Organic matter degradation in coral reef carbonate and silicate sediments

Dissertation

zur Erlangung des Doktorgrades der Naturwissenschaften

dem Fachbereich Biologie/Chemie der

Universität Bremen

vorgelegt von

Mohammed Y. M. Rasheed

Bremen
Juni 2002

„Gedruckt mit Unterstützung des Deutschen Akademischen
Austauschdienstes“

Tag des Promotionkolloquiums: 28. Juni 2002

Gutachter:

Prof. Dr. Bo. B. Jørgensen
Prof. Dr. Günter. O. Kirst

Prüfer:

Prof. Dr. Venugopalan Ittekkot
Dr. Markus Hüttel

Acknowledgements

I would like to deeply thank all the people who helped me during my work. Special thanks are due to Prof. Jørgensen for accepting me as his Ph.D. student.

My thanks are due to the Jordan-German Project (Red Sea Program III) for funding my study. Particular thanks are due to Prof. Hempel, and Dr. Claudio Richter.

I would like also to thank the DAAD (Deutcher Akademischer Austauschdienst) for financing my stay in Germany.

I am greatly indebted to Dr. Markus Huettel for his guidance, supervision and support. I am grateful for his constructive discussions, critical reading, helpful and suggestions, which improved this work significantly.

Special thanks are due to the members of the Marine Science Station in Jordan, for their support during my research in Aqaba. Particular thanks are due to Dr. Mohammed Badran for his support and comments. Many thanks are due to Ali, Khalid, Tariq Al-salman, Al.Qatawna, Al-sokhni, Huseen Al-najjar, Tariq Al-najjar, Al-momany and Fatima Al-fakhri, Abu Rami and Abu Moath for their help.

I would like to thank the stuff of Max Plank Institute for Marine Microbiology, Bremen especially the members of the flux group for their support. Special thanks are due to Martina Alisch, Antje Rusch, and Arzhang Al-khalili for their help.

I wish to thank the committee members of the thesis defense Prof. Jørgensen, Prof. Kirst, Prof. Ittikot, Dr. Markus Huettel, Markus Billerbeck and Holger Woyt for valuable comments and suggestions.

My thanks are due to my friends in Germany Saber, Fuad, Riyad, Bassam, Raied, Abdol, Al-sabi, Rami, Mohsen, Hamdan, Bashar, Khalid, Omar, Nidal, Rafat, Abu Al-heeja, Abu-shekha, Adrrienn, Agneiszka, Blerta, Ieva, Anna, Qustantina, Sara, Naomi, Eva for their support and encouragement.

Finally, my worm feeling and sincere gratitude to my **parents**, **brothers**, and **sisters** for their support and love.

Before and above all, I thank my Glorious God Allah

Table of contents

Summary

Our study addresses aspects of the cycling of matter in coral reef environments. These environments are characterized by extreme productivity and exhibit higher nutrient concentrations although the water enclosing the reef may be very low in nutrients. Our research program was designed to improve the understanding of the processes that lead to the increased nutrient concentrations and the ensuing high benthic production. Our main working hypothesis postulates that the reef framework and the coral sands play a key role in the cycling of matter in the reef, and that they are sites of intense mineralization. In order to test this hypothesis, the following research projects were conducted:

Assessment of the relative contributions of reef framework and bottom sediment to the nutrient supply in a coral fringing reef (results reported in Paper 1)

Detailed investigation of the reef framework community and its contribution to the mineralization of particulate organic matter (results reported in Paper 2)

Detailed investigation of particle filtration and seasonal nutrient dynamics in permeable reef sands in a coral fringing reef (results reported in Paper 3)

Assessment of the roles of sediment permeability and mineral composition on organic matter decomposition in reef and shelf sediments (results reported in Paper 3 and 4)

Investigation of the respiration rates and CO_2 production in permeable coral sands (results reported in Paper 5)

The following text summarized the main results of these studies.

In the reef waters, nutrient and chlorophyll a concentrations were significantly higher during summer than in the adjacent offshore waters. This was attributed to the release of nutrients from the reef framework and reef sediments. Reef sediments with their porous structure can filter and mineralize deposited organic material and subsequently release nutrients to reef waters. Nutrient concentrations in the sediment pore water exceeded those in the water overlying these sediment, which, under very calm conditions resulted in fluxes of 0.1 and 0.01 mmol m^{-2} d^{-1} for DIN and DIP respectively (see Paper 1).

Increased nutrient concentrations were also measured in the caves of the reef framework. An endoscopic video camera, developed to explore the internal structure and the macrofauna in the framework revealed a large internal surface (2.5-7.4 m^2 per projected

m^2 reef) dominated by encrusting filter feeders (up to 60% were sponges). The filtration activity of these coleobite communities that removes suspended particulate matter from the water penetrating through the framework results in high mineralization rates of organic matter (0.9 g C m^{-2} d^{-1}) which cause a relatively high nutrients release from the framework to the surrounding water (23.1 and 1.3 mmol m^{-2} d^{-1} for DIN and DIP respectively), (see Papers 1 and 2).

Seasonal investigations of the nutrient distribution in the pore water in permeable carbonate and silicate reef sediments showed that the concentrations were higher in the winter months than in summer months, following closely the concentrations of nutrients and organic matter in the water column. This demonstrates the close coupling between the water column and the permeable reef sediments emphasizing the role of advective transport for the exchange of solutes and particles between sea bed and overlying water (see Paper 3).

In order to investigate the impact of sediment chemical and physical properties on organic matter mineralization, we compared nutrient pore water distributions and organic matter mineralization rates in three sediments of the Gulf of Aqaba that differ in permeability and mineral composition. Two of the investigated sediments were shallow (5m depth) coarse permeable sands (> 1×10^{-12} m^2) with different mineral composition (carbonate and silicate sands, respectively), the third was a relatively impermeable (< 1×10^{-12} m^2) silt sediment from a deep site (825 m depth). DIN and DIP in the pore water of the shallow carbonate and silicate sands were higher than in the silt sediment, and the concentrations were significantly higher in the carbonate than in the silicate sands (factor of 1.7-14.0). In addition, organic matter and pigments (chl a, chl b, and Fucoxanthine) concentrations were also higher in the carbonate than in the silicate sands (1.7 fold for organic matter and 2.4 for pigments). These results indicated that the coarse permeable sands in the shallow shelf efficiently filtered and mineralized organic particles from the water column and that mineralization in the carbonate sand was more efficient as that in the silicate sand of same grain size. Despite their large grain size, the shallow sands were more active than the fine silt sediment and we attribute this finding to the biocatalytic filtration process (see Paper 4).

An investigation of the mineralization potential of the three investigated sediments was carried out in chamber incubations with dried *Spirulina* addition as an organic substrate. The mineralization rates of total organic carbon in the permeable carbonate (3.0 mg C m^{-2} d^{-1}) and silicate sands (2.0 mg C m^{-2} d^{-1}) exceeded that in the fine-grained sediment (1.4 mg C m^{-2} d^{-1}). Incubations of cleaned and sieved carbonate and silicate sands (250-500 µm) in the laboratory and in-situ revealed that in-situ, the sieved carbonate sand accumulated more organic matter and pigments, and developed higher nutrient

concentrations than the silicate sand. Lab experiments with the sieved sediments and fluoresceine as a solute tracer, showed a 1.4-fold higher fluid exchange rate in the carbonate than the silicate sands resulting in a 1.4-fold higher organic carbon mineralization rate in the carbonate (see Papers 3 and 4).

Field and laboratory experiments at the coral kay Heron Island (Great Barrier Reef), where the sediments are mainly permeable carbonate sands, revealed high oxygen respiration rates and high DIN and DIP fluxes. In these experiments we quantified oxygen respiration rates in-situ under different environmental conditions (light/dark, high/low pressure gradients causing advection) and thereby demonstrated the high sedimentary mineralization activity and its dependency on the boundary layer flow. Lab incubation experiments with sediments of different permeabilities showed the effect of the hydraulic conductivity for the organic matter decomposition in the sediment. Oxygen consumption rates in the chambers with high pressure gradient were approximately 2-fold higher than in the chambers with low gradient and 8-fold higher than in the chambers with stagnant water column (no stirring). A 3-fold higher permeability resulted in 2 to 3 fold higher oxygen consumption and DIC production rates. These results stressed the importance of advective pore water exchange for the mineralization of organic matter in permeable carbonate sands (see Paper 5).

