals. *Marine Biology* 127: 319-28.

Müller, W. E. G., Riemer, S., Kurelec, B., Smodlaka, N., Puskaric, S., Jagic, B., Müller-Niklas, G. & Queric, N. V. 1998 Chemosensitizers of the multixenobiotic resistance in amorphous aggregates (marine snow): etiology of mass killing on the benthos in the Northern Adriatic Sea. *Environmental Toxicology and Pharmacology* **6,** 229-238.

Muscatine, L. P., P. G. Falkowski, Z. Dubinsky, P. A. Cook, and L. R. McCloskey. 1989. The effect of external nutrient resources on the population dynamics of zooxanthellae in a reef coral. *Proc. R. Soc. Lond*. 236: 311-24.

Passow, U. & Alldredge, A. L. 1994 Distribution, size and bacterial colonization of transparent exopolymer particles (TEP) in the ocean. *Marine Ecology Progress Series* **113,** 185-198.

Passow, U. & Alldredge, A. L. 1995 A dye-binding assay for the spectrophotometric measurement of transparent exopolymer particles (TEP). *Limnology and Oceanography* **40,** 1326-1334.

Passow, U., Alldredge, A. L., & Logan, B. E. 1994 The role of particulate carbohydrate exudates in the flocculation of diatom blooms. *Deep-Sea Research* **41**, 335-357.

Philipp, E. & Fabricius, K. E. (in review) Photophysiological stress in scleractinian corals in response to short-term sedimentation.

Rogers, C. 1990 Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* **62,** 185-202.

Sato, M. 1985 Mortality and growth of juvenile coral *Pocillopora damicornis* (Linnaeus). *Coral Reefs* **4,** 27-33.

Stachowitsch, M. 1984 Mass mortality in the Gulf of Trieste: the course of community destruction. *P S Z N I Marine Ecology* **5,** 243-264.

Stafford-Smith, M. G. 1993 Sediment-rejection efficiency of 22 species of Australian scleractinian corals. *Marine Biology* **115,** 229-243.

Stafford-Smith, M. G. & Ormond, R. F. G. 1992 Sediment-rejection mechanisms of 42 species of Australian scleractinian corals. *Australian Journal of Marine and Freshwater Research* **43,** 683-705.

Statistical Sciences, 1999 *S-PLUS, Version 2000 for Windows.* Statistical Sciences, a division of Mathsoft Inc. Seattle, USA

Wild, C. 2000 Effekte von "marine snow" - Sedimentation auf Steinkorallen (Hexacorallia, Scleractinia) des Great Barrier Reef, Australien. Unpublished Diplom thesis, University of Bremen, Dept of Biology and Chemistry, 110 pp.

Wolanski, E. 1994 *Physical oceanographic processes of the Great Barrier Reef.* CRC Press, Boca Raton, 194 pp.

Wolanski, E. & Gibbs, R. J. 1995 Flocculation of suspended sediment in the Fly River Estuary, Papua New Guinea. *Journal of Coastal Research* **11,** 754-762.

Wolanski, E., Spagnol, S. & Ayukai, T. 1998 Field and model studies of the fate of particulate carbon in mangrove-fringed Hinchingbrook Channel, Australia. *Mangroves and Salt Marshes* **2,** 205-221.

Wolanski, E., Spagnol, S. & Lim, F. G. 1997 The importance of mangrove flocs in sheltering seagrass in turbid coastal waters. *Mangroves and Salt Marshes* **1,** 187-191.

Chapter 7

Degradation and mineralization of coral mucus in reef environments

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

[1]Max Planck Institute for Marine Microbiology, Celsiusstr.1, D-28359 Bremen, Germany

[2]Marine Science Station, University of Jordan and Yarmouk University, P.O. 195, Aqaba, Jordan

[3]Centre for Marine Studies, The University of Queensland, Brisbane QLD 4072, Australia

[4]Department of Oceanography, Florida State University, Tallahassee, FL 32306-4320, USA

This chapter has been accepted for publication in Marine Ecology Progress Series.

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 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 fast and significant increase in both O_2 consumption and dissolved inorganic carbon (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 the 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.

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 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 subjected to a range of physical and chemical processes that can cause the separation of mucus from the coral surface leading to 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 a 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), shrimp (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 (1500-5000 g C m^{-2} y^{-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 about 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 and 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.

MATERIAL 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 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 –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.

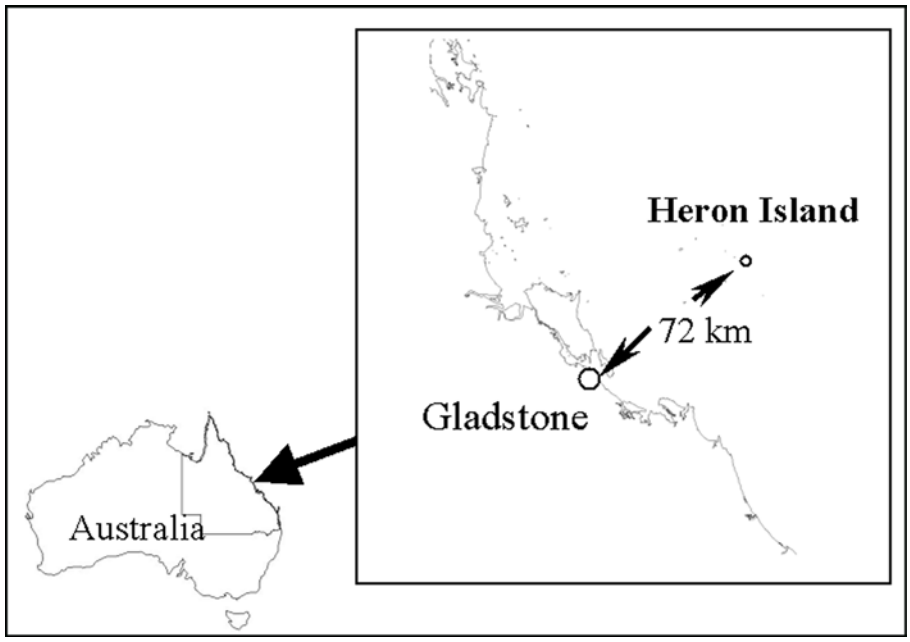

Figure 1: Location of the study site Heron Island.

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^{o}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 6N HCL until gas development ceased, and then washed twice with distilled water and dried at 60°C.

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 20s, 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 three more times. Bacteria were counted in subsamples from the combined supernatants. Aggregates were disintegrated by weak ultrasonic treatment (duration: 10-30s) when necessary. Bacteria were counted in natural *Shark Bay* sediments as well as in both sediment fractions used in the laboratory incubations (Table 1).

Table 1. Physico-chemical properties of and bacteria count in the sediments used for different experiments.

Sediment	Median grain size (µm)	Permeability (10^{-10} m²)	Porosity (%)	Surface area (m² 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

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 permit 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 (<2m 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 hours after 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 in-situ incubation experiment 1. As a control, bacteria were also counted in seawater sampled from the reef flat on the day of the mucus collection. All counts were performed using the standard AODC method (Hobbie et al. 1977).

Samples for particulate organic carbon 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 hours 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 hours. 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 local seawater in 30 ml Winkler bottles under dark conditions and at in-situ temperature (26-29° C). The O_2 concentrations in both treatments were measured parallel in 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 two laboratory and four 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 hours later. The laboratory incubations ran for 6 h. During all incubations, water samples (30-100 ml) were taken at pre-set time intervals (30-60 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 (one core per chamber) were collected for the analysis of sulfate reduction rates (SRR).

Table 2. Overview of all mucus chamber incubations done at *Heron Island*.

Date	Experiment	Mucus (Control) chambers	Water temperature/ Salinity(°C/PSU)	Parameters measured in chamberwater (-sediment)
2/4/01	insitu 1	3(4)	28,2/34,0	O2,DIC, NaBr
2/7/01	lab 1(coarse)	3(3)	27,2/34,5	O2,DIC
2/8/01	lab 2(fine)	3(3)	27,4/34,0	O2,DIC
1/15/02	in situ 2	2(2)	26,2/34,5	O2, (SRR)
1/21/02	in situ 3	2(2)	27,2/34,0	O2
1/25/02	in situ 4	2(2)	28,3/35,5	O2

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 about 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 in 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 about 8 cm marked by a ring of tape on the chamber wall and thus, included a water column of approximately 22 cm height. Then the chambers were 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 using Onset™ HOBO light loggers, made waterproof by shrink-wrapping them in transparent, non light absorbing clingwrap, and Tidbit temperature loggers revealed that no light intrusion and heating occurred in the chambers. Finally, the chambers were secured with lead weight 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, 150-280 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 chamberwall.

Laboratory chamber incubations

In order to assess the effect of sediment permeability on the degradation of coral mucus, two laboratory chamber incubations were conducted using sediments of different grain size. Sediment was collected from *Shark Bay* (06.02.2001) and separated with a sieve (500 µm) into a coarse and a medium grain size fraction (829 and 536 µm median grain size, respectively, see Table 1). The experiments were

conducted in a very 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 the incubation at in-situ temperature (26-28° C). The chambers were filled with 4.5 dm^3 of either the coarse (07.Feb.) or the medium (08.Feb.) 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 three of the chambers of each set. During the 6 hours 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* GmbH, Sensor type A, tip diameter < 50µm, for the measuring principle see (Klimant et al. 1995) mounted in the lids of the chambers or by 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 two-point calibration in oxygen-free (addition of sodium dithionite) and air-saturated seawater.

Dissolved inorganic carbon (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 standard for calibration.

In order to assess whether anaerobic decomposition contributed to the degradation processes associated with addition of coral mucus, sulfate reduction rates (SRR) were measured within 12 hours in sediment cores taken (one core from each chamber) at the end of in-situ experiment 2.

Sulfate reduction rates (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/ 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 6h at ambient temperatures (Exp 1: 33°C; Exp 2: 28°C). The sediment was subsequently sliced into 1 cm sections

and fixed in 20% ZnAc. Samples were processed using a cold chromium distillation procedure (Kallmeyer et al. 2003) with the slight modification that HCl was added until all carbonates were dissolved. The activity of $^{35}SO_4^{2-}$ and TRIS (Total Reduced Inorganic Sulfur) were determined using a liquid scintillation counter (Packard 2500 TR), 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:

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

SRR: sulfate reduction rates $(nmol \cdot cm^{-3} \cdot d^{-1})$

a_{TRIS}: activity (CPM) in TRIS per cm^3

α: correction factor for the expected isotopic fractionation (1.06)

SA : specific activity of sulfate; $SA = CPM_{Sulfate} \cdot l \cdot nmol_{Sulfate}^{-1} \cdot l^{-1}$ $(CPM \cdot nmol^{-1})$

t: time (d)

Oxygen profiles within the stirred chambers

The 2-dimensional oxygen distribution and penetration depths in the stirred chambers were measured using semi-transparent planar O_2 optodes. 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 are given in Glud et al. (1996b).

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) 2-dimensional 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 (x=200 x=250, x=300, x=350 and x=400). 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 x 19 mm and the spatial resolution was 40 x 40 µm pixel^{-1}.

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 that revealed approximately 100-fold increased 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 3-14 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 more than 15-fold increased O_2 consumption in coral mucus. This result was confirmed by the other 4 mucus incubation experiments, which showed O_2 consumption rates ranging from 130 to 445 µM O_2 d^{-1} and 5 to 41 µM O_2 d^{-1} for mucus and seawater incubations, respectively.

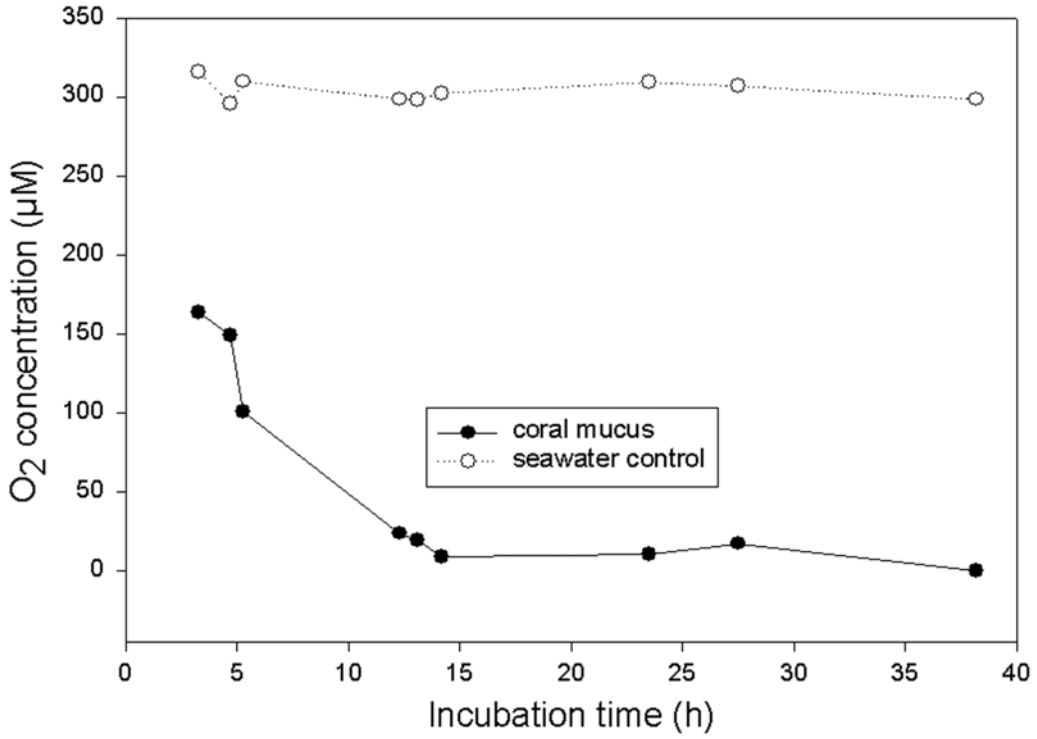

Figure 2. Oxygen concentrations in bottles filled with natural *Acropora* mucus (solid symbols) or seawater (open symbols) over time. The bottles were incubated at 28° C for 38 hours.

Chamber incubation experiments

The coarse *Shark Bay* sediment was highly permeable (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 x 10^9 bacteria cm^{-3} (Table 1).

In-situ chamber incubations

In the in-situ experiments, the addition of coral mucus (characteristics see Table 3) caused a 1.2-1.7 fold increase of the O_2 consumption rate in the amended chambers relative to the control chambers without mucus (Fig.3). In experiment 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 depth in 14 of 15 profiles (5 measured in each of 3 cores from Shark Bay) was 2.0 to 2.5 mm, only one profile showed an O_2 penetration up to 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.

Table 3. Carbon content and bacteria abundance in coral mucus used for the chamber incubations. Values are means ± standard error (n in replicates, n.d. = no data available).

Sampling date	used for	C (mg L^{-1})	Bacteria 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	n.d.	3.0 ± 1.7 (3)
06.02.2001	lab experiments	51.6 ± 7.7 (3)	292 ± 31 (3)
14.01.2002	in situ 2	30.9 ± 0.4 (3)	n.d.
14.01.2002	sw control	1.8 ± 0.1 (3)	n.d.
20.01.2002	in situ 3	12.1 (1)	n.d.
22.01.2002	sw control	0.3 ± 0.1 (3)	n.d.
25.01.2002	in situ 4	10.8 ± 0.8 (3)	n.d.
25.01.2002	sw control	0.43 ± 0.03 (3)	n.d.

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).