We conclude from the results of our study that the reef framework and the coarse permeable coral sands play an important role for the cycling of matter in coral reef ecosystems. The framework efficiently filters and mineralizes suspended matter due to the dense community of filter feeders that inhabit the cavities. The coral sands are highly active despite their low organic content, which is attributed to their high permeability, their mineralogy and the boundary layer flows. The characteristics of the coral sands, such as the high hydraulic conductivity, highly porous grains with large specific surface area, high sorption and pH buffer capacities enhance the filtration capacity and organic matter mineralization rates in these sediments. The coral sands and the coral framework, thus, act as biocatalytical filter systems within the reef ecosystem, efficiently removing the suspended particulate matter from the reef waters and returning nutrients to the reef after rapid mineralization in the permeable sediment and framework. This may sustain the high productivity of the coral reef in spite of the low nutrient concentrations in the surrounding waters.

Chapter 1

General Introduction

Introduction

Coral reef

Coral reefs are highly diverse, complex and productive biological communities, which live in oligotrophic tropical marine environments (30° N and 30° S of the equator) where average water temperature exceeds 18° C (Fig. 1). They cover about 30 % of the world coastline and are considered to be one of the most important ecosystems on the earth. Coral reefs are composed of consolidated areas of coral growth spread over areas of unconsolidated sediment containing coral and algal carbonate. Distress to coral reef ecosystem start to increase as a result of eutrophication of reef waters due to human activity. This gives research on nutrient regeneration and release in coral reef waters special importance.

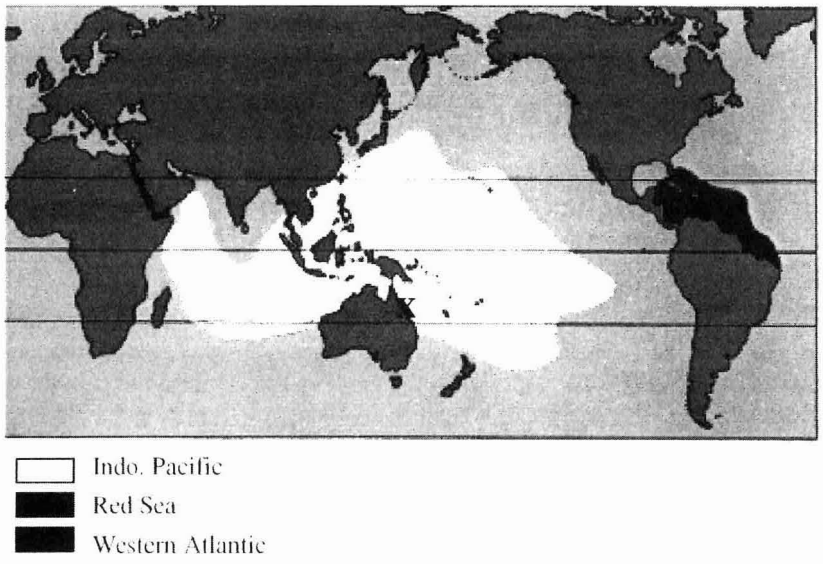


Fig. 1: Distribution of coral reef in the world. X: Sites of our study

Nutrients in reef ecosystem

Coral reef ecosystems belong to the most productive coastal marine ecosystem (Sorkin 1990, 1995) reaching rate of 3.5 kg C m^{-2} yr^{-1}. On the contrary, nutrient concentrations in the water of the coral reef ecosystems are known to be apparently below the level needed for phytoplankton growth with annual average inorganic nitrogen (nitrate, nitrite and ammonium) concentrations less than 1.5 µM, phosphate concentrations less than 0.5 µM and silicate concentrations less than 2.5 µM (Johannes et al. 1983, D'Elia and Wiebe 1990, Furnas et al. 1990, Larned 1998, Badran and Foster, 1998, Rasheed et al. in press.). However, nutrient concentrations in the reef waters are often higher than in the surrounding water (e.g. D'Elia and Wiebe 1990, Badran and Forster 1998, Rasheed et al. in press) a situation which is known as Darwin Paradox (Johannes et al. 1983, Tribble et al. 1990). This stimulated the scientists to search for the sources of nutrients that support such a high productivity in this ecosystem. Benthic sources and reef framework have been suggested as alternative to the water column in providing inorganic nutrients to the reef system. Benthic sources include trapping and decomposition of suspended organic material by macrofauna (Meyer and Schultz 1985, Williams and Carpenter 1988, Larned 1998), and meiofauna (Gray 1985), ground water inputs (D'Elia et al. 1981, Lewis 1987, Lapointe 1997). In addition, nitrogen fixation was considered to be a source of inorganic nitrogen in reef waters (Wilkinson et al. 1984, Capone et al. 1992), and occurred mainly by the living material in coral reefs community such as sponges (Wilkinson and Fay 1979), zoanthids (Shieh and Lin 1992), and some cyanobacteria (Paerl 1984, Larkum et al. 1988).

Reef framework as nutrient source

Several studies found nutrient rich, oxygen depleted, low pH water in the reef framework (Risk and Muller 1983, Sansone 1985, Buddemeier and Oberdorfer 1986, Sansone et al. 1988). The skeletons of the corals are porous and porosity may reach up to 50% of the framework (Ferrer and Szmant 1988, Richter and Wunsch 1999). The framework contains numerous cavities that are inhabited by a wide variety of low-light adapted organisms or coelobites (Ginsburg and Schroeder 1973). Among these organisms, macroborers such as sponges, microboresrs such as algae, fungi, and bacteria (Ferrer and Szmant 1988) cover almost the entire available substratum (Jackson et al. 1971). These

organism colonize the cavities of the framework and may act as filters for organic matters to be mineralized mainly to inorganic nitrogen and phosphate (Sanson et al. 1993, Tribble et al. 1990, Richter and Wunsch 1999, Richter et al. 2001).

Sediment as nutrient source

Remineralization of organic matter in the sediments of the coral reef which results in a net flux of dissolved inorganic nutrient from these sediments has been confirmed to be an important source for nutrient in the coral reef ecosystem (e.g. Smith et al. 1981, Capone et al. 1992, Boucher et al. 1994, Szmant and Forrester 1996, Stimson and Larned 2000). In the following sections we discuss the main characteristics of the reef sediments that are important for the mineralization processes.

Coral reef Sediment; carbonate sediment vs silicate sediment

Coral reef sediments are composed mainly of carbonate sands that contain more than 50% biogenic carbonate (Fig. 2.a). Silicate sediments (Fig 2.b) may be found adjacent to the reef e.g. in the reef valleys. These sediments cover approximately 10% of the continental shelves and are usually found in tropical and subtropical environments within coral reef ecosystems (Fig. 1). Carbonate and silicate sediments have different chemical and physical characteristics, such as porosity, light attenuation, surface structure, sorption and desorption characteristics, and dissolution kinetics (Schroeder and Purser 1986). Carbonate sands dissolve at faster rate than silicate (Banfield and Nealson 1998) and can act as a buffer for different reminarlization reactions through precipitation and dissolution of carbonate, which produce and or consume CO_2, HCO_3 and H^+, as shown in the following equations for precipitation and dissolution for calcium carbonate