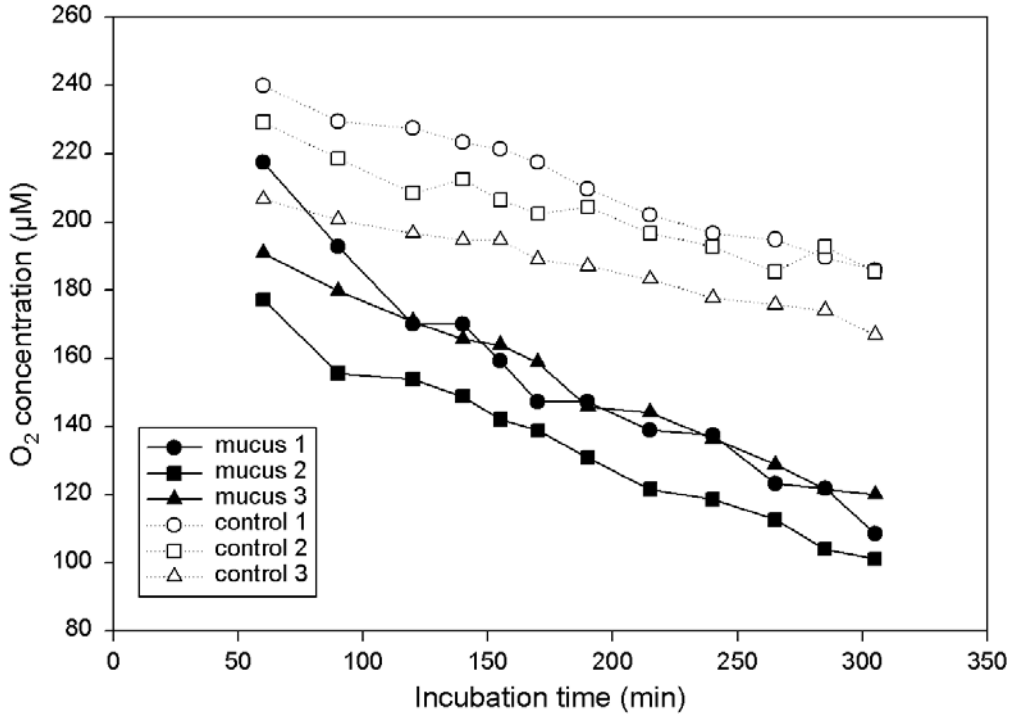

Figure 3. O_2 concentration in 6 benthic chambers during in situ experiment 1. Coral mucus was added to the 3 chambers represented by black symbols. Control chamber values are shown using open symbols.

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 200-280 min (coarse sand) and 300-360 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).

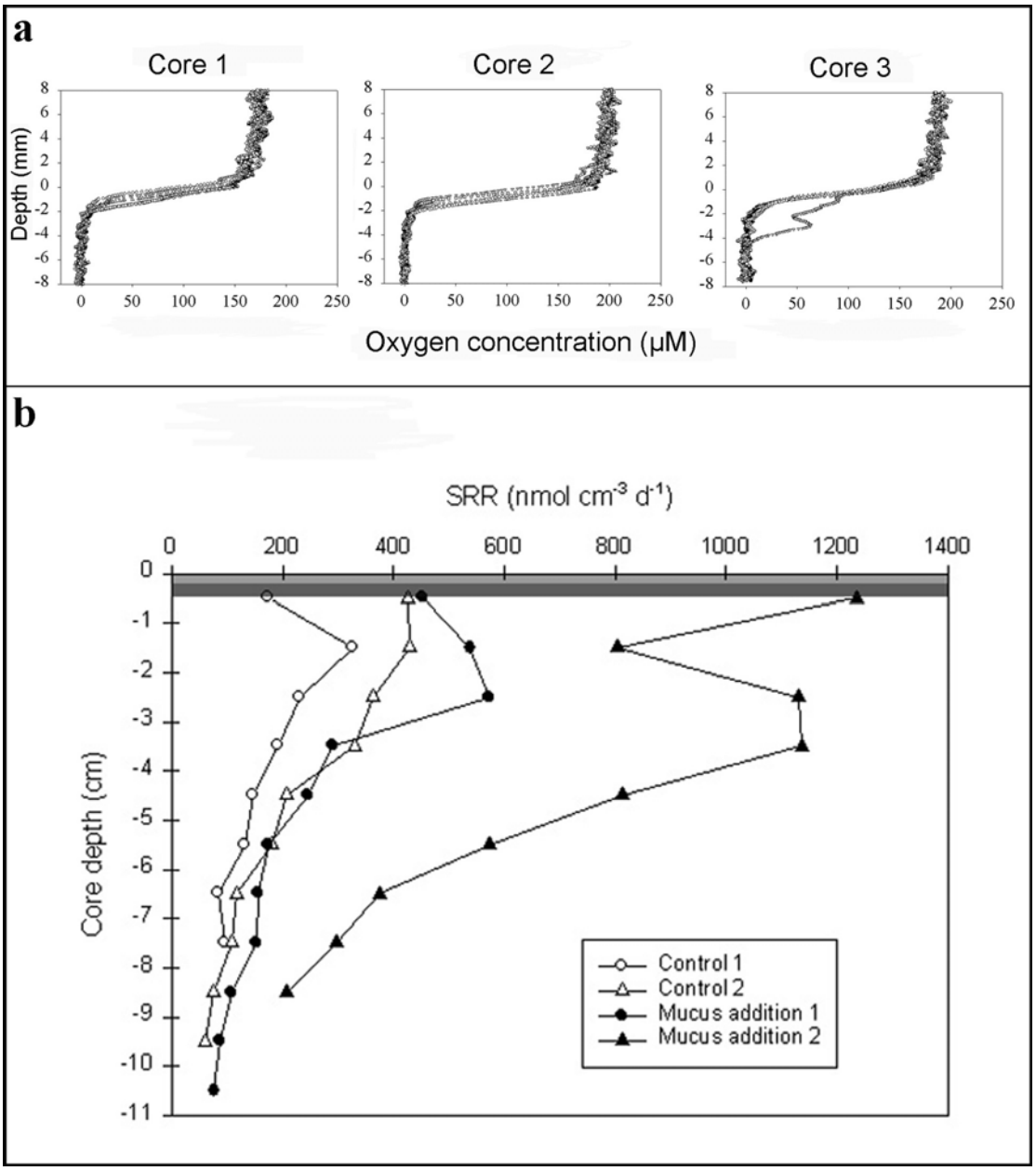

Figure 4. a) Oxygen distribution in three sediment cores from Shark Bay measured with planar optodes, **b)** Sulfate reduction rates (SRR) in sediment cores collected within all 4 chambers at the end of in situ experiment 2. Coral mucus was added to the chambers represented by black symbols. Control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

The amount of organic carbon added as mucus to the chambers ranged from 240 to 870 µmol (corresponding to 40-220 µmol POC l^{-1}) in all experiments (Table 4). In the laboratory experiments, the mucus concentrations in the chambers were highest (214-220 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).

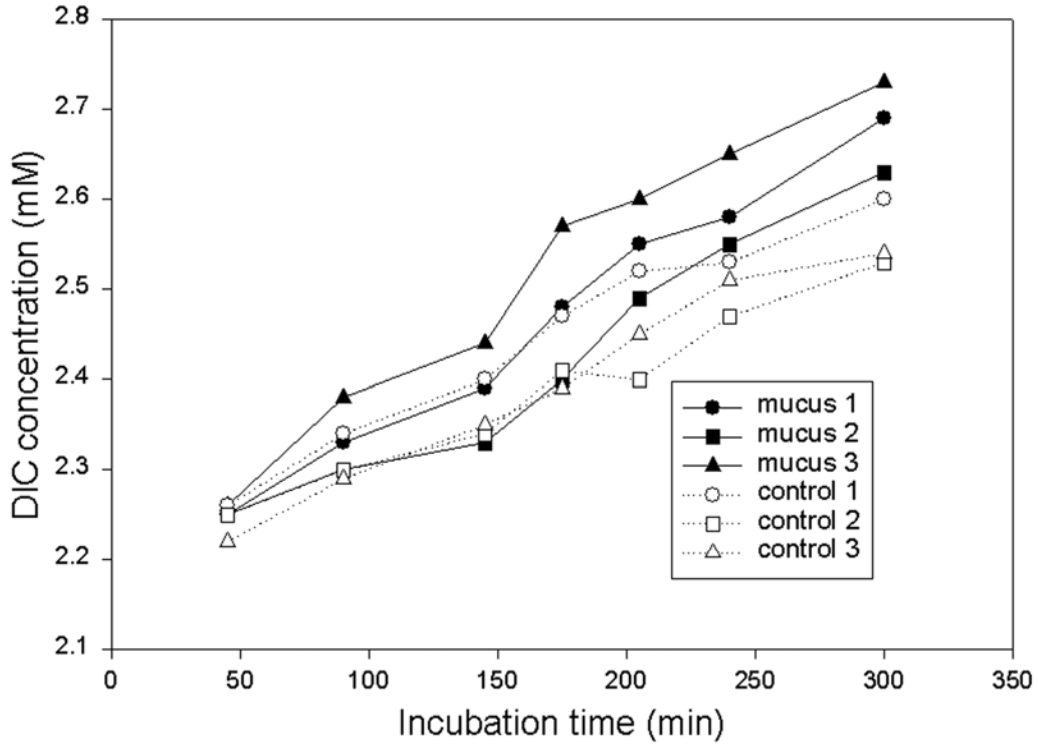

Figure 5. DIC concentration in 6 benthic chambers during in situ experiment 1. Coral mucus was added to the 3 chambers labeled with black symbols. Control chamber values are shown using open symbols.

The fluxes of O_2 and DIC calculated from all chamber experiments are summarised in Figure 8. In the 4 in-situ experiments we found in the chambers with mucus addition an increase in O_2 consumption of 17-46 mmol m^{-2} d^{-1} relative to the controls, while in the two laboratory experiments increases of 109-199 mmol m^{-2} d^{-1} were reached. A two-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 experiment 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) to the addition of coral mucus in the laboratory

experiments (176-298 mmol m^{-2} d^{-1} compared to 141 mmol m^{-2} d^{-1} for the in-situ experiment 1).

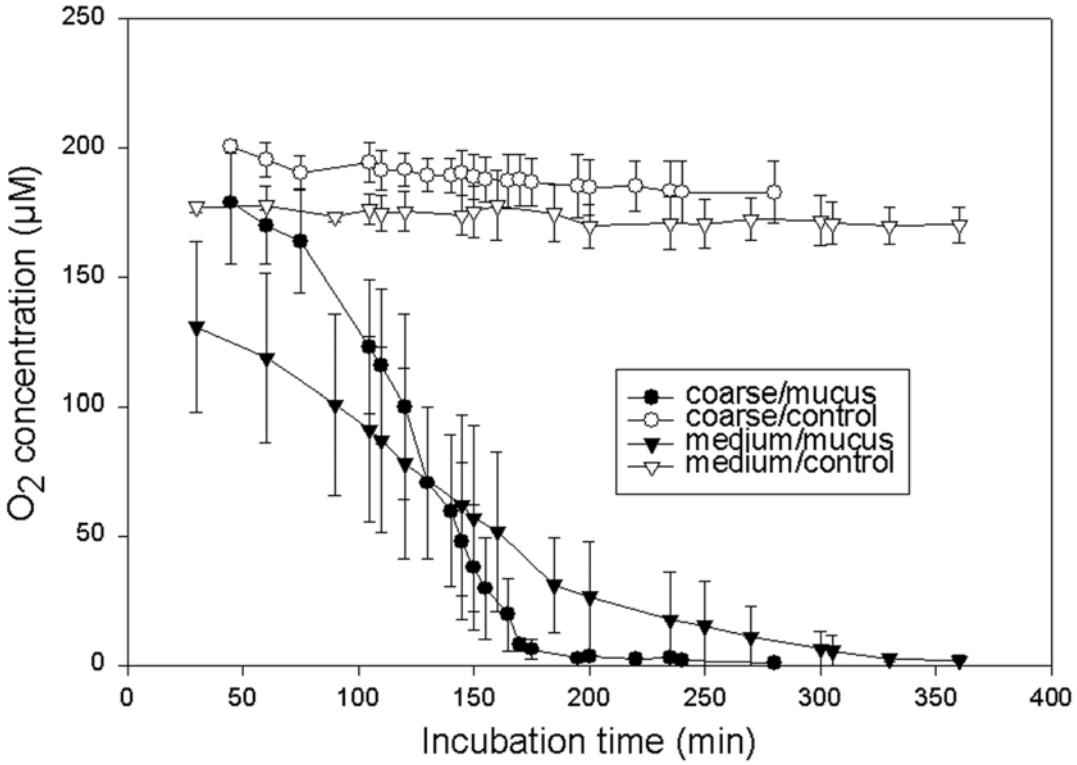

Figure 6. Mean O_2 concentrations in the incubation chambers during both lab experiments. Coral mucus was added to the chambers represented by black symbols. Control chamber values are shown by open symbols. Either carbonate sediment with medium (triangles) or coarse grain size (circles) was used. Error bars are indicating the standard deviation 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 experiment 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 a C turnover rates ranging from 7-18% h^{-1} during the in-situ experiments and rates from 13-24% h^{-1} and 26-41% h^{-1} in the lab 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 are similar, which can be caused by very similar permeabilities of both sediments (see Table 1).

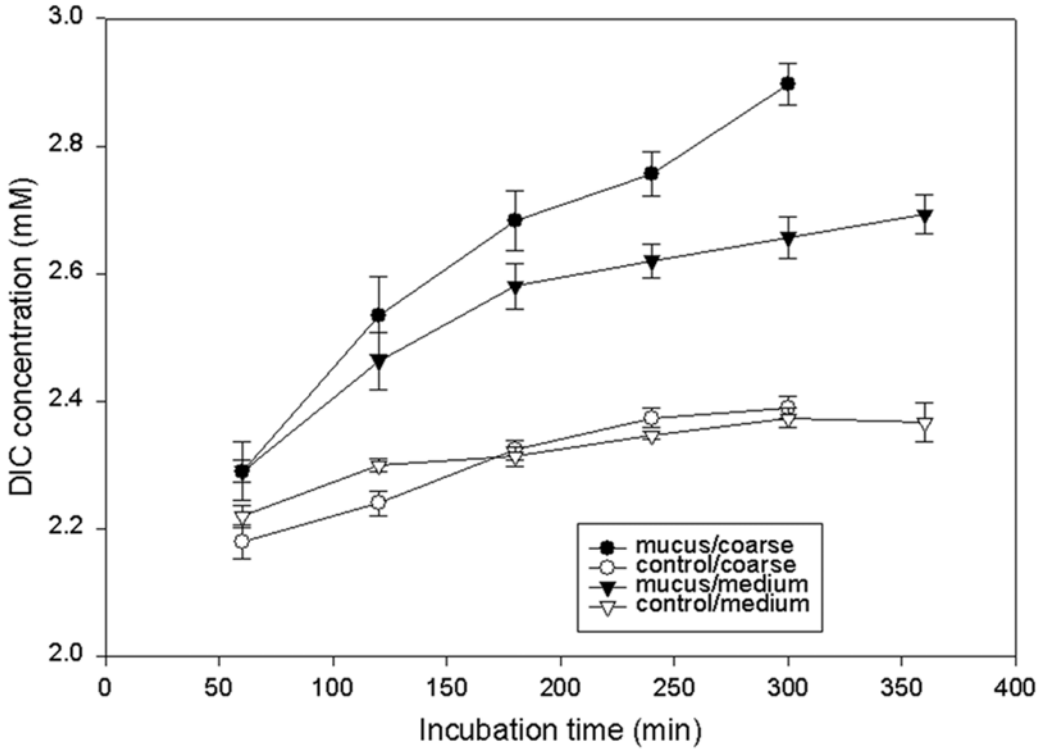

Figure 7. Mean DIC concentrations in the incubation chambers during both lab experiments. Coral mucus was added to the chambers represented by black symbols. Control chambers values are shown by open symbols. Medium (triangles) or coarse grain size (circles) was used. Error bars are indicating the standard deviation of 3 replicate chambers.

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

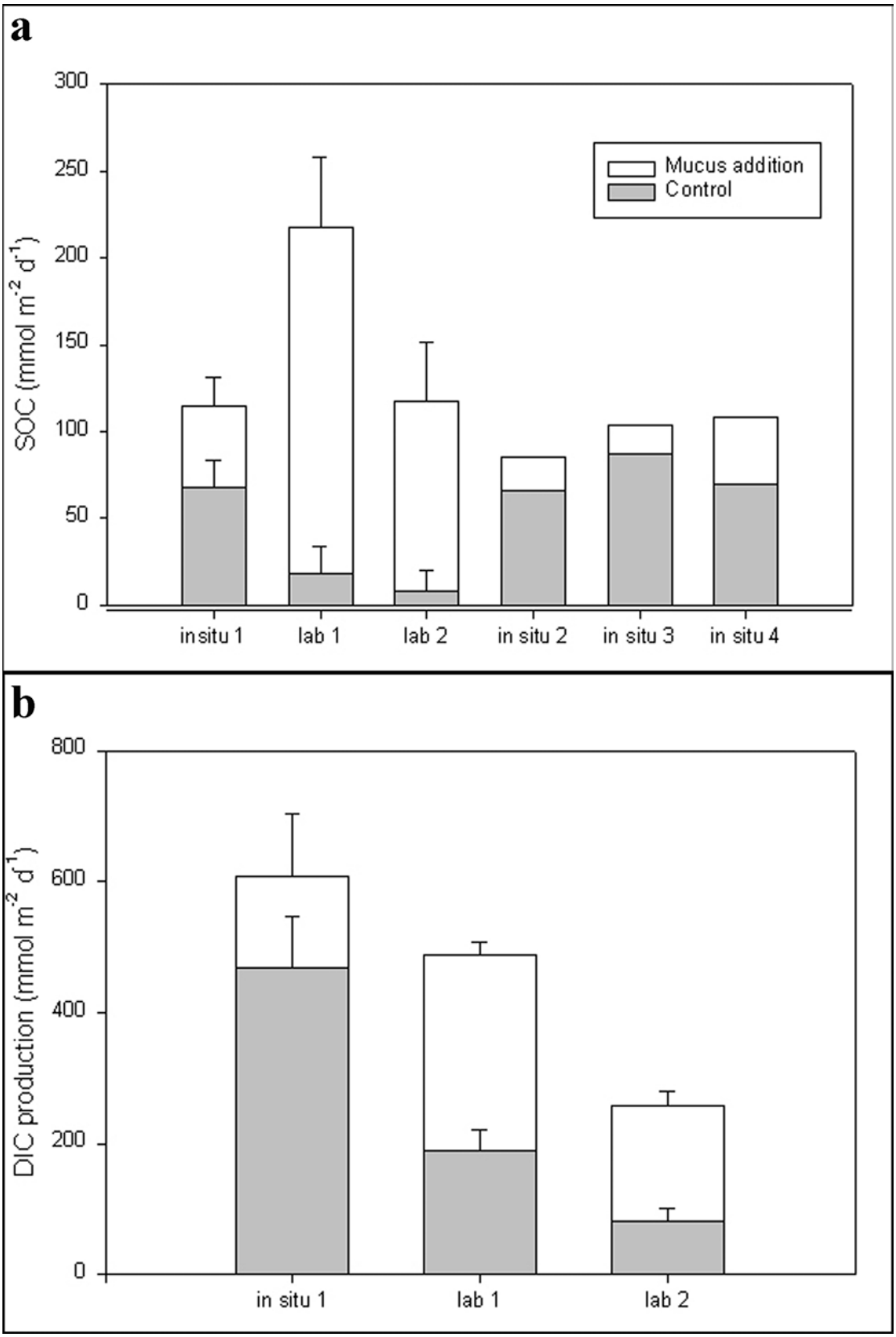

Figure 8. Sedimentary **a)** O_2 consumption and **b)** DIC release as calculated from all chamber incubation experiments. Open bars are indicating mean chamber values with mucus addition, gray bars show the control values. Error bars are indicating the standard deviation of all experiments with n=3.

Table 4. Degradation of reduced carbon derived from coral mucus. Amounts of carbon added to the chambers were calculated from carbon analysis in coral mucus (Table 3). Rates for DIC production and O_2 consumption are calculated from the rates measured in the mucus chambers subtracted 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 (upper part of table) or the increased consumption of O_2 (lower part of table) under the assumption that 1 mol of O_2 mineralizes 1 mol of reduced C.

Experiment	C added (µmol)	DIC prod.(µmol h^{-1})	C turnover (% h^{-1})
in situ 1	857.9	125.3	14.6
lab (coarse sand)	859.2	352.0	41.0
lab (medium sand)	872.5	208.0	23.8

Experiment	C added (µmol)	O2 cons.(µmol h^{-1})	C turnover (% h^{-1})
in situ 1	857.9	60.3	7.0
in situ 2	360.2	23.2	6.5
in situ 3	302.2	20.1	6.7
in situ 4	242.8	44.2	18.2
lab (coarse sand)	859.2	224.9	26.2
lab (medium sand)	872.5	113.6	13.0

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 just coral mucus as energy and nutrient source (Griffin 1999) and a significant number of the mucus colonising bacteria are able to grow on coral mucus as the only source of carbon (Pascal & Vacelet 1981). In addition, Moriarty et al. (1985) found in incubation experiments with and without mucus from *Acropora* and *Porites* 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 (1) found 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 days 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 130-445 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 experiment 1, we measured an O_2 consumption of 334 µM d^{-1}. According to this rate, addition of 280 mL of this mucus to chambers with an average volume of 6.9 L (as done during in-situ experiment 1) would lead to a calculated increase in O_2 consumption of approximately 14 µM d^{-1}. This consumption rate is about 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 the coral mucus added to the benthic chambers was primarily degraded in the carbonate sediment. The 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 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 like those used in the chamber experiments showed that suspended mucus can easily be transported into the carbonate sands with water flows percolating the sediment (Wild and Huettel, unpublished data). This may be an explanation why the results of this study did initially contradict 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. The 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 two 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 a 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 up to 1200 nmol cm^{-3} d^{-1} in a core taken from one of the mucus chambers at the end of in-situ experiment 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. Werner, unpublished data).

Our finding that O_2 can only penetrate 2-5 millimeters 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 increased stirring speed in the chambers for O_2 measurements with planar optodes compared to the stirring speed used for the in-situ and laboratory incubations. We therefore can state that the oxic surface layer of reef sands may even thinner than the 1 cm estimated by Skyring (1985).

Rasheed et al. (2003, in press) suggested that high permeability, porous grains, and the mineralogy of carbonate sands are important factors that make 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 as 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 the 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 after 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 indicated that the 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. This mechanism is another example for the short linked nutrient cycle between autotrophs and heterotrophs in coral reefs that may contribute to explain the high productivity of this ecosystem.

ACKNOWLEDGEMENTS

We thank B. B. Jørgensen for his support of this work and stimulating discussions. Thanks are also due to M. Alisch, S. Menger and S. Kremb for experimental assistance and help with the chemical analyses. We thank Ingo Klimant and Gregor Liebsch for fabrication of planar O_2 optodes. Gerhard Holst and Björn Grunwald are acknowledged for support with the MOLLI system. We acknowledge O. Hoegh-Guldberg and R. Forbes of Heron Island Research Station (HIRS) for making this research at HIRS possible and logistical assistance. All sample collections and in- situ experiments were done under the permits QC00/102, G01/479 and G01/601 of the Great Barrier Reef Marine Park Authority. This research was funded by the Max Planck Society (MPG), Germany and the Centre for Marine Studies (CMS) of the University of Queensland, Brisbane, Australia.

LITERATURE CITED

Benson A, Muscatine L (1974) Wax in coral mucus - energy transfer from corals to reef fishes. Limnol Oceanogr 19:810-814

Coffroth MA (1984) Ingestion and incorporation of coral mucus aggregates by a Gorgonian soft coral. Mar Ecol Progr Ser 17:193-199

Coffroth MA (1990) Mucous sheet formation on poritid corals - an evaluation of coral mucus as a nutrient source on reefs. Mar Biol 105:39-49

Coles S, Strathman R (1973) Observations on coral mucus flocs and their potential trophic significance. Limnol Oceanogr 18:673-678

Crossland C, Barnes D, Borowitzka M (1980) Diurnal lipid and mucus production in the staghorn coral *Acropora acuminata*. Mar Biol 60:81-90

Daumas R, Galois R, Thomassin B (1982) Biochemical composition of soft and hard coral mucus on a New Caledonian lagoonal reef. Proc 4th Int Coral Reef Symp 2:59-68

Dauwe B, Middelburg J, Herman P (2001) The effect of oxygen on the degradability of organic matter in subtidal and intertidal sediments of the North Sea area. Mar Ecol Prog Ser 215:13-22

Davies PS (1984) The role of zooxanthellae in the nutritional energy requirements of *Pocillopora eydouxi*. Coral Reefs 2:181-186

Ducklow H, Mitchell R (1979a) Bacterial populations and adaptations in the mucus layers on living corals. Limnol Oceanogr 24:715-725

Ducklow HW, Mitchell R (1979b) Composition of mucus released by coral reef coelenterates. Limnol Oceanogr 24:706-714

Ferrier-Pages C, Leclercq N, Jaubert J, Pelegri SP (2000) Enhancement of pico- and nanoplankton growth by coral exudates. Aquat Microb Ecol 21:203-209

Forster S, Huettel M, Ziebis W (1996) Impact of boundary layer flow velocity on oxygen utilisation in coastal sediments. Mar Ecol Prog Ser 143:173-185

Glud RN, Forster S, Huettel M (1996a) Influence of radial pressure gradients on solute exchange in stirred benthic chambers. Mar Ecol Prog Ser 141:303-311

Glud RN, Ramsing NB, Gundersen JK, Klimant I (1996b) Planar Optrodes - a new tool for fine scale measurements of two-dimensional O_2 distribution in benthic communities. Mar Ecol Prog Ser 140:217-226

Goldberg W (2002) Feeding behavior, epidermal structure and mucus cytochemistry of the scleractinian *Mycetophyllia reesi*, a coral without tentacles. Tissue Cell 34:232

Gottfried MRM (1983) Ingestion and incorporation of coral-mucus detritus by reef zooplankton. Mar Biol 72:211-218

Grange K (1991) Mutualism between the Antipatharian *Antipathes fiordensis* and the Ophiuroid *Astrobrachion constrictum* in New Zealand fjords. Hydrobiologia 216:297-303

Griffin DW (1999) Microbiological studies of Florida water quality. PhD thesis, University of South Florida,

Hall POJ, Aller RC (1992) Rapid, small-volume, flow injection analysis for ΣCO_2 and NH_4^+ in marine and freshwaters. Limnol Oceanogr 37:1113-1119

Herndl GJ, Velimirov B (1986) Microheterotrophic utilization of mucus released by the Mediterranean coral *Cladocora cespitosa*. Mar Biol 90:363-369

Hickel W (1974) Seston composition of the bottom waters of Great Lameshur Bay, St. John, US Virgin Islands. Mar Biol 24:125-130

Hobbie JE, Daley RJ, Jasper S (1977) Use of nucleopore filters for counting bacteria by fluorescence microscopy. Appl Environ Microbiol 33:1225-1228

Hubbard JAE, Pocock YP (1972) Sediment-rejection by recent scleractinian corals: a key to palaeo-environmental reconstruction. Geol Rundschau 61:598-626

Huettel M, Gust G (1992) Solute release mechanisms from confined sediment cores in stirred benthic chambers and flume flows. Mar Ecol Prog Ser 82:187-197

Huettel M, Rusch A (2000) Transport and degradation of phytoplankton in permeable sediment. Limnol Oceanogr 45:534-549

Ikeda Y, Miyachi S (1995) Carbon dioxide fixation by photosynthesis and calcification for a solitary coral, *Fungia* sp. Bul Inst Oceanogr, Monaco 14:61-67

Johannes R (1967) Ecology of organic aggregates in the vicinity of a coral reef. Limnol Oceanogr 12:189-195

Jørgensen BB (1977) The sulfur cycle of a coastal marine sediment (Limfjorden, Denmark). Limnol Oceanogr 22:814-832

Kallmeyer J, Ferdelman T, Weber A, Fossing H, Jørgensen B (2003) Evaluation of a cold chromium distillation procedure for recovering very small amounts of radiolabelled sulfide. Submitted to Biogeochemistry

Kautsky H (1939) Quenching of luminescence by oxygen. Trans Faraday Soc 35:216-219

Kinsey DW (1983) Standards of performance in coral reef primary production and carbon turnover. In: Barnes DJ (ed) Perspectives on coral reefs. Brian Clouston Publishing, A.C.T. Australia

Klimant I, Meyer V, Kühl M (1995) Fiber-optic oxygen microsensors, a new tool in aquatic biology. Limnol Oceanogr 40:1159-1165

Klute A, Dirksen C (1986) Hydraulic conductivity and diffusivity: laboratory methods. In: Klute A (ed) Methods of soil analysis -part 1- physical and mineralogical methods, 2nd edn. American Society of Agronomy

Kristensen E (2000) Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. Hydrobiologia 426:1-24

Krupp DA (1984) Mucus production by corals exposed during an extreme low tide. Pac Sci 38:1-11

Krupp DA (1985) An Immunochemical study of the mucus from the solitary coral *Fungia scutaria* (Scleractinia, Fungiidae). Bull Mar Sci 36:163-176

Lewis JB (1977) Processes of organic production on coral reefs. Biol Rev Camb Philos Soc 52:305-347

Lewis JB (1978) Feeding mechanisms in black corals (*Antipatharia*). J Zool 186:393-396

Lewis JB, Price WS (1976) Patterns of ciliary currents in Atlantic reef corals and their functional significance. J Zool 178:77-89

Marinelli RL, Jahnke RA, Craven DB, Nelson JR, Eckman JE (1998) Sediment nutrient dynamics on the South Atlantic Bight continental shelf. Limnol Oceanogr 43:1305-1320

Marsden J, Meeuwig J (1990) Preferences of planktotrophic larvae of the tropical serpulid *Spirobranchus giganteus* (Pallas) for exudates of corals from a Barbados reef. J Exp Mar Biol Ecol 137:97-104

Marshall M (1968) Observations on organic aggregates in the vicinity of coral reefs. Mar Biol 2:50-55

Moriarty DJW, Pollard PC, Alongi DM, Wilkinson CR, Gray JS (1985) Bacterial productivity and trophic relationships with consumers on a coral reef (MECOR 1). In: Proceedings of the fifth international coral reef congress, Tahiti., p 457-462

Odum HT, Odum EP (1955) Trophic structure and productivity of a windward coral reef community on Eniwetok atoll. Ecol Monogr 25:291-320

Pascal H, Vacelet E (1981) Bacterial utilization of mucus on the coral reef of Aqaba (Red Sea). Proc. 4th Int. Coral Reef Symp., Manila, Philippines 1:669-677

Patton W (1994) Distribution and ecology of animals associated with branching corals (*Acropora* spec.) from the Great Barrier Reef, Australia. Bul Mar Sci 55:193-211

Ploug H, Grossart HP (2000) Bacterial growth and grazing on diatom aggregates: Respiratory carbon turnover as a function of aggregate size and sinking velocity. Limnol Oceanogr 45:1467-1475

Richards GN, Meikle PJ, Yellowlees D (1983) Preliminary investigations into the chemical nature of mucus from the staghorn coral (*Acropora formosa*). Proc Inaug Great Barrier Reef Conf:353-359

Richman S, Loya Y, Slobodkin L (1975) Rate of mucus production by corals and its assimilation by the coral reef copepod *Acartia negligens*. Limnol Oceanogr 20:918-923

Rinkevich B, Wolodarsky Z, Loya Y (1991) Coral crab association-a compact domain of a multilevel trophic system. Hydrobiologica 216:279-284

Rublee P, Lasker H, Gottfried M, Roman M (1980) Production and bacterial colonization of mucus from the soft coral *Briarium asbestinum*. Bull Mar Sci 30:888-893

Schlichter D, Svoboda A, Kremer BP (1983) Functional autotrophy of *Heteroxenia fuscescens* (Anthozoa: Alcyonaria): carbon assimilation and translocation of photosynthates from symbionts to host. Mar Biol 78:29-38

Schuhmacher H (1977) Ability of fungiid corals to overcome sedimentation. Proc. 3rd Int. Symp. Coral Reefs:503-509

Shafir A, Loya A (1983) Consumption and assimilation of coral mucus by the burrowing mussel *Lithophaga lessepsiana*. Proc Int Conf Mar Sci Red Sea 9:135-140

Skyring GW (1985) Anaerobic microbial processes in coral reef sediments. Proc 5th Int Coral Reef Congress 3:421-425

Stachowicz JJ, Hay ME (1999) Mutualism and coral persistence: The role of herbivore resistance to algal chemical defense. Ecology 80:2085-2101

Thamdrup B, Canfield DE (1996) Pathways of carbon oxidation in continental margin sediments off central Chile. Limnol Oceanogr 41:1629-1650

Vacelet E, Thomassin B (1991) Microbial utilization of coral mucus in long term in situ incubation over a coral reef. Hydrobiologia 211:19-32

Wilkinson CR (1987) Microbial ecology on a coral reef. Search 18:31-33

Ziebis W, Huettel M, Forster S (1996) Impact of biogenic sediment topography on oxygen fluxes in permeable seabeds. Mar Ecol Prog Ser 140:227-237

Chapter 8

Coral mucus functions as energy carrier and particle trap in the reef ecosystem

Christian Wild[1], Markus Huettel[1,2], Stephan G. Kremb[3], Anke Klueter[4], Mohammed Y. M. Rasheed[5] and Bo B. Jørgensen[1]

[1]Max Planck Institute for Marine Microbiology, Celsiusstr. D-28359 Bremen, Germany

[2]Department of Oceanography, Florida State University, Tallahassee, FL 32306-4320, USA

[3]Alfred Wegener Institute for Polar and Marine Research, Department Benthic Ecosystems, Am Handelshafen 12, D-27570 Bremerhaven, Germany

[4]Centre for Marine Studies, The University of Queensland, Brisbane QLD 4072, Australia

[5]Marine Science Station, University of Jordan and Yarmouk University, P.O. 195, Aqaba, Jordan

This chapter has been submitted to Nature.