$$CO_2 + H_2O \leftrightarrow H_2CO_3$$

$$H_2CO_3 \leftrightarrow H^+ + HCO_3^-$$

$$HCO_3^- \leftrightarrow H^+ + CO_3^{2-}$$

$$CO_3^{2-} + Ca^{+2} \leftrightarrow CaCO_3$$

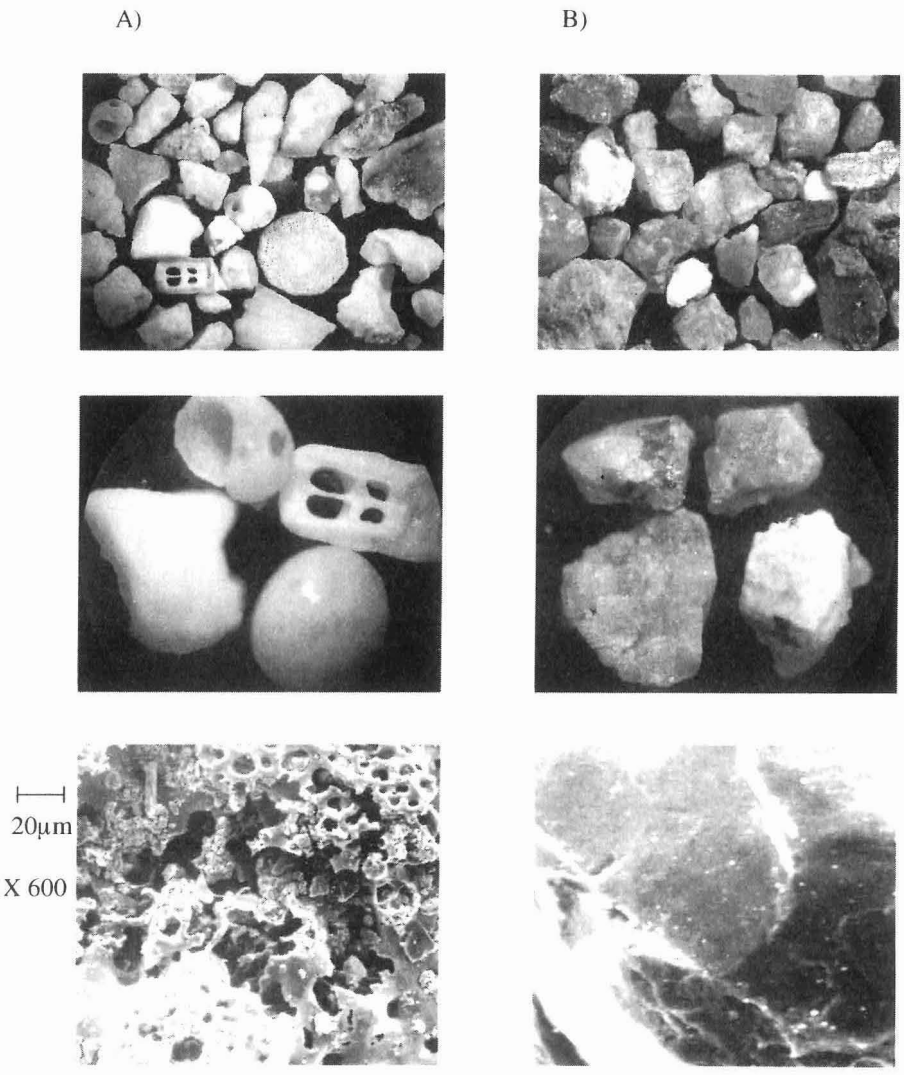


Fig.2: Some photos for a) carbonate, and b) silicate sands taken by Dissecting Microscope (the four above) and Electronic Scanning Microscope (the two below)

In most of the reef ecosystems carbonate sands cover roughly half of the surface area. In the Great Barrier Reef in Australia, sands occupy approximately 40% of the whole reef area (Furnas et al. 1995). The main component of these sands is carbonate of biological origin such as coral fragments, mollusc fragments, foraminiferans tests, and calcareous red algae. Terrigenous clastic materials composed mainly of silicate minerals may comprise 10-15% of these sediments (Milliman 1974). The largest fractions of reef sediments may be coral sands with particle sizes of 0.30-0.6 mm (Sorkin 1995) producing highly porous and permeable sediments ($>1\times 10^{-12}$ m^2).

The upper layers of coarse coral sands are well aerated and illuminated and are inhabited by dense populations of microalgae, bacteria and microzoobenthon (Sorkin 1995). This makes these sands one of the most active parts of the coral reef ecosystems, although they contain a relatively low organic carbon content (mostly 0.15-1%). Benthos organisms are the most important part in coral reef ecosystems with a productivity up to 10 times higher than that of the phytoplankton in the reef (Loban and Harrison 1997). Benthic microalgal production in reef sediments is responsible for 20-30% of the total primary production in the reef (Sorkin 1995). On the Great Barrier Reef in Australia, productivity of the sediments in coral reefs may contribute 50% of the total production (Lough and Barnes 2000). Degradation of organic matter in reef sediments may also influence the geochemical composition and preservation of reef sediments by indirectly driving carbonate mineral precipitation and dissolution reactions (Tribble 1993). The high porosity and permeability of carbonate sediments allow water currents to penetrate and resuspend these sands (Buddemeier and Oberdorfer 1986, Riegl 1995), which enhance advective transport through these sediments. This will necessarily enhance reminerlization rate in these sediments, as discussed in the following sections.

Degradation of organic matter in sediment

Coastal and shelf sediment

Shelf and coastal areas are considered the most productive parts of the ocean which comprise only 10% of the total ocean area, yet they contribute to 20 to 50% of the ocean total primary production. (Romankevich 1984). About 83% of the total organic matter sedimentation occurs in the shelf sediments (Jorgensen 1983). Due to this high capacity for organic matter, the sediments are expected to have an important regulatory and

buffering function in the ocean. The main source of organic matter to the shelf sediments is the deposition of detrital material from the local phytoplankton community in the overlying water. Most of the deposited organic materials are degraded, remineralized, and then recycled to the water column. About 10 % only are buried to form the steady state organic carbon concentration of shelf sediments. The importance of the bottom sediments to organic matter deposition and degradation increases with decreasing water column depth (Martin et al. 1987), which emphasise the importance of the shelf sediment in the coastal habitat food web.

Role of sediment in degradation of organic matter

Degradation and remineralization of organic matter in the sea are important process for the generation of inorganic material including nutrients, which sustain primary productivity in the ecosystem. The role of the sediment in these processes is substantial (e.g. Berner 1980, Zeitzschel 1980, Entsch et al. 1983, Charpy-Rouband et al. 1990, Ciceri et al. 1999). Nixon et al. (1980) suggested that mineralization of organic deposits in the sediment can be a main factor controlling nutrient availability in the shelf. Sedimentary mineralization is particularly important because of the high surface-volume ratio of the coastal sediments and the bacterial colonization of the sea floor (Dale 1974). Benthic metabolic activity limits the amount of organic matter, which can be retained in the sediment and determines the rate of nutrient release to the water column (Berner 1980). In tropical marine coastal systems, most of the productivity is associated with the benthos (Zieman 1982, D'Elia and Wiebe 1990).

Degradation of organic matter may occur aerobically or anaerobically depending on the oxidizing agent. When different organisms utilise oxygen as an energy source to decompose organic matter deposited to different inorganic products, this is called aerobic oxidation, which is represented simply by the following equation

$$CH_2O + O_2 \rightarrow CO_2 + H_2O$$

When dissolved oxygen become almost depleted, other processes may occur, which utilise nitrate, manganese oxides, iron oxides, sulphate and CO_2 as an energy source (Froelich et al. 1979, Canfield et al. 1993). These processes are anaerobic and represented in the following equations

Denitrification:

$5CH_2O + 4NO_3^- \rightarrow 2N_2 + 4HCO_3^- + CO_2 + 3H_2O$

Manganese oxide reduction:

$CH_2O + 2MnO_2 + 3CO_2 + H_2O \rightarrow 2Mn^{+2} + 4HCO_3^-$

Iron oxide reduction:

$CH_2O + 4Fe(OH)_3 + 7CO_2 \rightarrow 4Fe^{+2} + 8HCO_3^- + 3H_2O$

Sulphate reduction:

$2CH_2O + SO_4^{-2} \rightarrow H_2S + 2HCO_3^-$

Methane production:

$2CH_2O \rightarrow CH_4 + CO_2$

These reactions usually occur in the sequence listed below depending on their free energy yield (energy favourable), which follow the order (Latimer 1952, Berner 1971):

$$O_2 > NO_3^- > Mn^{4+} > Fe^{3+} > SO4^{2-}$$

However, many exceptions are known and overlap between the reaction zone is common. Oxic respiration is more efficient and most of the organic material in the surface layers decompose by this process (Berner 1980). However, anaerobic processes become particularly important when oxygen is depleted in the sediments which usually is the case of only a few millimetres depth in coastal sediments (Revsbech et al. 1980).