ABSTRACT

Zooxanthellae, endosymbiotic algae of reef-building corals, substantially contribute to the high productivity of coral reefs [1], but corals exude up to half of the carbon assimilated by their zooxanthellae as gel-like mucus [2,3], which contains carbohydrates, proteins and lipids [4,5].

We found that in the Great Barrier Reef, the dominant genus of hard corals, *Acropora,* exudes up to 4.8 L mucus m^{-2} reef area d^{-1}. Between 56 and 80% of these exudates rapidly dissolve in the reef water. The remainder forms gelatinous strings, which disengage from the corals. Drifting strings accumulate suspended particles that within two hours increase the initial organic C and N content by up to three orders of magnitude. Tidal currents concentrate the mucus into the reef lagoon, where it rapidly reaches highly permeable carbonate sands. Here, in-situ benthic chamber incubations revealed that freshly exuded coral mucus is degraded at a turnover rate of at least 7% h^{-1}. We show that coral mucus can efficiently transfer photosynthetic energy harvested by the zooxanthellae and trapped particles to primarily benthic degraders. This mechanism reduces loss of material from the reef system and leads to a release of regenerated nutrients, essential for autotrophic growth in the coral reef.

MANUSCRIPT MAIN TEXT

Assimilation products from zooxanthellae cover a major part of the energy requirement of their hosts via the transfer of photosynthetically fixed carbon to the coral [6]. Arabinose contents of 25-63% in the carbohydrate fraction of mucus collected from *Acropora millepora, A. nobilis, A. aspera and A. pulchra* indicate that a large fraction of the fixed carbon is released as mucus, because arabinose is usually not a constituent of animal cells [5].

Many different hard and soft corals release coral mucus continuously and in species-specific composition [5]. Known biological functions of these mucus exudates are to protect the corals against fouling [7], potential desiccation during exposure to air at extreme low tide [8], and sedimentation [9].

The adhesive matrix of coral mucus has the ability to trap particulate matter from the water and the light-collecting coral surfaces. Mucus and trapped particles are transported over the coral surface by ciliary currents and are released into the surrounding water [4]. Coral mucus can dominate suspended matter around reefs [10,11], and in water that has resided over living reefs for several hours, labile organic matter concentrations can double [12], which probably occurs as consequence of coral mucus release. Our measured C/N ratios of 5-14 also point towards the potential value of coral mucus as food source. 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 largely unknown.

We investigated release rates, chemical composition, contents and fate of mucus produced by *Acropora*, the coral genus with the highest areal coverage (15.8%) on the reef rim (crest + slope) of Heron Island (23° 27' S, 151° 55' E), a ring-shaped platform reef on the southern boundary of the Great Barrier Reef, Australia. Submerged *Acropora* released 1.7 L mucus m^{-2} reef area d^{-1}, not including the rapidly dissolving mucus fractions. In-situ measurements were also carried out after air exposure, a regular phenomenon caused by extreme low tides [13] and occurring during about 6 days per month at Heron Island (duration ca. 2h per day). These measurements revealed that reef

rim *Acropora* can release 4.8 L mucus m^{-2} reef area d^{-1} corresponding to 10-21 mmol particulate organic C (POC), 1.5-1.8 mmol N and 0.08–0.18 mmol P.

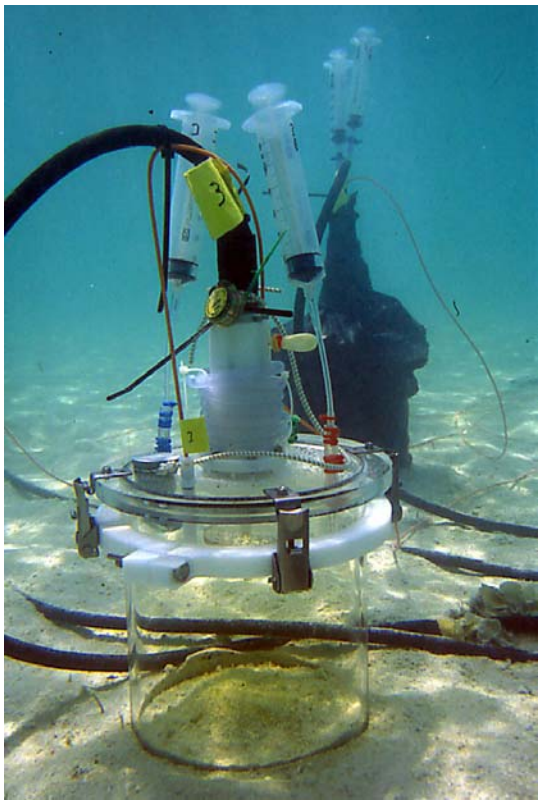

Table associated with Figure 1:

Date of in-situ experiment	Control (mmol O_2 m^{-2} d^{-1})	Mucus addition (mmol O_2 m^{-2} d^{-1})	Increase (%)
04.02.01	52; 58; 80	99; 111; 133	41
15.01.02	64; 67	71; 100	23
21.01.02	82; 92	95; 113	16
25.01.02	49; 92	106; 110	35

Figure 1 Benthic degradation of coral mucus studied with stirred benthic chambers. Values in the table represent the O_2 consumption given as mmol m^{-2} d^{-1} calculated from the O_2 concentration decrease in the enclosed water of each chamber. For these experiments only dark chambers were used (see background) in order to prevent any artifacts caused by photosynthesis. Addition of 140 - 300 mL freshly collected gel-like coral mucus to the chamber water (corresponds to 500-1500 µg POC L^{-1} compared to 171-488 µg POC L^{-1} measured in waters from the Heron Island reef flat, n=56) caused a significant O_2 consumption increase in the dark benthic chambers (two-sided U-test after Wilcoxon, Mann and Whitney, α=0.002) relative to the controls. Only less than 10% of this increase can be attributed to the water column degradation of mucus indicating that more than 90% of the added mucus was degraded in the permeable reef sands. Yellow color of chamber water is due to the addition of fluoresceine tracer to quantify advective water exchange.

More than half (56-80%) of the released gel-like coral mucus dissolves in the seawater, where this dissolved fraction provides a food source for planktonic bacteria [7,14]. Respiration measurements with freshly exuded mucus showed high O_2 consumption rates of 130-445 µmol O_2 L^{-1} d^{-1} compared to 5-41 µmol O_2 L^{-1} d^{-1} in the surrounding seawater. This is caused by 100-fold higher bacterial numbers in the mucus ($2.7*10^7$ vs. $3.0*10^5$ cells mL^{-1}, n = 3-6, measurement after Hobbie [15]).

Flux measurements with 4 to 6 stirred benthic chambers (Fig.1, picture), deployed simultaneously on the permeable lagoon sands, show that freshly produced coral mucus is also a substrate for the benthic community. Experimental addition of mucus to the water enclosed in these chambers enhanced O_2 consumption immediately by 16 to 41% (Fig.1, data). Oxygen consumption by mucus degrading water column bacteria (as quantified in the respiration experiments described above) only accounted for less than 10% of the total measured O_2 consumption, demonstrating that the benthic community decomposed more than 90% of the added mucus. The increased benthic O_2 uptake of 17-47 mmol m^{-2} d^{-1} suggests that at least 7% of the C added as coral mucus was turned over per hour, which, with the measured C:N:P ratio of 84:7:1 for coral mucus, corresponds to a conversion and potential release of 3.9 mmol N m^{-2} d^{-1} and 0.6 mmol P m^{-2} d^{-1}.

The less soluble fraction (20-44%) of the exuded gel-like mucus forms transparent filaments and strings (Fig.2a) that are detached from the coral branches and subsequently aggregate to mucus flocs. Positive buoyancy caused by enclosed gas bubbles and lipid content results in a slow ascent of these flocs. On the way through the water column, their sticky surface traps bacteria, algal cells and small carbonate particles. (Fig.2b). Enriched mucus flocs then accumulate at the water surface and form milky films that are concentrated by currents and winds producing whitish mucus coatings. Accumulation and subsequent fusion of these coatings generate 1.5 to 3.0 cm thick mucus floats (Fig.2c) with up to 2 m width and 10 m length and a cohesiveness that traps larger particles including filamentous algae, small zooplankton and sand grains (Fig.2d). Two hours after low tides with air exposure of the corals, the gel-like transparent mucus released from the corals has turned into a yellow, bubbly custard that smells strongly of dimethylsulfide and contains on average 2250 ± 230 mM POC, 220 ± 40 mM N and 2 ± 0.1 mM P (carbonate grains excluded, n=4-8).

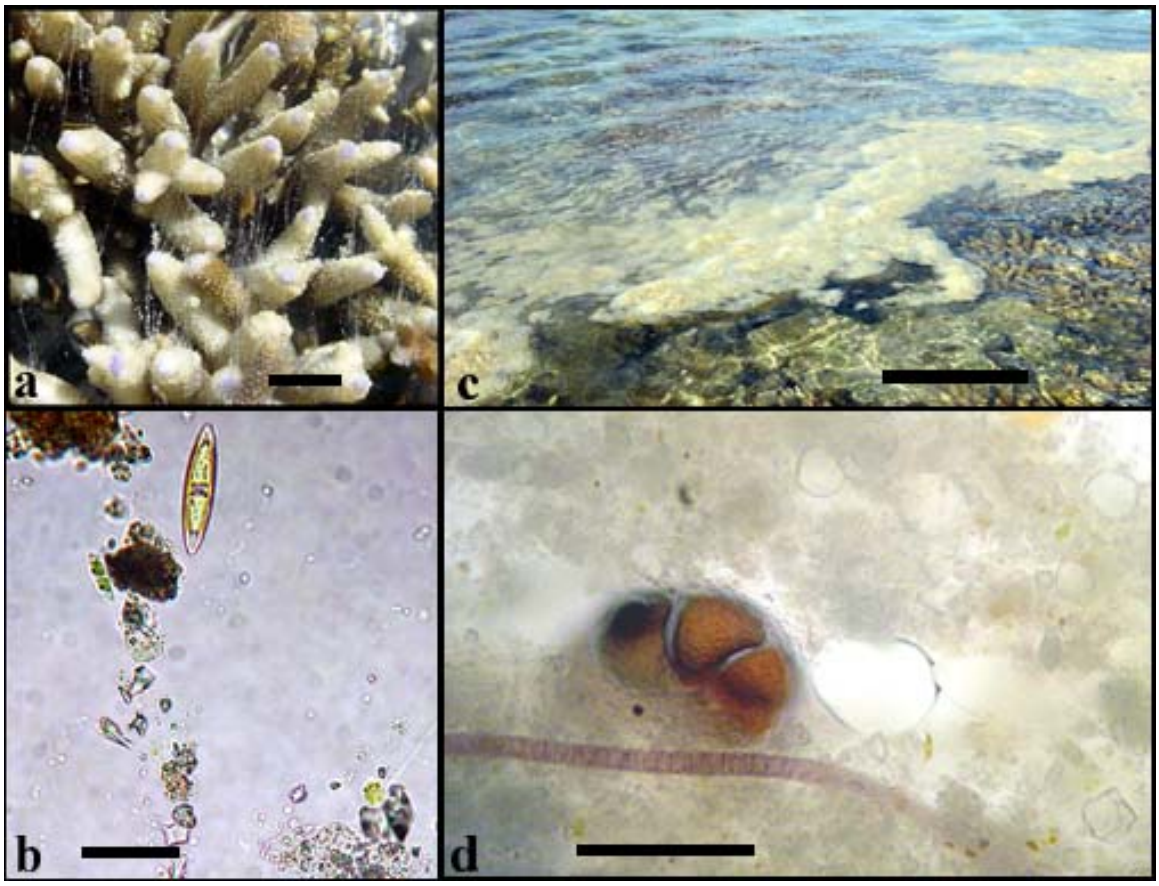

Figure 2. Changes of coral mucus during its ageing process. Picture **(a)** shows freshly produced mucus strings by *Acropora* spec. attached to the coral (scale bar = 1cm), **(c)** shows large mucus floats drifting in lagoon direction on the water surface (bar = 1m). Microscopic observations indicate significant content changes between freshly produced mucus **(b)** and mucus floats **(d)**. Scale bars in **(b)** and **(d)** represent 50 µm. In **(b)**, a diatom (above, center), a dinoflagellate (below, right) and few carbonate grains are seen attached to the mucus strings, whereas the aged mucus shown in **(d)** accumulated a large foraminifer (brown, center) and a filamentous algae (below) in addition to heavy loads of carbonate grains.

Table associated with Figure 2. The table summarizes compositional analyses of both mucus stages in comparison, giving enrichment factors for the measured parameters. All values are averages ± standard error.

	freshly exuded mucus	**mucus floats**	**enrichment factor**	**n**
Dry mass (g L^{-1})	0.3 ± 0.1	107 ± 45	357	6
POC (mmol L^{-1})	2.3 ± 1.2	2253 ± 227	980	8
PN (mmol L^{-1})	0.2 ± 0.1	218 ± 36	1089	8
C/N ratio	12 ± 3	11 ±1		8
P total (µmol L^{-1})	32 ± 13	1835 ± 71	58	4
Chl a (µg L^{-1})	3.7 ± 0.5	8134 ± 2809	2198	8

Roller table experiments after Shanks [16] using sea water or coral mucus each mixed with a suspension containing either zooxanthellae, fine carbonate grains (< 10 µm), or bacteria showed that after 3 to 14 h of slow rotation, aggregates had formed only in the cylinders with mucus. This demonstrates that mucus exudates function as trap for particles and cause the formation of aggregates. The resulting mucus/particle aggregates had a volume 300-fold smaller than the volume of mucus initially added due to compaction. Likewise, natural mucus floats loaded with particles trapped from the reef waters (Fig. 2c) showed reduced average water contents of only 60 ± 1 vol. % (n=6). Using the enrichment factors presented in Figure 2 and correcting these factors for compaction leads to an 8-fold C and a 9-fold N, but no P increase relative to the original exuded mucus.

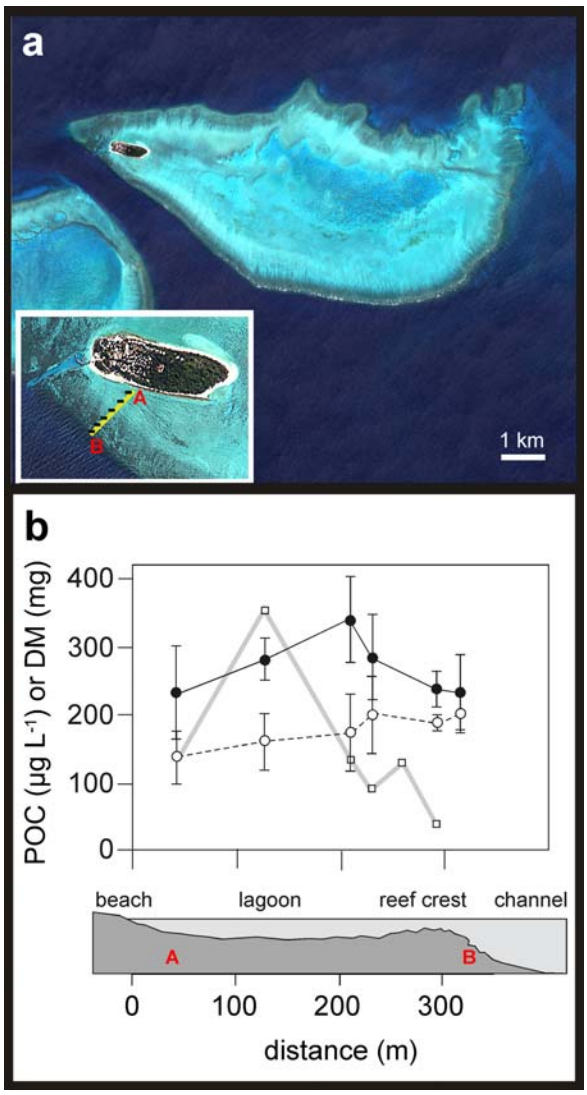

Figure 3. Transect studies at Heron Island. **(a)** The Heron Island Reef (copyright "Space Image"). The brownish-gray reef rim encloses the light-colored sandy lagoon. Yellow line in insert shows position of sampling transect A-B with black bars indicating the 6 sampling stations. **(b)** POC is highest at the lagoonward edge of the reef crest during flooding after coral exposure (solid circles), doubling the ebb tide POC concentrations (open circles). Plankton nets caught the main load of mucus aggregates in the lagoon (gray line, open squares, DM=dry mass). Microscopic examination of the aggregates caught in the nets proved that these were indeed mucus aggregates similar to those shown in Figure 2d.