The degradation pathways, aerobic or anaerobic, are affected by several factors such as temperature, sediment compositions, physical and chemical properties of the sediments, sedimentation rate, hydrodynamics, bioturbation and irrigation (Goldhaber et al. 1977, Emerson et al. 1984, Haddad et al. 1992, Keil et al. 1994, Mayer 1994, Henrichs 1995, Adams and Bustin 2001).

Fluxes of solutes from the sediment

Degradation of organic deposits result in mineralization of organic nitrogen, phosphate and silicate to inorganic forms. The accumulation of these inorganic nutrients in the sediments produces solute concentration gradients between pore water and the overlying sea water. This concentration gradient drives the solute back to the water column, which means fluxes of these nutrients to the overlying waters. In aerobic sediment, oxic respiration can supply nitrate and nitrite for the water column (Hammond et al 1983, Berelson et al. 1998). In anaerobic sediment, ammonium can be supplied from nitrate reduction, phosphate remains soluble under anaerobic conditions (Libes 1992). Flux of inorganic nutrient from the sediment can then supply a significant amount of nutrient required for primary productivity in the overlying water (Boynton et al. 1980, Nixon and Pilson 1983, Furrer et al. 1996). Benthic flux of nutrients is controlled mainly by the rate of the degradation processes, diffusive transport, advection processes, pore waters pumping which is influenced by bioirrigation and bioturbation from different burrowing organisms, as well as the physical and chemical properties of the sediment and the bottom waters.

Advective transport in bottom surface sediment

This process can be defined as flow of water through sediment pores as a result of pressure gradients (Fig. 3) that can be created by action of currents (Huettel and Gust 1992) interacting with biogenic or physical sediment topography (Forster et al. 1996, Ziebs et al. 1996). Waves can, however, also induce exchange across flat sediments (Riedl et al. 1972, Shum 1993). Gradients of less than 1 Pa cm^{-1} can cause significant advective water flow through the top layers of sandy sediments (Huettel and Gust 1992). Interfacial fluid exchange depends mainly on flow velocity (Forster et al. 1996), topography height (Huettel et al. 1996) and permeability of the sediment (Huettel and Gust 1992). In the upper layer of the sediment (from surface down to 5cm), a minimum permeability of 1×10^{-12} m^2 is required for advective transport to take place (Huettel and Gust 1992).

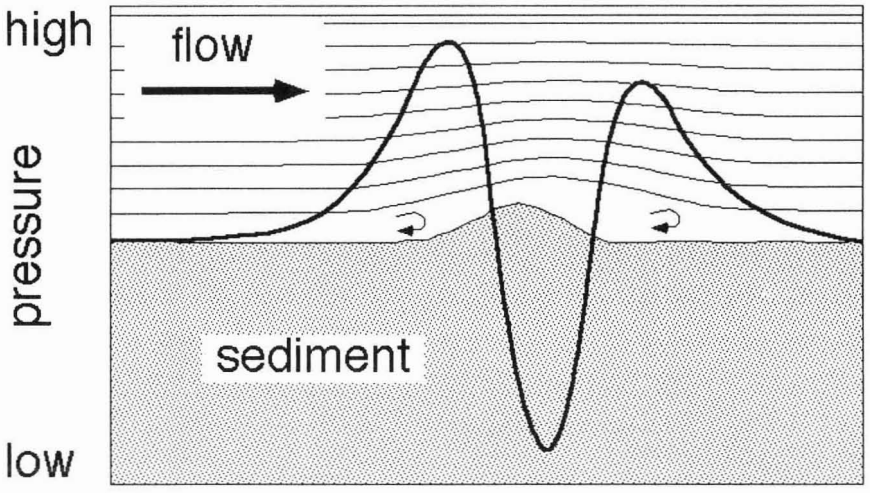


Fig. 3: The pressure distribution (thickline) at a mound on the sedimet surface exposed to boundary layer flow (Huettel et al. 1996).

Permeable sediments are dominant on continental shelves (Emery 1968, Riedl et al. 1972, Shum and Sundby 1996). These sediments contain relatively small amounts of organic carbon (0.1-1.0 mostly). However, advective transport, which occurs in these sediments increases degradation and mineralization of organic matter to form mineralization products like nutrients, which support the high productivity of the coastal ecosystems (Huettel et al. 1998).

Transport in cohesive sediments that have a permeability of less than 1×10^{-12} m^2 occurs by molecular diffusion and bioturbational irrigation maintaining organic matter degradation in these sediments (Froelich et al. 1979, Berner 1980, Jorgensen 1996).

Influence of advective transport on remineralization of organic matter

Mineralization of organic matter increases as a result of advective transport of solute through the sediment (Huettel and Gust 1992, Forster and Graf 1995, Shum and Sundby 1996, Falter and Sansone 2000). The assimilation rate of bacteria attached to particles

increases several fold by a fluid flow of 20 m d^{-1} (Logan and Kirchman 1991). Oxygen consumption increases in permeable sediments as well. Forster et al. (1996) demonstrated oxygen utilization increase of 91%±23% in a sediment of permeability 5×10^{-12} m^2 when flow velocity increased from 3 to 14 cm s^{-1}, while in less permeable sediment (5×10^{-12} m^2) the change was not significant. The authors showed that the mineralization of added algae also increase in the coarser sand. Advective flows increase oxygen consumption by increasing oxygen penetration depth (Ziebis et al. 1996). Some investigations have shown that oxygen consumption may be enhanced in organic poor sediment due to advective transport (Andersen and Helder 1987, Rowe et al. 1988), which may reflect rapid mineralization in such sediments.

Objectives

This study had two main goals. First is a better understanding of the relationship between reef productivity and nutrient availability in coral reef ecosystems found in tropical or subtropical oligotrophic waters. This includes the contributions of reef framework and sediments to the nutrient recycling in reef ecosystem. The second is to investigate the degradation and remineralization rates of organic matter in carbonate sediments in comparison to silicate sediments. The impact of mineral composition, physical and chemical characteristics of the sediments in degradation rate of organic matter have also been investigated. The results show the role of carbonate sands for the recycling of nutrients in reef ecosystems.

The main objectives of the study are to:

1- Investigate the role of reef framework and reef sediments in nutrient cycles in the coral reef ecosystem.

2- Investigate the effect of the physical and chemical properties of carbonate and silicate sediments, including permeability, porosity, mineral composition, and surface area on organic matter degradation and remineralization

3- Quantify the nutrient and organic carbon concentrations in the pore water of shallow sediment sites of the Gulf of Aqaba, including carbonate and silicate sediments during summer and winter, and identify seasonality in nutrient and organic carbon distribution in both sediments.

4- Study of nutrient and oxygen exchange in shallow coarse sediments and deep cohesive sediment of the Gulf of Aqaba, and quantify the rate of organic matter degradation in these sediments.

5- Assess oxygen consumption and CO_2 production in permeable carbonate sediments.

Publications outline:

The thesis includes five articles. Four of them have been submitted to international journals and the fifth will be submitted soon. Two of the articles investigated nutrient dynamics in the coral reef and the effect of reef framework and sediments (mainly carbonate) on nutrient cycling in the reef waters. The other three articles investigated the importance of carbonate sediments for the degradation of organic matter in reef environments and compared mineralization rates of organic material in carbonate and silicate sediments.

1) Rasheed M., Badran M., Richter C. and Huettel, M.
Effect of reef framework and bottom sediment on nutrient enrichment in a coral reef of the Gulf of Aqaba

This study was initiated and carried out by M. Rasheed, M. Badran, M. Huettel and C. Richter. M. Rasheed evaluated the data and wrote the manuscript with editorial help by M. Huettel and M. Badran. This article is accepted for publication in Marine Ecology - Progress Series.

2) Richter C., Wunsch M., Rasheed M., Kötter I. and Badran M.
Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges

C Richter initiated this study, who also carried out the experiments with M. Wunsch, M. Rasheed, I. Kötter and M. Badran. C. Richter wrote the manuscript. This article was published in Nature 413, 18.Oct. 2001.