Continuous compaction and accumulation of resuspended carbonate grains gradually decreases the positive buoyancy of the mucus floats. Water movement of the incoming tide transports the mucus into the lagoon and disintegrates the floats. Agitation and separation of the resulting mucus clusters liberates trapped air bubbles, which initiates a rapid sinking (4-8 cm s^{-1}) to the sandy bottom of the reef lagoon. A series of plankton nets (26 cm diameter, 500 μm mesh, each net fixed at 20 cm above the sediment), deployed along the transect shown in Figure 3, caught pieces of mucus aggregates close to the lagoon floor, revealing sedimentation of mucus aggregates more than 150 m inward of the reef crest (Fig.3b).

The lagoon seafloor is characterised by medium to coarse-grained carbonate sands with a high permeability ($1.2 \pm 0.4 * 10^{-10}$ m^2, n=7), high porosity (44 ± 2 vol.%, n = 8) and a large specific surface area of the sands grains (0.18-0.74 m^2 g^{-1}).

Small mucus aggregates arriving at the surface of such lagoon sands can be transported into the sands via advective interfacial water flows caused by wave pumping [17] and tide-induced water level differences (up to 0.5 m at Heron Island) between the reef lagoon and the deeper water body outside the reef [18,19]. These sedimentary and hydrodynamic properties in combination with a dense population of benthic bacteria ($5.8 * 10^8$ to $6.3 * 10^9$ cells cm^{-3}) convert the reef lagoon sands into a large filter system that removes suspended matter, e.g. mucus, from the enclosed water column.

In order to calculate the contribution of coral mucus to the energy and nutrient demand of the lagoon sediments we used an aerial photograph of Heron Island (Fig. 3a) and derived a total coral covered surface area of 6.87 km^2 and a lagoon sediment surface area of 19.50 km^2. The genus *Acropora* on the Heron Island reef rim exuded at least 4.9 t dry mass mucus d^{-1} (conservative estimate, submerged) corresponding to 1.8 t carbohydrate polymers, 1.0 t protein and 0.2 t lipids (*Acropora* carbohydrate: protein: lipid ratio from Meikle [5]). Due to the circular shape of the reef, approximately 50% of the dissolved and particulate mucus drift into the lagoon. After aerial exposure of the reef rim, the incoming tide may push up to 100% of the mucus into the lagoon because of a pressure gradient between the low water level in the lagoon and the higher level outside the reef. Within the lagoon, energy and nutrients contained in mucus and trapped particles are transferred

to the water column [20] and to benthic food chains including bacteria, benthic invertebrates and fish [8,11,21,22].

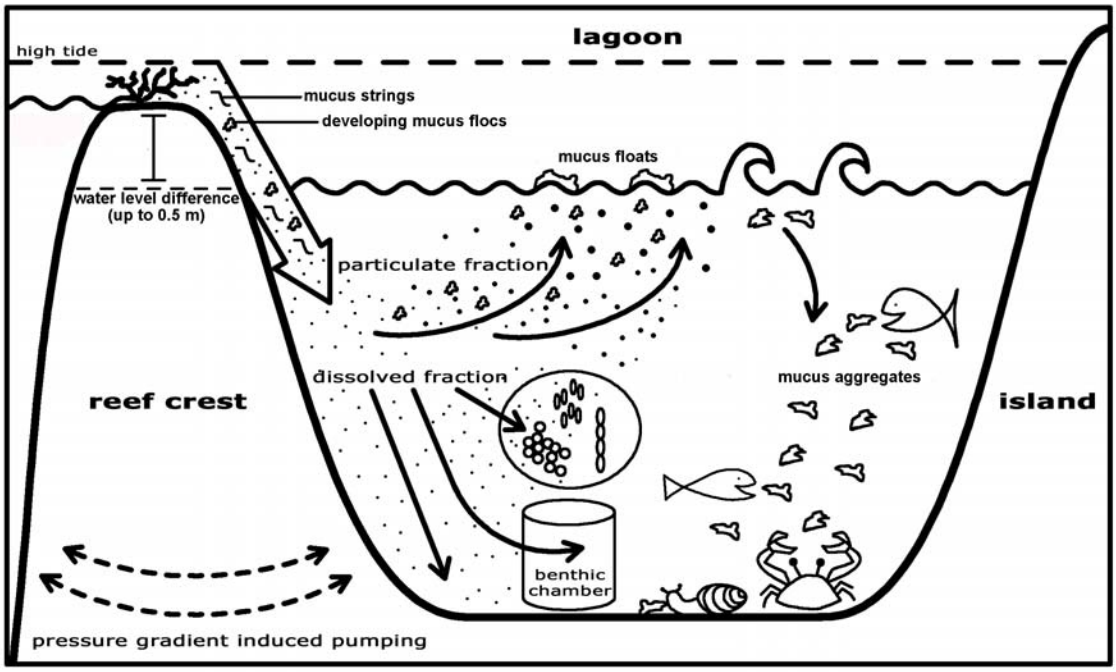

Figure 4. The coral mucus cycle suggested for the Heron Island reef and lagoon. During low tide, mucus is produced in large quantities by air exposed corals on the reef rim. Tidal currents dissolve a large fraction of the mucus, detach the mucus strings from the corals and transport at least 50% of mucus into the lagoon. Here, the dissolved fraction fuels bacteria and algae of the planktonic food chain and is also transported into the permeable reef sands enhancing benthic metabolism. Floating mucus aggregates trap suspended particles, sink and fuel the benthic food chain. Pelagic and benthic mineralization of mucus and trapped particles returns regenerated nutrients to the corals.

The relative importance of coral mucus as carrier of energy and nutrients to consumers in the reef lagoon increases with the ratio between the coral-covered area and the lagoon area. Conservative estimates were made assuming only 20% of the total mucus production was in the particulate fraction. The contribution by the dissolved mucus fraction, particles trapped in the mucus and increased rates of mucus production due to aerial exposure were not included. This estimate suggests that in the Heron Island reef *Acropora* mucus production contributes at least 0.7-1.3% C, 0.4-0.7% N and 1.0-1.9% P to the measured sedimentary C, N, P consumption. Assuming a comparable mucus

production by the other hard corals, and based on a measured total hard coral coverage of the rim of 40%, the coral mucus production by the Heron Island rim hard corals covers 1.7-3.3%, 1.0-1.8% and 2.6-4.9% of the sedimentary C, N and P demand, respectively. Adding the particulate matter trapped by the mucus and with the assumption that a large fraction of these particles originate from the water transported into the reef, the contribution of energy and nutrients transported by coral mucus to the sedimentary metabolism increases to 14-26 % for C, 12-22 % for N and 2-3 % for P, highlighting the importance of this process for the energy and nutrient supply of the lagoon sands. Without the presence of the "mucus trap" in the reef water, many suspended particles would pass through the reef without being available for benthic degradation [23].

Coral reef and lagoon sediment together form a recycling entity linked by coral mucus as an important carrier of energy and nutrients. By producing and shielding an enclosed or landward lagoon, coral reefs generate a biocatalytic filter system that accumulates and retains energy and nutrients in the reef ecosystem. The coral barrier protecting the lagoon provides the calm hydrodynamic conditions and tidal induced pressure gradients, which are necessary to increase the volume of water and particles filtered by the lagoon sands. Benthic organisms living on and in the lagoon sands are able to degrade organic matter from the water forced through the permeable coral sands and return nutrients to the water. Filtering through the coral reef framework adds to this recycling process [24].

We conclude that coral mucus acts as energy carrier and particle trap in the reef system, linking primary production of the zooxanthellae to the pelagic and especially benthic food chains of the reef. The permeable lagoon sands are an important filter that mineralizes mucus and trapped particles to inorganic nutrients essential for autotrophic growth. Due to this tight recycling mechanism and the trapping function of the mucus, the release of almost 50% of the net fixed carbon by the corals could be a profitable energetic investment. This mechanism may contribute to explain the high primary productivity characterizing coral reefs growing in oligotrophic oceans.

METHODS

Sediment characteristics

Sediment permeability was assessed after Klute [25]. Sediment specific surface areas were determined by dinitrogen adsorption using a Quantachrome Quantasorb instrument.

Mucus collection

Coral mucus was collected from the staghorn corals *Acropora millepora, A. pulchra, A. nobilis and A.aspera*. Individual coral colonies (max. 30 cm in diameter), anchored with their lower branches in the carbonate sands, were lifted, exposed to air and subsequently released 0.1 - 0.3 L liquid mucus. The initial mucus release (30 sec) containing water was discarded and afterwards mucus was collected for 2 min.

Mucus characterization

Carbohydrate composition

Mucus samples were desalted through dialysis membranes and freeze-dried. Purified mucus was hydrolysed using 1 M methanolic-HCl for 16 h at 80°C. Released sugars were derivatized with Tri-Sil and measured by employing a GC and a *Supelco* column with myo-inositol (10 µg) as internal standard.

C, N analyses

Mucus aliquots (5-10 mL) were filtered onto precombusted GF/F filters (Whatman) and frozen at –20° C. Carbonate grains were removed by exposing the filters to fuming HCl. Particulate organic carbon (POC) and particulate nitrogen (PN) then were measured using a Fisons NA1500 element analyser.

Sedimentation velocity

Sedimentation velocities of mucus aggregates of different ageing stages (n = 4-16 each) and freshly collected from the field were timed in a graded cylinder (38 cm in height, 8 cm in diameter) filled with ambient seawater at in-situ temperature.

Mucus solubility

One of two identical volumes of freshly collected gel-like mucus from *Acropora* was diluted (1:1 with 0.2 µm filtered seawater), than each of the two volumes was added to a 5 mL graded cylinder with saturated NaCl containing rhodamine dye (n=11 replicates for

each treatment). Not dissolved mucus raised to the surface where it could be detected and quantified due to its not-stained appearance. Mucus solubility was calculated from the ratio of the relative volume of the dissolved mucus fraction and the total volume of the gel-like mucus in percent.

In-situ quantification of mucus release

Mucus release of *Acropora* during naturally occurring exposure to air at low tide was quantified in 5 in-situ experiments. Individual colonies were transferred to three 10 L containers without exposure to air, three containers with seawater only were used as controls. During ebb tide, a gauze-covered (125 μm) opening permitted falling of the water level in the containers at the same rate as in the reef, thus finally exposing the incubated colonies to air. Exposure times were the same as those of the corals on the reef rim (15-105 min). The flooding tide slowly re-filled the containers through the gauze-covered openings. As soon as the corals were submerged again, the openings were closed and for exactly 3 minutes a water current equivalent to ambient currents was generated by an electric pump causing detachment of mucus from the corals. Then the corals were removed and the water was thoroughly mixed before water samples (50-150 mL, n = 3 for each analysis) from all six containers were collected for dry mass, POC and PN measurements. The results were related to the 3D-surface area of the coral branches assessed by a wax-coating method [26]. Mucus production of fully submersed colonies of *A. millepora* and *A. aspera* (n= 8 in each of 2 independent experiments) was quantified according to the incubation technique described in Herndl [27].

Daily mucus release of *Acropora* corals per reef area was calculated using a factor of 3.8 to recalculate the 3-dimensional surface area of the corals to the two-dimensional reef rim area covered by *Acropora*. This recalculation factor was derived from the ratio of measured coral surface area to the 2-dimensional area (length * width) of the same coral colonies (n=15). The naturally coral covered area on the Heron Island Reef rim was calculated from the satellite picture shown in Fig. 3a.

Hard coral coverage

Spatial distribution of hard corals on the reef rim were determined along nine randomly placed line transects. A counting grid (1 m^2) was moved 10 times along each line transect (10 m in length). Hard corals were identified down to species level [28] permitting calculation of the cover of *Acropora* (%).

Oxygen consumption in suspended mucus

Freshly collected *Acropora* mucus and separately ambient seawater were incubated in 30 mL bottles in the dark and at *in situ* temperature (26-29° C). O_2 concentrations in the incubated solutions were measured simultaneously in time series using the Winkler titration method [29]. O_2 consumption rates were derived from linear regression with at least 4 data points. Measurements were repeated for 5 different mucus samplings.

Water level measurements

Tide-induced water level differences between the lagoon and the water surrounding the Heron Reef were measured during two spring low tides with a hydraulic potentiometer. A 100 m long water-filled hose (2 cm inner diameter) was placed across the reef rim such that one opening was located in the lagoon and the other opening at a boat anchored in the channel outside the reef. At low tide, the water level difference could be assessed by measuring the height difference between the water level in the reef channel and the water level in the vertical end of the hose located at the boat.

In-situ benthic chamber incubations

Benthic degradation of coral mucus was studied with 4 independent in-situ incubations using stirred benthic chambers similar to those described in Huettel [30]. A horizontally rotating (20 rpm) disk agitating the water in the chambers was adjusted to a rotational velocity (20 rpm) generating a pressure gradient at the sediment surface of 1.2 Pa between the center and the periphery that was in the same order of magnitude as the gradients developing when sediment topography and boundary flows as found at the study site interact [30]. Such pressure gradients lead to advective transport of fluid and particles in permeable sediments and an exchange between the overlying water and the

pore water. The chambers were inserted into the sediments to a depth of about 8 cm, closed and sealed from light by wrapping with opaque black PVC foil (see background Fig.1). At the onset of each experiment, between 140 and 300 mL of freshly collected *Acropora* mucus was added to half of the 4-6 deployed chambers (Volume: 6.8-7.0 L) via a syringe port. During the following 2-7 hour incubations, O_2 was measured either synchronously with fiber-optic sensors or by taking water samples every 30 to 60 min for O_2 determination using Winkler titration. Fluxes of O_2 were evaluated by linear regression of O_2 concentrations over time.

Water collection transect

Two days with similar tidal amplitudes and weather conditions were chosen for collection of water samples along a transect extending from the lagoon to the outer reef edge (Figure 3a). The corals on the reef rim were exposed to air to a comparable extent and duration. At regular time intervals between high and low tide, water samples (2 L) for POC, PN (see above) were taken simultaneously at the six sampling stations along the transect.

ACKNOWLEDGEMENTS

We thank M. Alisch, S. Menger, H. Woyt, S. Gonelli and L. Hönemann for experimental assistance and help with the chemical analyses. We acknowledge O. Hoegh-Guldberg, R. Johnstone, R. Forbes and the other staff members of Heron Island Research Station for logistical assistance and C. Richter, H. Zech, P. Cook and R. Tollrian for improving the manuscript. A. Peiter is acknowledged for help in figure preparing. All sample collections and in situ experiments were done under the permits QC00/102, G01/479 and G01/601 of the Great Barrier Reef Marine Park Authority. The Max Planck Society, Germany funded this research.

REFERENCES

1. Goreau, T.F., Goreau, N.I. & Goreau, T.J. Corals and coral reefs. *Scientific American* 241, 124-135 (1979).
2. Crossland, C., Barnes, D. & Borowitzka, M. Diurnal lipid and mucus production in the staghorn coral *Acropora acuminata*. *Marine Biology* 60, 81-90 (1980).
3. Davies, P.S. The role of zooxanthellae in the nutritional energy requirements of *Pocillopora eydouxi*. *Coral reefs* 2, 181-186 (1984).
4. Coles, S. & Strathman, R. Observations on coral mucus flocs and their potential trophic significance. *Limnology and Oceanography* 18, 673-678 (1973).
5. Meikle, P., Richards, G. & Yellowlees, D. Structural investigations on the mucus from 6 species of coral. *Marine Biology* 99, 187-193 (1988).
6. Muscatine, L., McCloskey, L.R. & Marian, R.E. Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration. *Limnology and Oceanography* 26, 601-611 (1981).
7. Ducklow, H. & Mitchell, R. Bacterial populations and adaptations in the mucus layers on living corals. *Limnology and Oceanography* 24, 715-725 (1979).
8. Krupp, D.A. Mucus production by corals exposed during an extreme low tide. *Pacific Science* 38, 1-11 (1984).
9. Schuhmacher, H. Ability of fungiid corals to overcome sedimentation. *Proceedings of the third international coral reef symposium, Miami, Florida* , 503-509 (1977).
10. Marshall, M. Observations on organic aggregates in the vicinity of coral reefs. *Marine Biology* 2, 50-55 (1968).
11. Johannes, R. Ecology of organic aggregates in the vicinity of a coral reef. *Limnology and Oceanography* 12, 189-195 (1967).
12. Sorokin, Y.I. Role of plankton in the turnover of organic-matter on the Great-Barrier-Reef, Australia. *Hydrobiologia* 308, 35-44 (1994).
13. Romaine, S., Tambutte, E., Allemand, D. & Gattuso, J.P. Photosynthesis, respiration and calcification of a zooxanthellate scleractinian coral under submerged and exposed conditions. *Marine Biology* 129, 175-182 (1997).
14. Moriarty, D.J.W., Pollard, P.C. & Hunt, W.G. Temporal and spatial variation in bacterial production in the water column over a coral reef. *Marine Biology* 85, 285-292 (1985).
15. Hobbie, J.E., Daley, R.J. & Jasper, S. Use of nucleopore filters for counting bacteria by fluorescence microscopy. *Applied and Environmental Microbiology* 33, 1225-1228 (1977).
16. Shanks, A.L. & Edmondson, E.W. Laboratory-made artificial marine snow - a biological model of the real thing. *Marine Biology* 101, 463-470 (1989).
17. Shum, K.T. & Sundby, B. Organic matter processing in continental shelf sediments - The subtidal pump revisited. *Marine Chemistry* 53, 81-87 (1996).

18. Parnell, K.E. Water movement within a fringing reef flat, Orpheus Island, North Queensland, Australia. *Coral Reefs* 5, 1-6 (1986).
19. Oberdorfer, J.A. & Buddemeier, R.W. Coral-reef hydrology: field studies of water movement within a barrier reef. *Coral Reefs* 5, 7-12 (1986).
20. Marsden, J. & Meeuwig, J. Preferences of planktotrophic larvae of the tropical serpulid *Spirobranchus giganteus* (Pallas) for exudates of corals from a Barbados reef. *Journal of Experimental Marine Biology and Ecology* 137, 97-104 (1990).
21. Benson, A. & Muscatine, L. Wax in coral mucus - energy transfer from corals to reef fishes. *Limnology and Oceanography* 19, 810-814 (1974).
22. Richman, S., Loya, Y. & Slobodkin, L. Rate of mucus production by corals and its assimilation by the coral reef copepod *Acartia negligens*. *Limnology and Oceanography* 20, 918-923 (1975).
23. Wilkinson, C.R. Microbial ecology on a coral reef. *Search* 18, 31-33 (1987).
24. Richter, C., Wunsch, M., Rasheed, M., Kotter, I. & Badran, M.I. Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. *Nature* 413, 726-730 (2001).
25. Klute, A. & Dirksen, C. Hydraulic conductivity and diffusivity: laboratory methods. in *Methods of soil analysis -part 1- physical and mineralogical methods* (ed. Klute, A.) (American Society of Agronomy, 1986).
26. Stimson, J. & Kinzie, R.A. The temporal pattern and rate of release of zooxanthellae from the reef coral *Pocillopora damicornis* (Linnaeus) under nitrogen-enrichment and control conditions. *Journal of Experimental Marine Biology and Ecology* 153, 63-74 (1991).
27. Herndl, G.J. & Velimirov, B. Microheterotrophic utilization of mucus released by the Mediterranean coral *Cladocora cespitosa*. *Marine Biology* 90, 363-369 (1986).
28. Wallace, C.C. Staghorn corals of the world: a key to species of Acropora. *CSIRO Publishing, Melbourne* (1999).
29. Winkler, L.W. The determination of dissolved oxygen in water. *Berichte der Deutschen Chemischen Gesellschaft* 21, 2843-2857 (1888).
30. Huettel, M. & Gust, G. Solute release mechanisms from confined sediment cores in stirred benthic chambers and flume flows. *Marine Ecology Progress Series* 82, 187-197 (1992).

Chapter 9

Rapid recycling of coral mass spawning products in permeable reef sediments

Christian Wild[1], Ralph Tollrian[2] and Markus Huettel[1,3]

[1]Max Planck Institute for Marine Microbiology, Celsiusstr. D-28359 Bremen, Germany

[2]Department Biology II and GeoBioCenter, Ludwig-Maximilians University, Karlstr. 23-25, D- 80333 Munich, Germany

[3]Department of Oceanography, Florida State University, Tallahassee, FL 32306-4320, USA

This chapter has been submitted to Marine Ecology Progress Series.

ABSTRACT

During the annual synchronous release of gametes by corals, a large amount of energy-rich organic material is released to the reef environment. In November 2001, we studied a minor spawning event at Heron Island in the Great Barrier Reef (GBR), Australia. Laboratory experiments showed that egg release by the staghorn coral *Acropora millepora* amounted to 19 ± 15 g dry mass (mean ± standard error, n = 8) per m² coral surface. Carbon content reached 60.1 ± 4.0% and nitrogen content 3.6 ± 0.4% of the egg dry mass. During this minor spawning period, *Acropora* corals from the reef crest released 7 g C and 0.4 g N as eggs per square meter reef. Our calculations suggest that all hard corals from the Heron Island Reef (26 km^2) may release approximately a total of 310 t C and 18 t N during the spawning event. In-situ experiments (n=11) using benthic chamber measurements revealed that the sedimentary O_2 consumption (SOC) increased sharply immediately after the coral spawning. Two days after the event, extreme SOC rates of 230 mmol O_2 m^{-2} d^{-1} were reached, exceeding the pre-spawning rate by a factor of 2.5. This maximum was followed by a steep decrease in SOC rates that gradually levelled of and reached pre-spawning values 11 days after the event. The immediate and strong response of SOC shows that the coral spawning event provides a strong food impulse to the benthic food chain. Our results demonstrate high decomposition efficiency of permeable carbonate reef sands and underline the role of these sediments as a biocatalytical recycling system in the oligotrophic reef environment.

INTRODUCTION

In 1981, scientists for the first time discovered a spectacular phenomenon in the Central Great Barrier Reef (GBR), Australia: the synchronous mass release of gametes by many species of coral (Harrison et al. 1984). They called this event coral spawning and found out that it only happens during a few predictable nights each year, in the GBR typically during the week following full moons from October to December (Harrison 1993). Besides the lunar phase, other factors like temperature change, salinity, current velocity, tidal amplitudes (Oliver et al. 1988, Hayashibara et al. 1993) and even chemical messengers (Atkinson & Atkinson 1992) are suggested as possible triggers for the coral spawning event.

Simultaneous multi-species coral spawning has also been observed in other regions, including Singapore (Guest et al. 2002), American Samoa (Itano & Buckley 1988), Japan (Van Woesik 1995) and the Gulf of Mexico (Gittings et al. 1992, Hagman et al. 1998), but not in the Red Sea (Shlesinger & Loya 1985) and the Caribbean (Szmant 1986). Synchronous release of sexual products is also known from a variety of planktonic and other benthic marine invertebrates including polychaetes (Itano & Buckley 1988), hydrozoan fire corals (Soong & Cho 1998) and gorgonians (Lasker et al. 1996). It was also observed that green algae on coral reefs show a mass spawning behaviour (Clifton 1997).

Research in the GBR revealed that at least 140 coral species participate in the mass spawning event (Babcock et al. 1986, Oliver et al. 1988) that occurs throughout the whole GBR region (Oliver et al. 1988). Typical for the Great Barrier Reef corals is a broadcast spawning (buoyant gamete release) with external fertilisation (Harriott 1992). During the very brief spawning period, a large amount of organic matter is released into the reef ecosystem as so-called egg-sperm bundles. The bundles float to the sea surface, because their high lipid content makes them positively buoyant (Arai et al. 1993). Soon after, the buoyant egg-sperm bundles break apart releasing eggs and sperm into the surrounding water (Coll et al. 1994). Visible surface aggregations (coral spawn slicks) can form from the coral eggs and embryos as a consequence of local hydrodynamic features like fronts between water parcels, wakes and eddies behind a reef (Oliver & Willis 1987, Willis & Oliver 1990). Coral eggs and slicks are transported to other reefs

by wind and currents (Wolanski et al. 1989, Sammarco et al. 1991) or stay within the same reef due to self-seeding patterns (Andrews et al. 1988, Wolanski et al. 1989).

It is very likely that parts of the released gametic material are reaching the reef sediments after a short pelagic period, because of an intense coupling between water column and sediments in these shallow water environments. Wolanski et al. (1989) found that coral eggs were partly trapped in the lagoon of the studied reef. Simpson et al. (1993) observed at Ningaloo Reef, Western Australia, that large amounts of coral spawn were trapped in a bay and formed extensive slicks on the sediment surface.

In this study we investigated the response of the lagoon sediments to a coral spawning event in order to assess the contribution of the coral sands to the decomposition of the organic material released by the corals. For these investigations, benthic chambers were deployed in the lagoon of the Heron Island Reef, Australia, and the sedimentary O_2 consumption (SOC) was measured before, during and after the coral spawning event in November 2001.

MATERIAL AND METHODS

Study site

All sample collections and experiments were done in November 2001 at Heron Island, a platform reef system with a total area of 26.4 km², located in the Southern Great Barrier Reef (23° 27' S, 151° 55' E), Australia (Fig.1). Egg release was quantified in the laboratory facilities of the Heron Island Research Station (HIRS). The benthic chamber experiments took place in Shark Bay, a shallow water environment (max. water height 2.5 m) situated on the Southeastern edge of the island.

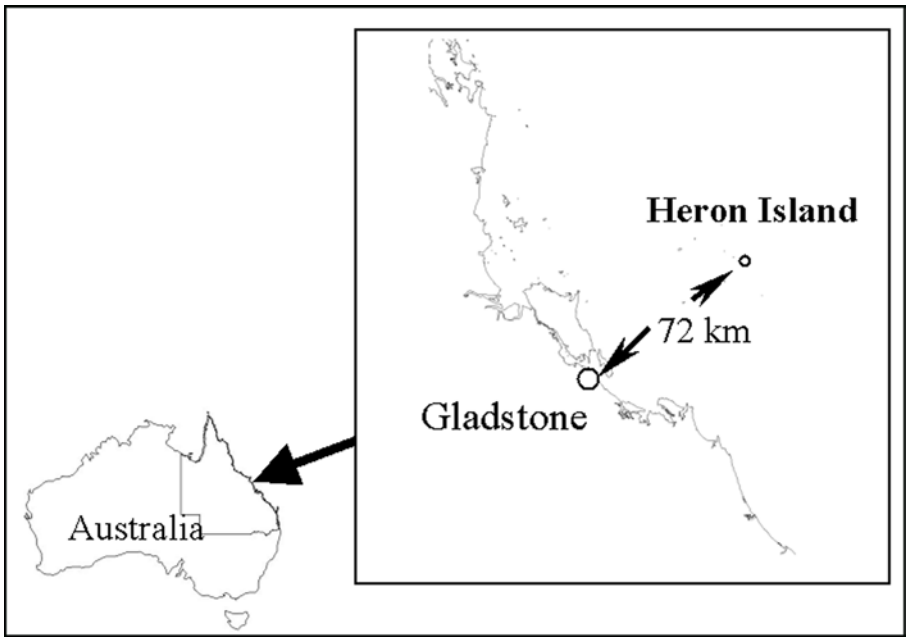

Figure 1. Location of Heron Island on the Australian Great Barrier Reef.

Sediment characteristics

We took sediment cores (n = 7) in Shark Bay and measured a permeability of 1.2 ± 0.34 x 10^{-10} m^2 (mean ± standard deviation) using a constant head permeameter as described by Klute & Dirksen (1986). Sediment porosity was 44.3 ± 1.9 % wt/wt (n = 9) calculated from weight loss of wet sediment after drying at 60°C for 24 h. Particulate organic carbon (POC) and nitrogen (PON) contents were measured using a CHNO-rapid elemental analyser (Heraeus, Hanau, Germany) 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. Measurements showed values of 0.24% for POC and 0.042% for PON. Median grain size of Shark Bay sands was 838 µm characterising the sediment as dominated by coarse sands.

Egg release quantification

On 4.11.01, dominant *Acropora* species of the Heron Island reef flat were examined for signs of spawning readiness by inspecting the cross-sections of coral branches. Only a few species, *A. millepora, A. digitata and A. pulchra,* showed pinkish-reddish septal contents indicating the production of gametes. The other tested species *A. aspera, A. nobilis and A. formosa* did not show any recognisable maturation of eggs. Between two and three colonies (size approx. 40 x 40 x 30 cm) from each of the three species with visible gametes were collected and transferred to aerated flow-through tanks at HIRS without exposure to air. One of the *A. millepora* colonies was split into 8 similar sized fragments, which were left in a separate aquarium for 3 days to recover.

Every day at sunset starting on 7.11.01, these fragments were transferred to 500 mL glass beakers filled with unfiltered fresh seawater and kept in complete darkness. These beakers were examined for gamete release every 30 min until 10 p.m. using a torch covered with a red transparent film. Spawning of all eight *A. millepora* fragments occurred on 9.11.01 at 9 pm lasting for about 45 min (Figure 2a). Egg-sperm bundles (Figure 2d) floating to the water surface of each beaker were filtered through gauze (50 µm) to separate eggs and sperm. The eggs then were filtered on pre-weighed Whatman #1 filters and dried for 48 h at 40° C. Egg dry weights were related to the surface area of the parental *A. millepora* fragments. These surface areas were assessed by the wax method described by Stimson & Kinzie (1991).

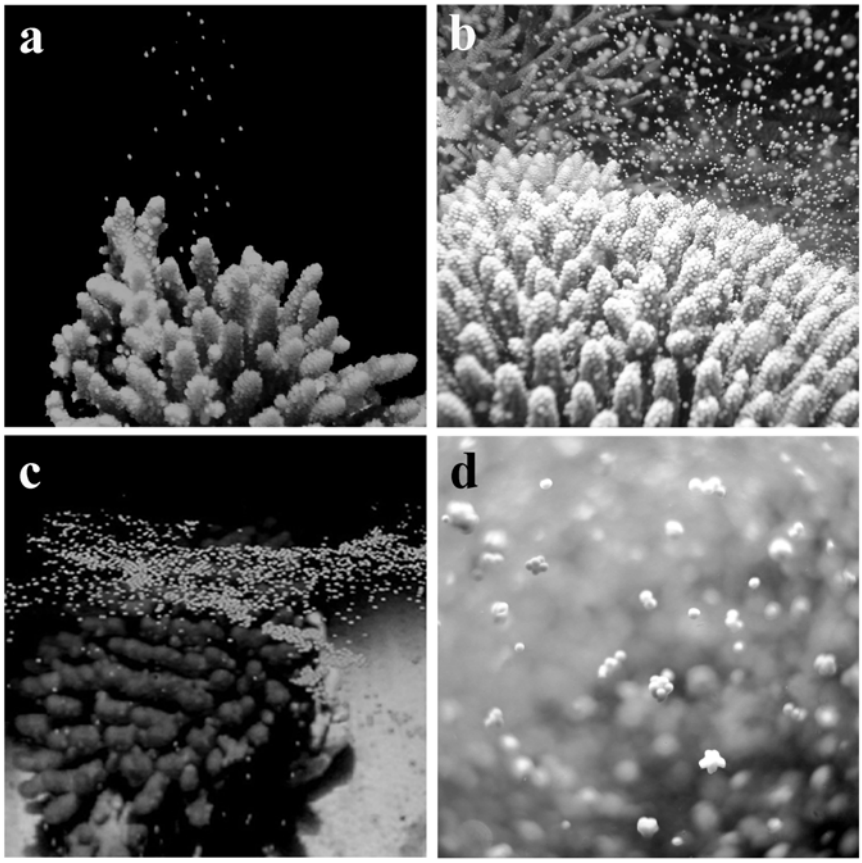

Figure 2. (a) A colony of *Acropora millepora*, placed in an aquarium, is releasing its gametes during the November spawning 2001. **(b)** Hard corals of the genus *Acropora* on the Heron Island reef crest during the more pronounced spawning in November 2002. **(c)** Egg-sperm bundle form slicks on the water surface. **(d)** Detail photograph of egg-sperm bundles released by corals of the genus *Acropora*.