3) Rasheed M., Badran M. and Huettel M.
Particulate matter filtration and seasonal nutrient dynamics in permeable carbonate and silicate sands of the Gulf of Aqaba, Red Sea

This study was initiated by M. Huettel and M. Rasheed who also carried out the study with a help of M. Badran. M. Rasheed evaluated the data and wrote the manuscript with editorial help and input by M. Huettel. This article has been submitted to Coral Reefs.

4) Rasheed M., Badran M. and Huettel M.
Influence of sediment permeability and mineral composition on organic matter decomposition in three sediments from the Gulf of Aqaba, Red Sea

The contributions of the authors are the same as in the last article. This article has been submitted to Estuarine, Coastal and Shelf Science.

5) Rasheed M., Wild C., and Huettel M.
Benthic respiration in permeable carbonate lagoon sediments from the Heron Island atoll, Great Barrier Reef, Australia

This study was initiated by M. Huettel. The experiments for this study were carried out by M. Huettel, M. Rasheed and C. Wild. M. Rasheed evaluated the data and wrote the manuscript with editorial help and input of M. Huettel. This article will be submitted to Estuarine, Coastal and Shelf Science.

References

Adams RS, Bustin RM (2001) The effects of surface area, grain size and mineralogy on organic matter sedimentation and preservation across the modern Squamish Delta, British Columbia: the potential role of sediment surface area in the formation of petroleum source rocks. Internat J Coal Geol 46:93-112

Andersen F, Helder W (1987) Comparison of oxygen microgradients, oxygen flux rates and electron transport system activity in coastal marine sediments. Mar Ecol Prog Ser 37:259-264

Badran MI, Foster P (1998) Environmental quality of the Jordanian coastal waters of the Gulf of Aqaba, Red Sea. Aquatic Ecosystem Health and Management 1:75-89

Banfield JF, Nealson KH (1998) Geomicrobiology: interactions between microbes and minerals. In: Ribbe PH (ed) Rev in Mineral, vol 35

Berelson WM, Heggie D, Longmore A, Kilgore T, Nicholson G, Skyring G (1998) Benthic nutrient recycling in Port Phillip Bay, Australia. Est Coast Shelf Sci 46:917-934

Berner RA (1971) Principle of Chemical Sedimentology. McGraw-Hill, New York

Berner RA (1980) Early Diagenesis-A Theoretical Approach. Princeton University Press, Princeton, New Jersey

Boucher G, Clavier J, Garrigue C (1994) Estimation of bottom ammonium affinity in the New-Caledonia Lagoon. Coral Reefs 13:13-19

Boynten WR, Kemzp WM, Osborne CG (1980) Nutrient fluxes across the sediment-water interface in the turbid zone of a coastal plain estuary. In: Kennedy VS (ed) Estuarine Perspective. Academic Press, New York, pp 93-109

Buddemeier RW, Oberdorfer JA (1986) Internal hydrology and geochemistry of coral reefs and atoll islands: key to diagenetic variations. In: JH Schroeder and Purser BH (eds) Reef Diagenesis. Springer, Berlin, pp 91-112

Canfield DE, Jorgensen BB, Fossing H, Glud R, Gundersen J, Ramsing NB, Thamdrup B, Hansen JW, Nielsen LP, Hall POJ (1993) Pathways of organic carbon oxidation in three continental margin sediments. Mar Geol 113:27-40

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

Charpy-Roubaud CJ, Charpy L, Cremoux JL (1990) Nutrient budget of the lagoonal waters in an open Central South-Pacific Atoll (Tikehau, Tuamotu, French-Polynesia). Mar Biol 107:67-73

Ciceri G, Ceradini S, Zitelli A (1999) Nutrient benthic fluxes and pore water profiles in a shallow brackish marsh of the lagoon of Venice. Annali Di Chimica 89:359-375

D'Elia CF, Webb KL, Porter JW (1981) Nitrate-rich groundwater inputs to Discovery Bay, Jamaica: A significant source of N to local coral reefs. Bull Mar Sci 31:903-910

D'Elia CF, Wiebe WJ (1990) Biogeochemical nutrient cycles in coral-reef ecosystem. In: Dubinsky Z (ed) Ecosystems of the world. Coral reef, vol 25. Elsevier, Amsterdam, pp 49-74

Dale NG (1974) Bacteria in intertidal sediments - factors related to their distribution. Limnol Oceanogr 19:509-518

Emerson S, Jahnke R, Heggie D (1984) Sediment-water exchange in shallow-water estuarine sediments. J Mar Res 42:709-730

Emery KO (1968) Relict sediments on continental shelves of the world. Am Assoc Petrol Geol 52:445-464

Entsch B, Boto KG, Sim RG, Wellington JT (1983) Phosphorus and nitrogen in coral-reef sediments. Limnol Oceanogr 28:465-476

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

Ferrer LM, Szmant AM (1988) Nutrient regeneration by the endolithic community in coral reef skeletons Proceedings of the 6th International Coral Reef Symposium, vol 3, Australia

Forster S, Graf G (1995) Impact of irrigation on oxygen flux into the sediment: intermittent pumping by *Callianassa subterranea* and "piston pumping" by *Lanice conchilega*. Mar Biol 123:335-346

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

Froelich PN, Klinkhammer GP, Bender ML, Luedtke NA, Heath GR, 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. Geochim Cosmochim Acta 43:1075-1090

Furnas MJ, Mitchell AW, Gilmartin M, Revelante N (1990) Phytoplankton biomass and primary production in semienclosed reef lagoons of the Central Great-Barrier-Reef, Australia. Coral Reefs 9:1-10

Furnas M, Mitchel AW, Skuza M (1995) Nitrogen and phosphorus budgets for the Central Park Authority, vol 35, Townsville

Furrer G, vonGouten V, Zobrist J (1996) Steady-state modelling of biogeochemical processes in columns with aquifer material 1. Speciation and mass balance. Chem Geol 133:15-28

Ginsburg RN, Schroeder JH (1973) Growth and submarine fossilization of algal cup reefs, Bermuda. Sedimentology 20:575-614

Goldhaber MB, Aller RC, Cochran JK, Rosenfeld JK, Martens CS, Berner RA (1977) Sulfate reduction, diffusion, and bioturbation in Long-Island Sound sediments - report of foam group. Amer J Sci 277:193-237

Gray JS (1985) Nitrogenous excretion by meiofauna from coral-reef sediments - Mecor-5. Mar Biol 89:31-35

Haddad RI, Martens CS, Farrington JW (1992) Quantifying early diagenesis of fatty-acids in a rapidly accumulating coastal marine sediment. Org Geochem 19:205-216

Hammond DE, Giordani P, Montanari G, Rinaldi A, Poletti R, Rovatti G, Astorri M, Ravaioli M (1983) Benthic flux measurements in NW Adriatic coastal waters. Memoirs of the Society for Geology Italy 27:461-467

Henrichs SM (1995) Sedimentary organic matter preservation: an assessment and speculative synthesis - a comment. Mar Chem 49:127-136

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

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 GI (1998) Advective transport affecting metal and nutrient distribution and interfacial fluxes in permeable sediments. Geochim Cosmochim Acta 62:613-631

Jackson JBC, Goreau TF, Hartman WD (1971) Recent brachiopod-coralline sponge communities and their paleoecological significance. Science 173:623-625

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

Jorgensen BB (1983) Processes at the sediment-water interface. In: Bolin B, Cook RB (eds) The Major Biochemical Cycles and Their Interactions, vol 21. John Wiley, New York, pp 477-515

Jorgensen BB (1996) Material flux in the sediment. In: Jorgensen BB, Richardson K (eds) Eutrophication in Coastal Marine Ecosystems, vol 52. American Geophysical Union, pp 115-135

Keil RG, Montlucon DB, Prahl FG, Hedges JI (1994) Sorptive preservation of labile organic-matter in marine- sediments. Nature 370:549-552

Lapointe BE (1997) Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnol Oceanogr 42:1119-1131

Larkum AWD, Kennedy IR, Muller WJ (1988) Nitrogen fixation on a coral reef. Mar Bio 97:503-506

Larned ST (1998) Nitrogen- versus phosphorus-limited growth and sources of nutrients for coral reef macroalgae. Mar Biol 132:409-421

Latimer WM (1952) Oxidation Potentials. Prentic-Hall, Englewood Cliffs, N. J.