Carbon and nitrogen measurements in coral eggs

Freshly released and filtered eggs (sperms were removed) from *A. millepora, A. digitata and A. pulchra* were also dried for 48 h at 40° C. Dried eggs were subsequently frozen at –20° C until further analysis. Total organic carbon (TOC) and nitrogen (TON) were measured using an element analyser (Fisons NA1500) with sulphanilamide as the calibration standard.

Determination of sedimentary O_2 consumption (SOC)

In total, 11 in-situ chamber experiments were carried out before, during and after the coral spawning event. All experiments were done in Shark Bay, always starting two hours after low tide (water height approximately 0.5 m) and ending between two and seven hours later. Cylindrical stirred benthic chambers as described in Huettel & Gust (1992) were used. 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. A horizontally rotating disk (20 rpm) agitated the water in the chamber and generated a pressure gradient at the sediment surface of 1.1 Pa between the centre and the chamber wall. Pressure gradients in this order of magnitude develop when sediment topography and boundary flows found at the study site interact (Huettel & Gust 1992, Glud et al. 1995), and can induce advective transport of water and solutes into permeable sediments.

For each experiment, three of the described benthic chambers were used with the exception of the first two experiments, where we could only use 1 chamber each because of technical problems. 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 clips.

All chambers were protected from light by wrapping them with black PVC foil and secured with weight belts to prevent movement caused by wind and waves. Recording of light intensity and temperature under the PVC foil and in the surrounding seawater at least every 2 min using Onset™ HOBO and Tidbit dataloggers showed that no light intrusion and heating took place in the chambers during the in-situ incubations. In-situ water temperature was between 22 and 29° C in all chamber experiments.

Oxygen concentration in the chamber water was measured in regular intervals using the Winkler titration method (Winkler 1888). SOC was calculated from linear regression of the O_2 concentration decrease in the chambers.

Respiration measurements in the water column

In order to quantify the O_2 consumption of the water column and to relate it to the results of the chamber experiments, surface water from Shark Bay was collected on 17.11., filled in nine 30 mL Winkler bottles and incubated under dark conditions and at in-situ temperature (26-29° C). The O_2 concentrations were measured in a time series using the Winkler titration method, and O_2 consumption rates were derived from linear regression of O_2 concentrations over time.

RESULTS

In-situ and lab observations during the spawning period

The coral-spawning event in November 2001 at Heron Island was not very pronounced. Only a few coral species collected from the Heron Island Reef showed morphological signs for spawning preparation. The release of egg-sperm bundles (Figure 2c) through corals was only directly observed in the laboratory aquarium, but not in the field, although the water temperature on the reef flat (range 22-29° C) was identical with the aquarium temperature (range 22-25° C). Spawning of the corals in the lab occurred between 8.30 and 10.00 pm on 3 following nights (9-11.11.). This is later than the predicted week after full moon (1.11.). The spawning event was small, because the typical odour or beach slicks of coral spawning products could not be detected on the mornings during the spawning period. Nevertheless, divers observed slicks of spawning material at the water surface in the lagoon near Shark Bay during high tide on 10.11.

The corals in the aquarium showed a species-specific behaviour with *A. millepora* spawning on 09.11. (8 fragments, 2 larger colonies) and 11.11. (1 larger colony), and *A. digitifera* and *A. pulchra* just spawning on 10.11. (2 larger colonies each). A species-specific spawning behaviour was also observed by Hagman et al. (1998) for corals in the Gulf of Mexico.

Released egg-sperm bundles of 2 different colonies of *A. pulchra* (tot. vol. 1 ml) incubated in aerated 1 L glass beakers showed that sperm and eggs separate within 30 min. Sperm then was suspended in the water, whereas intact eggs were floating at the water surface. The beakers were examined five times a day, whereby the dead material was removed 10% of the water volume was replaced with fresh seawater. Within 48 hours, 50% of the eggs lost their coloration, died and sank to the beaker bottom. Pigmented eggs were still floating at the water surface after 48 hours, afterwards gradually loosing their positive buoyancy and changing to oval shaped moving planula larvae. The latter were observed for the first time after 5 days incubation time.

Carbon and nitrogen in coral eggs

Coral eggs released during the spawning event had a high carbon content of 57-66% (dry mass), whereas nitrogen only accounted for 3-4% of the egg dry mass (Table 1). Thus, the C:N ratio showed values of 16-21. There were no species-specific differences in C and N content.

Egg release by *Acropora* spec.

The measurements revealed a release of 19 ± 15 g egg dry mass per square meter coral surface (n = 8) by *Acropora millepora* during the November spawning event. This corresponds to at least 11.6 and 0.7 g C and N respectively released per square meter coral surface as eggs.

Table 1. Carbon and nitrogen contents of eggs released by three species of the genus *Acropora* in relation to egg dry mass (dm). Values are means ± standard deviation.

Coral species	No. of replicates	C (mg/g dm)	N (mg/g dm)	C:N ratio
A.digitifera	6	572 ± 59	38 ± 9	16 ± 4
A.pulchra	3	659 ± 43	32 ± 9	21 ± 4
A.millepora	6	601 ± 43	36 ± 4	17 ± 2

In-situ chamber experiments

Despite the relatively small volume of gametes released during the spawning event we investigated, the benthic response to the organic matter input was immediate and strong. The average pre-spawning SOC of 94 ± 2 mmol m^{-2} d^{-1} (mean ± standard error, n = 4) increased by a factor of 2.5 to a maximum of 230 mmol m^{-2} d^{-1} on the second day after the spawning event (Fig.3).

The decrease in the O_2 consumption rate was nearly as steep as the increase, however, significantly increased ($\alpha = 0.025$, one-sided U-test after Wilcoxon, Mann and Whitney) SOC rates compared to the pre-spawning values (5.-8.11, n = 5) could still be measured 9 days after the spawning (Fig.3).

Eleven days after the start of the spawning event, SOC was not significantly different compared to the measured pre-spawning values ($\alpha > 0.2$, two-sided U-test after

Wilcoxon, Mann and Whitney). SOC rates measured 11 days after the spawning event ranged from 93 to 95 mmol m^{-2} d^{-1}. These values are on the upper limit of SOC values derived from in-situ chamber incubations made during the previous (52-80 mmol m^{-2} d^{-1}, n=3) and following Australian summer (49-92, n = 6) at Heron Island outside the spawning period (see chapter 7).

O_2 consumption in the water column

On 17.11., when SOC rates were still increased, we measured an O_2 consumption rate for Shark Bay waters of 15.4 µmol L^{-1} d^{-1}, thus not higher than the values of between 5 and 41 µmol L^{-1} d^{-1} measured by Wild et al. (unpublished data) in Shark Bay waters in January 2002. Using the water O_2 consumption rate measured on 17.11. to calculate the water O_2 consumption in the benthic chambers (max. 7L), this results in rates of 3.9 mmol m^{-2} d^{-1} when related to the enclosed sediment surface. That is about 3% of the O_2 consumption rates of the previous (16.11.: 142.6 mmol m^{-2} d^{-1}) and following day (18.11.: 122.3 mmol m^{-2} d^{-1}). This means that the O_2 consumption in the chambers originated by more than 95% from the sedimentary metabolism and only by a minor fraction from water column respiration.

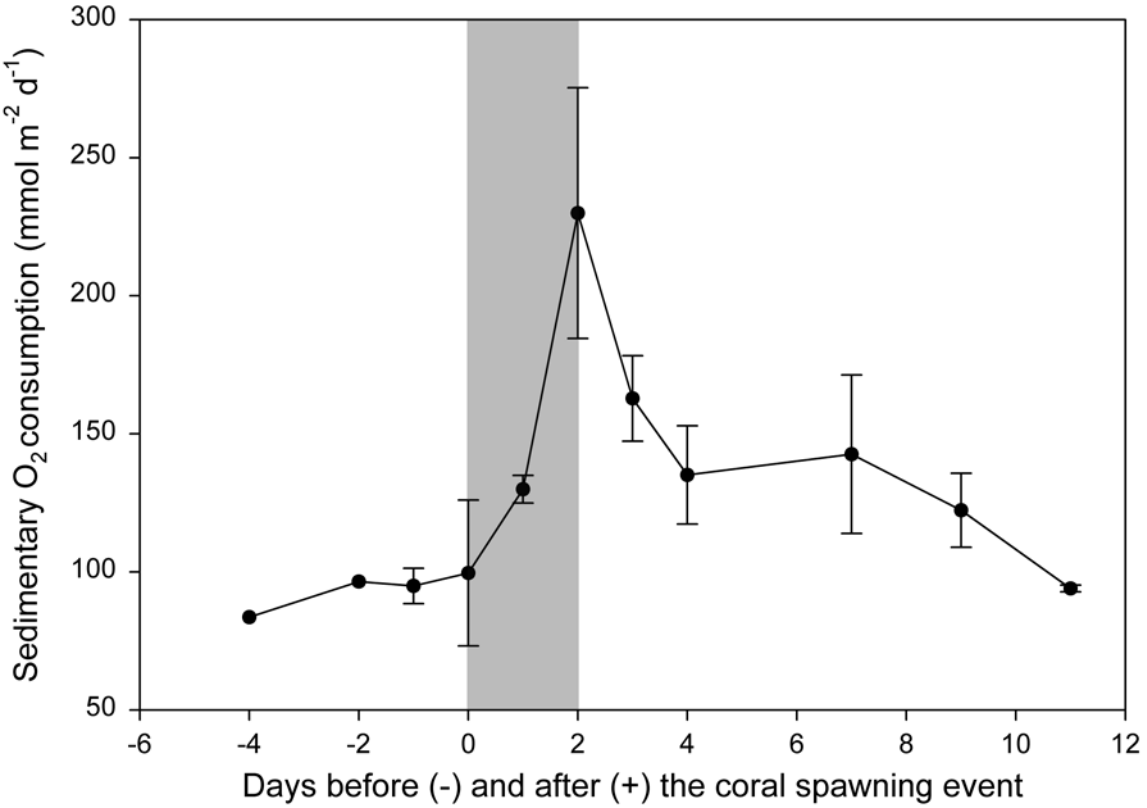

Figure 3. Sedimentary O_2 consumption (SOC) measured in 11 chamber experiments before, during and after the coral spawning period. Error bars are indicating the standard deviation. The number of replicate chambers used in each experiments was 3, except the first two experiments. Point zero on the horizontal axis labels the day where spawning was observed for the first time. The grey area highlights all days where spawning was also noticed.

DISCUSSION

In 2001, the coral spawning at Heron Island was split into a minor November spawning and a major December spawning (S. Dove, S. Ward, pers. communication). In 2002, this scenario was reversed with a large spawning in November and a smaller one in December (R. Tollrian, pers. communication). Figure 2b shows a large spawning on the Heron Island reef crest in November 2002.

In 2001, we were able to study the smaller event and showed that even a relatively small coral spawning can increase the SOC significantly for more than a week. In order to explain the measured temporal link between the coral spawning event and the enhanced SOC rates we first of all have to assume that a fraction of the spawning products reached the sediment soon after the release from the corals.

This can be caused by direct sedimentation of eggs, which is supported by our incubation experiments where we observed that within 48 hours 50% of the eggs lost their pigments, died and sank to the ground. Oliver & Willis (1987) also observed that coral spawn slicks appearing on the days after coral spawning consisted to over 99% of dead eggs and breakdown products. Bacteria possibly degrade low-density components (e.g. lipids) of this material, which then leads to the loss of buoyancy and sedimentation of the dead spawning products.

A second source of organic matter may be the intrusion of diluted sperms into the sediment. Sperm cells are not positively buoyant and are diluted once released from the egg-sperm bundles.

Additionally, spawning products can also reach the sediment via food chain transfer processes. Many different coral reef organisms, e.g. fish and zooplankton (Westneat & Resing 1988, Baird et al. 2001, Pratchett et al. 2001) intensely feed on the spawning products and process them into fecal pellets. Fecal pellets are generally known to increase the sedimentary flux of organic material (Turner 2002).

All these factors lead to an increased sedimentation of organic matter derived from the spawning event. No matter how the spawning products reached the reef sediments, in these permeable reef sands advective processes are found to play an important role for the rapid and efficient degradation of organic matter (Rasheed et al. 2003, in press at Estuarine Coastal Shelf Science, Wild et al. 2003, in press at MEPS).

Release of organic C and N during the coral spawning event

Corals of the genus *Acropora* are covering 15.7% of the Heron Island rim, which includes the reef crest and slope (A. Klueter, unpublished data). From a satellite picture we calculated that the Heron Island rim covers a total area of about 6.9 km^2. Hard corals of the genus *Acropora* therefore exclusively cover approximately 1.1 km^2 of the Heron Island reef rim. Because of the three-dimensional structure of the corals, this *Acropora*-covered rim surface area corresponds to an actual coral surface area 3.8-fold as large (approximately 4.2 km^2). Our results show that 11.6 g C and 0.7 g N were released per square meter coral surface by the staghorn coral *A. millepora* as eggs during the coral spawning event in 2001. Extrapolated to the reef rim area and assuming that the other *Acropora* species are releasing roughly the same amount of eggs, this would account for a release of 7.1 g C and 0.4 g N m^{-2}. Our data further suggest that all hard corals from Heron Island may release roughly 310 t C and 18 t N as eggs during the coral spawning, whereas the simultaneous release of sperm is not even included in this estimate.

Coral spawning affecting SOC

With values exceeding 200 mmol m^{-2} d^{-1}, the SOC in the coarse carbonate sands of Heron Island after the spawning event reached rates exceeding those measured in most coastal sediments (Table 2). Higher SOC rates are measured only in microbially highly active sediments, e.g. those beneath cages of a salmon farm (Nickell et al. 2003). Diffusive oxygen uptake rates of the seafloor range usually between 10 and 30 mmol m^{-2} d^{-1} with maximum rates of approximately 94 mmol m^{-2} d^{-1} (Jørgensen 2001).

Ehrenhauß & Huettel (2003) simulated the sedimentation of a phytoplankton bloom by adding dead diatoms (amount of added material comparable to the amount of material reaching the sediment after a spring algal bloom) to benthic chambers identical to those used in this study. The SOC in very fine to coarse sands from the German North Sea afterwards increased by a factor of 2.0 – 3.3, which is similar to the maximum increase observed in this study. This indicates that the coral spawning event may have a similar effect on SOC as the sedimentation of an algal bloom. The measured SOC rates in the silicate sediments (63-1000 µm grain size) used by Ehrenhauß & Huettel (2003) were between 1.2 and 6.7 mmol m^{-2} d (without algae addition) and 6.7 – 11.0 mmol m^{-2} d^{-1}

(after algae addition) indicating that much more organic matter can be mineralised in the carbonate sands from Heron Island with a similar grain size (838 μm).

Table 2. Sedimentary O_2 consumption (SOC) measured in different marine shelf sediments with benthic chamber incubations.

Location	SOC (mmol m^{-2} d^{-1})	Reference	Kind of sediment
Douro River Estuary (Portugal)	< 96	(Magalhaes et al. 2002)	silicates
Salmon farm Loch Creran (Scotland)	9-468	(Nickell et al. 2003)	silicates
North and Baltic Sea	42-170	(Forster et al. 1999)	silicates
Balearic Islands (Spain)	195	(Lopez et al. 1995)	silicates
Bay of Cadiz (Spain)	138	(Forja et al. 1994)	silicates
Shellfish farm Carteau Bay (France)	< 105	(Barranguet et al. 1994)	silicates
Bay of Cadiz (Spain)	99-189	(Gomezparra & Forja 1993)	silicates
South Atlantic Bight	35	(Marinelli et al. 1998)	silicates
New Caledonia	11-54	(Grenz et al. 2003)	carbonates
New Caledonia	18	(Boucher et al. 1994)	carbonates
New Caledonia	84-230	This study	carbonates

SOC was enhanced compared to the pre-spawning level (94 ± 2 mmol m^{-2} d^{-1}) for 9 days after the spawning event (see Fig.3). Integration of the additional SOC due to the spawning event (measurements were interpolated for days on which no measurements were made) results in 490 mmol O_2 m^{-2}. If it is assumed that 1 mol of O_2 oxidises 1 mol of reduced carbon (in this case coral eggs) then 41 mg of C was oxidised per square meter Heron Island reef flat area during the 9-day period. This is equivalent to 800 kg C for the entire reef flat area of 19.5 km². We calculated an egg production of 66 t C for *Acropora* and 310 t C for all hard corals of the Heron Reef (see above). As such between 0.2% (spawning of all hard corals) and 1.6% (only *Acropora* spawned) of the egg dry mass could have produced the observed SOC rate increase.

These numbers could be even smaller, because we could not include the organic matter derived from coral sperm in this calculation. The sedimentary community can rapidly degrade sperm, because they are diluted and transported into the permeable sediments via advection. However, it cannot be concluded that only a very small fraction of all coral

eggs is degraded in the reef system. The shallow location where the chamber measurements were done is exposed to tidal currents and waves. Thus, sedimentation of low-density materials, like spawning products, in this area is inhibited and therefore relatively small. Much higher sedimentation of spawning products can be expected in deeper or calm parts of the lagoon as supported by reports of Wolanski et al. (1989) and Simpson et al. (1993).

The fast SOC response of the Heron Island sediments hints to a rapid input of organic matter to the sediments. The effect of the spawning event, however, is not restricted to additional C and N being released to the reef. Atkinson & Atkinson (1992) measured that during a coral spawning event the total phosphate concentrations in the water column increased 600-fold. High P concentrations in the water column can stimulate the growth of bacteria in the water column and in the sediment of oligotrophic reef systems (Kuffner & Paul 2001). This may also contribute to the high SOC rates observed in this study.

Even a small coral spawning event, like the one we studied, delivers enough organic material and nutrients to keep the sedimentary metabolism above the initial level for at least a week. A more pronounced spawning (like the November spawning 2002 shown in Figure 2) or split spawning likely can cause an even longer increased SOC level.

Our findings show that the coral spawning event may play a periodical but important role for the nutrition of benthic (microbial) reef communities. The result of this study hint to an important trophic link between the corals and the sedimentary community especially during the spawning period, in addition to the proposed trophic link via spawning products between corals and reef fish (Pratchett et al. 2001).

The trapping of spawning products in the reef lagoon and rapid processing of the products by reef organisms reduces the loss of organic matter from the reef and therefore is a recycling process that retains and accumulates nutrients in the oligotrophic reef system.

ACKNOWLEDGEMENTS

We thank Bo Barker Jørgensen for his support of this work. Thanks are also due to L. Hönemann who helped with the C/N analyses. We acknowledge R. Forbes of Heron Island Research Station (HIRS) for logistical assistance and S. Ward for taxonomic advice. Thanks are due to P. Cook who helped to improve the manuscript. All sample collections and in situ experiments were done under the permit G01/479 of the Great Barrier Reef Marine Park Authority. This research was funded by the Max Planck Society (MPG), Germany.

LITERATURE CITED

Andrews J, Gay S, Sammarco P (1988) Influence of circulation on self-seeding patterns at Helix Reef, Great Barrier Reef. Proc 6th Int Coral Reef Symp 2:469-474

Arai T, Kato M, Heyward A, Ikeda Y, Iizuka T, Maruyama T (1993) Lipid-composition of positively buoyant eggs of reef building corals. Coral Reefs 12:71-75

Atkinson S, Atkinson MJ (1992) Detection of estradiol-17-beta during a mass coral spawn. Coral Reefs 11:33-35

Babcock RC, Bull GD, Harrison PL, Heyward AJ, Oliver JK, Wallace CC, Willis BL (1986) Synchronous spawning of 105 scleractinian coral species on the Great Barrier Reef. Mar Biol 90:379-394

Baird AH, Pratchett MS, Gibson DJ, Koziumi N, Marquis CP (2001) Variable palatability of coral eggs to a planktivorous fish. Mar Freshw Res 52:865-868

Barranguet C, Alliot E, Plantecuny MR (1994) Benthic microphytic activity at 2 Mediterranean shellfish cultivation sites with reference to benthic fluxes. Oceanol Acta 17:211-221

Boucher G, Clavier J, Garrigue C (1994) Oxygen and carbon-dioxide fluxes at the water-sediment interface of a tropical lagoon. Mar Ecol Prog Ser 107:185-193

Clifton KE (1997) Mass spawning by green algae on coral reefs. Science 275:1116-1118

Coll JC, Bowden BF, Meehan GV, Konig GM, Carroll AR, Tapiolas DM, Alino PM, Heaton A, Denys R, Leone PA, Maida M, Aceret TL, Willis RH, Babcock RC, Willis BL, Florian Z, Clayton MN, Miller RL (1994) Chemical aspects of mass spawning in corals .1. Sperm- attractant molecules in the eggs of the Scleractinian coral *Montipora digitata*. Mar. Biol. 118:177-182

Ehrenhauß S, Huettel M (2003) Advective transport and decomposition of chain-forming planktonic diatoms in permeable sediments. submitted to J Sea Research

Forja JM, Blasco J, Gomezparra A (1994) Spatial and seasonal variation of in-situ benthic fluxes in the Bay of Cadiz (South-West Spain). Estuar Coast Shelf Sci 39:127-141

Forster S, Glud RN, Gundersen JK, Huettel M (1999) In situ study of bromide tracer and oxygen flux in coastal sediments. Estuar Coast Shelf Sci 49:813-827

Gittings SR, Boland GS, Deslarzes KJP, Combs CL, Holland BS, Bright TJ (1992) Mass spawning and reproductive viability of reef corals at the East Flower Garden Bank, Northwest Gulf of Mexico. Bull Mar Sci 51:420-428

Glud RN, Gundersen JK, Revsbech NP, Jorgensen BB, Huettel M (1995) Calibration and performance of the stirred flux chamber from the benthic lander Elinor. Deep-Sea Res Pt I-Oceanog Res 42:1029-1042

Gomezparra A, Forja JM (1993) Benthic nutrient fluxes in Cadiz Bay (SW Spain). Hydrobiologia 252:23-34

Grenz C, Denis L, Boucher G, Chauvaud L, Clavier J, Fichez R, Pringault O (2003) Spatial variability in sediment oxygen consumption under winter conditions in a lagoonal system in New Caledonia (South Pacific). J Exp Mar Biol Ecol 285:33-47

Guest JR, Chou LM, Baird AH, Goh BPL (2002) Multispecific, synchronous coral spawning in Singapore. Coral Reefs 21:422-423

Hagman D, Gittings S, Deslarzes K (1998) Timing, species participation, and environmental factors influencing annual mass spawning at the Flower Garden Banks (Northwest Gulf of Mexico). Gulf of Mexico Science 16:170-179

Harriott VJ (1992) Recruitment patterns of Scleractinian corals in an isolated subtropical reef system. Coral Reefs 11:215-219

Harrison PL (1993) Coral spawning on the Great Barrier Reef. Search 24:45-48

Harrison PL, Babcock RC, Bull GD, Oliver JK, Wallace CC, Willis BL (1984) Mass spawning in tropical reef corals. Science 223:1186-1189

Hayashibara T, Shimoike K, Kimura T, Hosaka S, Heyward A, Harrison P, Kudo K, Omori M (1993) Patterns of coral spawning at Akajima Island, Okinawa, Japan. Mar Ecol Prog Ser 101:253-262

Huettel M, Gust G (1992) Solute release mechanisms from confined sediment cores in stirred benthic chambers and flume flows. Mar Ecol Prog Ser 82:187-197

Itano D, Buckley T (1988) Observations of the mass spawning of corals and Palolo (Eunice viridis) in American Samoa. Report of the Department of Marine and Wildlife Resources, American Samoa:14 pp

Jørgensen BB (2001) Life in the diffusive boundary layer. In: Boudreau BP, Jørgensen BB (eds) The Benthic Boundary Layer. Oxford University Press, Oxord New York, p 395

Klute A, Dirksen C (1986) Hydraulic conductivity and diffusivity: laboratory methods. In: Klute A (ed) Methods of soil analysis-part 1-physical and mineralogical methods, 2nd edn. American Society of Agronomy

Kuffner IB, Paul VJ (2001) Effects of nitrate, phosphate and iron on the growth of macroalgae and benthic cyanobacteria from Cocos Lagoon, Guam. Mar Ecol Prog Ser 222:63-72

Lasker H, Brazeau D, Claderon J, Coffroth M, Coma R, Kim K (1996) In situ rates of fertilization among broadcast spawning gorgonian corals. Biol Bull 190:45-55

Lopez P, Vidal M, Lluch X, Morgui JA (1995) Sediment metabolism in a transitional continental marine area - the Albufera-Fo-Majorca (Balearic-Islands, Spain). Mar Freshw Res 46:45-53

Magalhaes CM, Bordalo AA, Wiebe WJ (2002) Temporal and spatial patterns of intertidal sediment-water nutrient and oxygen fluxes in the Douro River estuary, Portugal. Mar Ecol Prog Ser 233:55-71

Marinelli RL, Jahnke RA, Craven DB, Nelson JR, Eckman JE (1998) Sediment nutrient dynamics on the South Atlantic Bight continental shelf. Limnol Oceanogr 43:1305-1320

Nickell LA, Black KD, Hughes DJ, Overnell J, Brand T, Nickell TD, Breuer E, Harvey SM (2003) Bioturbation, sediment fluxes and benthic community structure around a salmon cage farm in Loch Creran, Scotland. J Exp Mar Biol Ecol 285:221-233

Oliver J, Babcock R, Harrison P, Willis B (1988) Geographic extent of mass coral spawning: Clues to ultimate causal factors. Proc 6th Int Coral Reef Symp 2:803-810

Oliver JK, Willis BL (1987) Coral-spawn slicks in the Great Barrier Reef - preliminary observations. Mar Biol 94:521-529

Pratchett MS, Gust N, Goby G, Klanten SO (2001) Consumption of coral propagules represents a significant trophic link between corals and reef fish. Coral Reefs 20:13-17

Sammarco P, Andrews J, Risk M (1991) Coral reef geomorphology as a function of seasonal prevailing currents and larval dispersal. Palaeogr Palaeoclimatol Palaeoecol 88:1-12

Shlesinger Y, Loya Y (1985) Coral community reproductive patterns: Red Sea versus the Great Barrier Reef. Science 228:1333-1335

Simpson CJ, Cary JL, Masini RJ (1993) Destruction of corals and other reef animals by coral spawn slicks on Ningaloo Reef, Western Australia. Coral Reefs 12:185-191

Soong K, Cho LC (1998) Synchronized release of medusae from three species of hydrozoan fire corals. Coral Reefs 17:145-154

Stimson J, Kinzie RA (1991) The temporal pattern and rate of release of zooxanthellae from the reef coral *Pocillopora damicornis* (Linnaeus) under nitrogen enrichment and control conditions. J Exp Mar Biol Ecol 153:63-74

Szmant AM (1986) Reproductive ecology of Caribbean reef corals. Coral Reefs 5:43-53

Turner JT (2002) Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. Aquat Microb Ecol 27:57-102

Van Woesik R (1995) Coral communities at high latitude are not pseudopopulations: Evidence of spawning at 32 degree N, Japan. Coral Reefs 14:119-120

Westneat M, Resing J (1988) Predation on coral spawn by planktivorous fish. Coral Reefs 7:89-92

Willis BL, Oliver JK (1990) Direct tracking of coral larvae - implications for dispersal studies of planktonic larvae in topographically complex environments. Ophelia 32:145-162

Winkler LW (1888) The determination of dissolved oxygen in water. Ber Deutsch Chem Ges 21:2843-2857

Wolanski E, Burrage D, King B (1989) Trapping and dispersion of coral eggs around Bowden Reef, Great Barrier Reef, following mass coral spawning. Cont Shelf Res 9:479-496

Chapter 10

Thesis conclusions

THESIS CONCLUSIONS

This study presents new findings on transport and biogeochemical reactions in permeable shelf sediments. Special emphasis was put on in-situ studies, which confirmed that advection plays a pivotal role concerning the transport of water, dissolved gases and organic matter (dissolved or particulate) into permeable shelf sediments. New insights were gained in the reactivity of subtropical permeable carbonate sands that differ strongly in their sedimentological and geochemical characteristics from silicate sediments of temperate shelves.

Chapter 2 shows that the deposition of fecal pellets on the surface of fine-grained sediments can strongly increase the sediment permeability. This secondary permeability generates advective transport of water and dissolved O_2 into the pelletized layer leading to a higher O_2 penetration depth and availability compared to the non-pelletized sediment. Degradation of organic compounds is therefore faster in the pelletized layer compared to the surrounding sediment and depends on the flow velocity in the boundary layer. We could prove that pelletization is an important factor for the sediment-water coupling by influencing the exchange processes between water and sediment and, thus, benthic degradation.

In chapter 3, a new measuring techniques using iodide as tracer was deployed to quantify pore water flow velocity in permeable sediments in-situ, at a station on the Atlantic Shelf of the US coast. These measurements revealed that rapid advective transport of water and solutes takes place in these beds, reaching down to several centimeters depth. Both, chapters 2 and 3 also showed that the sedimentary O_2 consumption rates are positively correlated with the flow rates through the sedimentary pore space. This supports the hypothesis that permeable shelf sediments may function as biocatalytical filter systems.

Chapter 4 is directly connected to chapter 3, because the same sediments have been studied. The experiments discussed in this chapter demonstrate a rapid response of the microbial community in these permeable sediments to the addition of dissolved organic matter leading to a fast increase in sedimentary O_2 consumption. Advection transports both O_2 and dissolved organic matter into the permeable sediments and to the consumers within the sediment, thus enabling a fast reaction to changes in water column DOC concentration down to several centimeter depth.

Chapter 5 highlights the extreme role of carbonate sediments within permeable shelf sediments. Coral reef sediments, mainly composed of very permeable sands, showed high primary production and O_2 consumption rates compared to silicate sediments. Solute exchange rates were high and depending on the friction velocity of the overlying water. O_2 consumption and DIC release increased with increasing sediment permeability. These findings suggest that advective transport may be even more important in reef sands compared to silicate sands and indicate a very intensive coupling between the shallow water column and the sediments in coral reef systems.

Chapter 6 addresses an important pathway of particulate matter from the water column to the sea floor in tropical environments. This research shows that transparent exopolymer particles (TEP) in Great Barrier Reef inshore waters can reach very high concentrations and the mucoid marine snow aggregates reach lengths of 20-40 mm. Scavenging of suspended muddy particles by sticky marine snow aggregates resulted in a fast sedimentation of the TEP-sediment aggregates. Young corals, covered by large amounts of this material on the rocky seafloor, died to a high degree. In reef environments and adjacent waters, sticky marine snow and mucus aggregates provide a rapid pathway of particulate matter from the water column to the benthos and, thus, intensify benthic-pelagic coupling and recycling of matter.

In the work presented in chapter 7, in-situ chamber experiments demonstrate the reaction of the benthic community in permeable carbonate reef sediments on settling coral mucus and highlights the rapid and intense reaction of these relatively coarse lagoon sands. The coral mucus added to the chamber water immediately increased O_2 consumption and DIC production. This reaction can be mainly attributed to benthic degraders that use coral mucus as organic substrate for aerobic and also anaerobic metabolism. The conclusion of this work was that coral mucus, a dominant organic substrate in reef systems can be efficiently recycled in the permeable carbonate sediments of the reef lagoon. Again, the sediment permeability allowing advective transport of water and solutes into the sediments seems to play an important role for the trapping and degradation of this material in the carbonate sands.

The work presented in chapter 8 tracks the pathway of coral mucus from the coral to the reef sediments and concludes that mucus represents an important energy and nutrient carrier in the reef ecosystem. Mucus, exuded in large quantities by hard and soft corals into the surrounding water, partly dissolves and partly transforms to marine snow trapping particles from the water column. Evolving mucus aggregates are transported by tidal currents into the reef lagoon where they sink down to the carbonate sands due to their density increasing with particle accumulation. In the lagoon sediments coral mucus can efficiently be degraded. Coral mucus, thus, seems to act as particle trap preventing the export of material from the oligotrophic reef system. It also carries energy and nutrients, enclosed in the mucus matrix and the attached particles, to the permeable sediments where the organic matter is mineralized and nutrients are released. Coral mucus thereby covers a part of the C, N and P demand of the lagoon sediments. This work confirms that coral mucus represents an important link for the exchange of matter between water-column and reef sediments.

Chapter 9 points to coral sexual products as other important coral-derived organic substrates. The reef sediments reacted to the release of gametes, caused by the annual coral mass spawning event, with a 2.5-fold increased O_2 consumption rate two days after the coral spawning. This indicates that at least a part of the organic matter released by the corals as gametes is directly or via food chain processes linked to degradation on and within the reef sands. Even the relatively small coral spawning event studied caused significantly increased O_2 consumption rates for more than a week and suggests that the seasonal input of coral spawning products is an important event for the benthic community.

Chapters 7-9 therefore underline the importance of carbonate reef sediments for the recycling of matter in coral reefs and show that coral-derived organic matter has an important function for the nutrition of reef sediments.