Lewis JB (1987) Measurments of ground water seepage flux onto a coral reef: spatial and temporal variations. Limnol Oceanogr. 32:1165-1169

Libes SM (1992) An Introduction to Marine Biogeochemistry. John Wiley and Sons, New York

Loban CS, Harrison PJ (1997) Seaweed Ecology and Physiology. University Press, Cambridge

Logan BE, Kirchman DL (1991) Uptake of dissolved organics by marine bacteria as a function of fluid motion. Mar Biol 111:175-181

Lough JM, Barnes DJ (2000) Environmental controls on growth of the massive coral Porites

Martin JH, Knauer GA, Karl DM, Broenkow WW (1987) Vertex - carbon cycling in the Northeast Pacific. Deep-Sea Res Part a-Oceanogr Rese Papers 34:267-285

Mayer LM (1994) Surface-area control of organic-carbon accumulation in continental-shelf sediments. Geochim Cosmochim Acta 58:1271-1284

Meyer JL, Schultz ET (1985) Tissue condition and growth-rate of corals associated with schooling fish. Limnol Oceanogr 30:157-166

Milliman JD (1974) Marine Carbonates. Springer Verlag, New York

Nixon SW, Kelly JR, Furnas BN, Oviatt CA, Hale SS (1980) Phosphorus regeneration and the metabolism of coastal marine bottom communities. B: In: Tenore KR, Coull BC (eds), Marine Benthic Dynamics, University of South Carolina Press, Columbia: 219-243

Nixon SW, Pilson MEQ (1983) Nitrogen in estuarine and coastal marine ecosystems. In: Carpenter EJ, Capone DG (eds) Nitrogen in the Marine Environment. Academic Press, New York, pp 565-648

Paerl HW (1984) N_2 Fixation (nitrogenase activity) attributable to a specific *Prochloron* (Protochlorophyta)-ascidian association in Palau. Micronesia. Mar Biol 81:251-254

Rasheed M, Badran MI, Richter C, Huettel M (in press.) Effect of reef framework and bottom sediment on nutrient enrichment in a coral reef of the Gulf of Aqaba, Red Sea. Mar Ecol Progr Ser

Revsbech NP, Sorensen J, Blackburn TH, Lomholt JP (1980) Distribution of oxygen in marine sediments measured with microelectrodes. Limnol Oceanogr 25: 403-411

Richter C, Wunsch M (1999) Cavity-dwelling suspension feeders in coral reefs - a new link in reef trophodynamics. Mar Ecol Prog Ser 188:105-116

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

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

Riegl B (1995) Effects of sand deposition on scleractinian and alcyonacean corals. Mar Biol 121:517-526

Risk MJ, Muller HR (1983) Porewater in coral heads - evidence for nutrient regeneration. Limnol Oceanogr 28:1004-1008

Romankevich EA (1984) Geochemistry of organic matter in the Ocean. Springer-Verlag, New York

Rowe GT, Theroux R, W. P, Quinby H, Wilke R, Koschoreck D, Whitledge TE, Falkowski PG, Fray C (1988) Benthic carbon budgets for the continental shelf south of New England. Continental Shelf Res 8:511-527

Sansone FJ (1985) Methane in the reef flat porewaters of Davies Reef, Great Barrier Reef, Australia. Proc. Fifth Int. Coral Reef Congress 3: 415-419

Sansone FJ, Andrews CC, Buddemeier RW, Tribble GW (1988) Well-point sampling of reef interstitial water. Coral Reefs 7:19-22

Sansone FJ, Chanton JP, Haberstroh PR, Bozeat R (1993) Methane cycling in coral reef frameworks. In: R Guerrero and C Pedros-Alio (eds) Trends in Microbial Ecology. Spanish Soc Microbiol pp. 157-162

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

Shieh WY, Lin YM (1992) Nitrogen fixation (acetylene reduction) associated with the zoanthid *Palythoa tuberculosa* Esper. J Exp Mar Biol Ecol 163:31-41

Shum KT (1993) The effects of wave-induced pore water circulation on the transport of reactive solutes below a rippled scdiment bed. J Geophysical Res-Oceans 98:10289-10301

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

Smith SV, Kimmerer WJ, Laws EA, Brock RE, Walsh TW (1981) Kaneohe Bay sewage diversion experiment: Perspectives on ecosystem responses to nutritional perturbation. Pacific Sci 35:279-402

Sorkin YI (1990) Aspects of trophic relations, productivity and energy balance in coral-reef ecosystems. In: Dubinsky Z (ed) Ecosystem of the World. Coral Reef, vol 25. Elsevier, Amsterdam, pp 401-410

Sorkin YI (1995) Coral reef ecology. Ecological studies, vol 192. Springer-Verlag, Berlin

Stimson J, Larned ST (2000) Nitrogen efflux from the sediments of a subtropical bay and the potential contribution to macroalgal nutrient requirements. J Exp Mar Biol Ecol 252:159-180

Szmant AM, Forrester A (1996) Water column and sediment nitrogen and phosphorus distribution patterns in the Florida Keys, USA. Coral Reefs 15:21-41

Tribble GW, Sansone FJ, Smith SV (1990) Stoichiometric modeling of carbon diagenesis within a coral- reef framework. Geochim Cosmochim Acta 54:2439-2449

Tribble GW (1993) Organic matter oxidation and aragonite diagenesis in a coral reef. J Sediment Petrol 63:523-527

Wilkinson CR, Fay P (1979) Nitrogen fixation in a coral reef community. Science 188:257-259

Wilkinson CR, Williams DM, Sammarco PW, Hogg RW, Trott LA (1984) Rates of nitrogen-fixation on coral reefs across the continental-shelf of the Central Great Barrier-Reef. Mar Biol 80:255-262

Williams SL, Carpenter RC (1988) Nitrogen-limited primary productivity of coral-reef algal turfs - potential contribution of ammonium excreted by diadema- antillarum. Mar Ecol Progr Ser 47:145-152

Zeitzschel B (1980) Sediment-water interactions in nutrient dynamics. B: In: Tenore KR, Coull BC (eds) Marine Benthic Dynamics, University of South Carolina Press, Columbia: 195-219

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

Zieman JC (1982) The ecology of the seagrasses of South Florida: a community profile. US Fish and Wildlife Service Program FWS/OBS-82/25 123

Chapter 2

Effect of reef framework and bottom sediment on nutrient enrichment in a coral reef of the Gulf of Aqaba, Red Sea

Mohammed Rasheed [1,2], Mohammed Badran[2], Claudio Richter[3], Markus Huettel[1]

[1] Max Plank Institute for Marine Microbiology, Bremen University, 28359 Bremen, Germany

[2] Marine Science Station, University of Jordan and Yarmouk University, Aqaba Jordan

[3] Center for Tropical Marine Ecolgy, Bremen University, Bremen, Germany

This chapter has been accepted in Marine Ecology Progress Series

Effect of reef framework and bottom sediment on nutrient enrichment in a coral reef of the Gulf of Aqaba, Red Sea

Summary

Inorganic nutrients and chlorophyll a concentrations were measured bi-weekly in a transect across a coral reef in the Gulf of Aqaba over a period of 1 year. The nutrient and chlorophyll concentrations were compared to those in adjacent offshore waters (400 m depth). In reef and offshore waters, nutrient (ammonia, nitrite, nitrate, phosphate and silicate) and chlorophyll a data showed seasonal changes, with high concentrations in winter and low concentrations in summer. However, throughout the summer, nutrient concentrations in the coral reef waters significantly exceeded those in the offshore waters, while this difference was less pronounced in winter. This difference was caused by nutrient release from regenerative space in the reef framework and coral sand. In the reef framework water (i.e. cavity water), nutrient concentrations were 1.2 to 2.3-fold higher than those in the surrounding waters, corresponding to fluxes of 14.5 mmol m^{-2} d^{-1} for ammonia, 7.7 mmol m^{-2} d^{-1} for nitrate, 0.9 mmol m^{-2} d^{-1} for nitrite, and 1.3 mmol m^{-2} d^{-1} for phosphate. In the less permeable reef sediments, nutrient concentrations exceeded those of the free-stream waters by factors of 15 to 80. Here, the calculated diffusive fluxes were 0.06 mmol m^{-2} d^{-1} for ammonia, 0.03 mmol m^{-2} d^{-1} for nitrate, 0.01 mmol m^{-2} d^{-1} for nitrite, 0.01 mmol m^{-2} d^{-1} for phosphate, and 0.07 mmol m^{-2} d^{-1} for silicate. Our results highlight the importance of the reef framework and coral sand for the trapping and mineralization of particulate organic matter and the regeneration of nutrients in oligotrophic coral reef waters.

Introduction

Although most coral reefs grow in oligotrophic waters (Furnas 1992), they belong to the most productive coastal marine ecosystems (Sorokin 1993). The exchange of substances between reef, open water, land and atmosphere is small relative to their concentrations and turnover within the coral reefs. The high biomass and productivity of coral reefs is explained by the tight internal recycling of matter (Wiebe et al. 1975, Andrews and Müller 1983, Risk and Müller 1983). Gross primary production in coral reef waters has been shown to be 1 to 2 order of magnitude higher than in the surrounding oligotrophic water (d'Elia and Wiebe 1990, Adey 1998). Reef-related physical and biogeochemical processes mediate intensive exchange of dissolved and particulate matter between the coral reef and the water in the reef environment. Coral sands and reef framework may play important roles in this exchange process.

In most reef ecosystems, corals occupy roughly half the surface area and sands cover the other half. Due to the porous structure of the coral sand, its permeability is relatively high and the porosity of the reef sediment can reach 50%. Pore water analyses in these calcareous sediments revealed elevated nutrient concentrations relative to the overlying bottom water (Engvall 1978, Holm 1978, Smith et al. 1981, Arenas and de la Lanz 1983, Entsch et al. 1983, Nixon and Pilson 1983, Williams 1984, Williams et al. 1985, Furnas et al. 1993, Szmant and Forrester 1996).

Beneath the living surface of the coral reefs, coral skeletal remains and other calcareous biogenic materials form a highly permeable framework, where the volume of coral reef cavities may reach up to half the bulk volume (Ginsberg 1983). These framework cavities are inhabited by a wide variety of organisms (Kobluk and van Soest 1989). Organic matter trapped within the framework or imported by the reef fauna is consumed by the organisms that colonize the cavities and which return ammonia and phosphate to the framework water (Ferrer and Szmant 1988). Nutrient concentrations in reef cavities, therefore, exceed those of waters surrounding the reef (Risk and Müller 1983, Ayukai 1993, Richter et al. 2001).

Because of their large specific surface areas, coral sands and reef framework may have an important biocatalytic function and may act as nutrient buffers in reef ecosystems exposed to seasonal nutrient changes. Seasonal variability of the nutrient supply in coral reef environments has received little attention due to the perception that seasonal fluctuations are less pronounced in tropical climates. Nonetheless, high-latitude reefs, such as those of the Gulf of Aqaba, undergo strong seasonal variations in primary productivity (Kinsey 1977) that are unexpected on the basis of temperature and light fluctuation alone.

Our understanding of the relationship between reef productivity and nutrient availability is limited, despite the importance of nutrients for the growth and health of corals (Ward 1990, Torrance 1991, Hallock et al. 1993, Atkinson et al. 1995). In this study, we investigated the seasonal changes of chlorophyll a and nutrients in the water column and in a fringing reef ecosystem of the Gulf of Aqaba, and we measured coral framework and sediment pore-water nutrient concentrations in order to assess the importance of framework and sediment in the nutrient balance of the coral reef.

Materials and methods

The study was conducted in a well-developed coral reef located in the northern Gulf of Aqaba in a marine reserve close to the Marine Science Station in Aqaba. Water samples were collected concurrently from the reef site and an offshore site 3 km from the Marine Science Station (Fig. 1A). Along the reef transect, surface and bottom water (ca 50 cm above the sediment) were sampled biweekly at stations ranging 5, 10, 20, and 30 m from the bottom. At the stations of 20 and 30 m water depth, additional samples were taken at 10 m depth intervals. The offshore reference station was sampled at water depths of 0 and 25 m. The bottom-water samples were collected by divers, while all other samples were collected with Niskin bottles. Samples were kept on ice until analysis. In the laboratory, the 1 l samples were filtered through pre-rinsed 0.45 µm cellulose-membrane filters and analyzed for ammonia, nitrite, nitrate, phosphate and silicate concentrations according to Strickland and Parsons (1972). The material on the membrane filter was used for the determination of chlorophyll a based on the method published by Arar and Collins (1992), using a Turner Designs, TD-700 fluorometer.

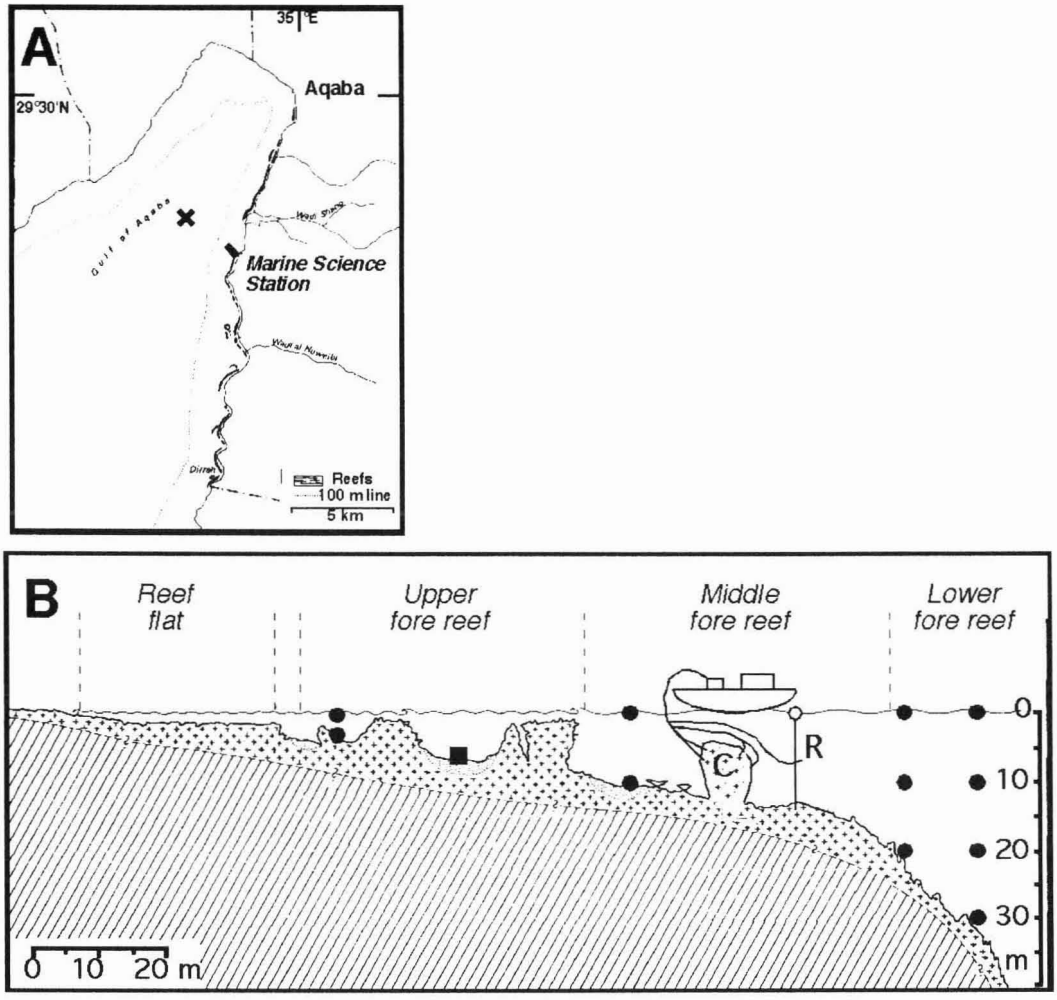


Fig. 1: A. Study area in the northeastern Gulf of Aqaba, Red Sea, showing the reference station ~3 km offshore (×) and the coral reef transect in front of the Aqaba Marine Science Station, Jordan. Modified after Wells (1988). B. Coral reef transect with the sampling locations for the nutrient distribution in coral reef waters (l), nutrient fluxes between coral reef waters and sediment (n) and fluxes between freestream waters (F) and framework cavities (C). Boat is anchored with 8 tubes penetrating into pinnacle (only 4 shown) and R tubes fixed to 2 (only 1 shown) bouys. Modified after Schuhmacher and Mergner (1985).

In June and December 1998, water samples from coral reef cavities and free-flowing reef waters were simultaneously taken at hourly intervals over a period of 24 hours (Fig. 1B). Water was collected using a multichannel peristaltic pump mounted on a boat, using 10 m long, 5 mm diameter silicone tubing inserted into 8 randomly selected cavities within a 4 m diameter coral pinnacle located at a depth of 3 to 6 m. Tubes were fixed axially into ~6 cm wide, ~30 cm deep cavities using elastic plastic rods. Tubes were inserted two-thirds of the way into the cavities, i.e. at ~20 cm distance from the entrance. Free-flowing water was collected with 2 tubes fixed on moorings 3 m upstream from the pinnacle; 100 ml samples were drawn at 50 ml min^{-1} and taken to the laboratory for subsequent analysis of nutrients. Between samplings, the flow was reversed, using double distilled water at rates of 2 ml min^{-1} to avoid fouling of the tubing. With an average volume of the sampled cavities of ~3 l and a water residence time of less than 5 min, we found no dilution effect of the freshwater on salinity in the cavities. Nutrient fluxes between coral reef cavities and free flowing waters were calculated according to the formula

$$F = \Delta N \times Vc \times T^{-1}$$

where ΔN is the concentration difference between the cavity and free-flowing reference (mmol m^{-3}), Vc is the volume of cavities per unit area of reef (m^3 m^{-2}), and T is the residence time of water in the cavities. For the upper 0.2 m of framework investigated, Vc was 0.07 m (Richter et al. 2001). A conservative estimate for T is 300 s (Richter and Wunsch 1999). From June 1999 until March 2000, interstitial water of the coral reef sediments were sampled at a 5 m deep reef site (Fig. 1B) using a method similar to that described by Hesselein (1976). The sediments in this site consist mainly of carbonate sands, with a medium grain size of 500 μm, an average porosity of 47%, a permeabilty of 143 x 10^{-12} m^2, an organic content of 0.5%, and a calcium carbonate content of 80%. 50 ml of the filtered pore water were diluted to 250 ml with distilled deionized water for nutrient analyses. The pore-water nutrient concentrations were compared to those of the bottom water overlying the sediment. Minimum fluxes of NH_4^+, NO_2^-, NO_3^-, PO_4^{-3} and $Si(OH)_4$ from the sediment were calculated according to Fick's first law of diffusion:

$$F = \phi D dCdz^{-1}$$

where F is the flux (mmol m^{-2} d^{-1}), ø is sediment porosity, D is the coefficient of diffusion (m^2 d^{-1}), and $dCdz^{-1}$ is the concentration gradient at the sediment-water interface (mmol m^{-4}). Diffusion coefficients for ammonia, nitrate, nitrite and phosphate were taken from Li and Gregory (1974) for a water temperature of 25°C and corrected for a tortuosity using a porosity of 0.47 and the tortuosity-porosity relationship reported by Beekman (1990). The value for silicate was taken from Lerman (1979) and Callender and Hammond (1982) and corrected for tortuosity. The calculated diffusion coefficients were 8.85, 6.66, 6.7, 2.97 and 5.89 x 10^{-5} m^{-2} d^{-1} for ammonia, nitrate, nitrite, phosphate and silicate respectively.

To assess whether nutrients were significantly different in coral reef waters from those in the offshore waters, ANOVA analysis (5% significance level) was performed based on a calculation of the differences in the average of concentrations between coral reef waters and offshore waters in summer and winter.

Results

In order to compare nutrient concentrations of reef and offshore waters, surface and 25 m samples of the offshore waters were averaged and plotted with the average of the coral reef waters from various depths against time (Fig. 2). Nutrient and chlorophyll a concentrations in reef and offshore waters showed seasonal changes, with high concentrations in winter and low concentrations in summer. The concentrations began to increase in October. Nutrient and chlorophyll a concentrations in the reef waters exceeded those in the offshore waters (Fig. 2, Table 1), particularly in summer, when inorganic nitrogen and phosphate concentrations exceeded offshore values by up to 3 times. The pattern was less consistent during winter, when gradient reversals occurred, both for inorganic nitrogen (e.g. nitrate, February through April: Fig. 2) and chlorophyll a (January through March: Fig. 2).

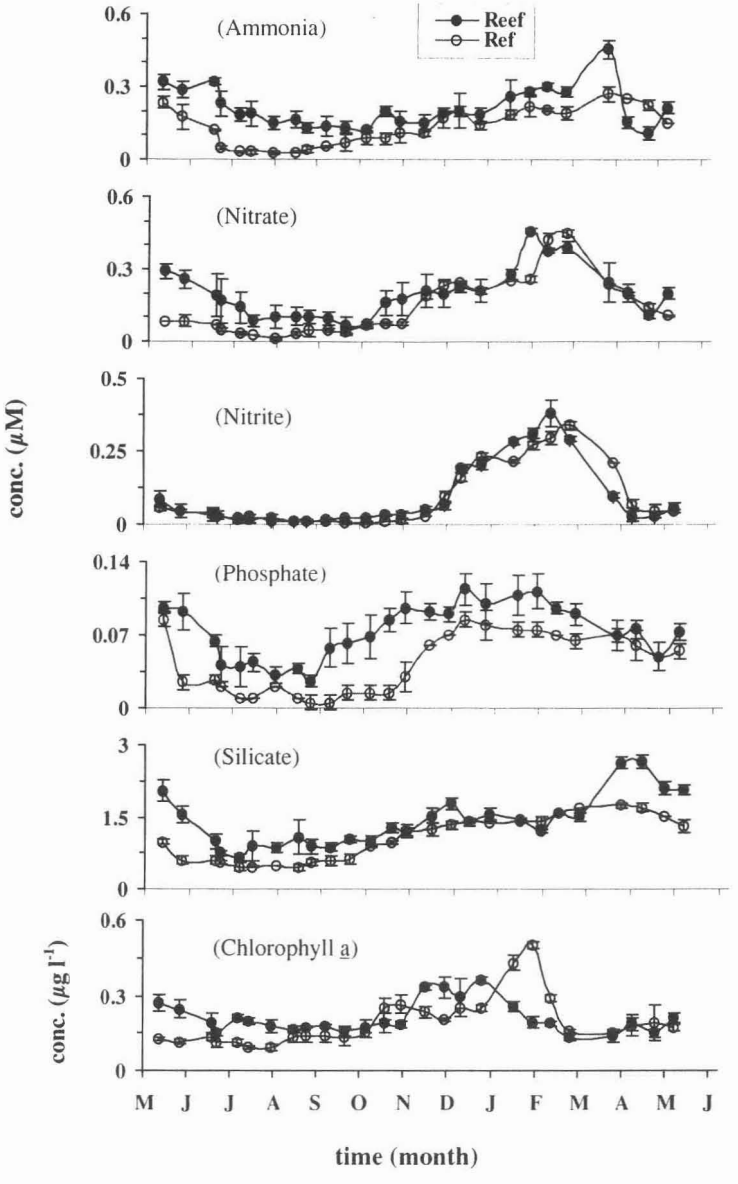


Fig. 2: Nutrient (μM) and chlorophyll a ($\mu g\ l^{-1}$) concentration records in coral reef (closed circles) and offshore reference (opened circles) waters during the period May 97 to May 98.

As a result, moderate cross-shore differences were found only for phosphate and silicate in winter, as opposed to strong and highly significant differences for all parameters in summer (Table 2).

Parameter	*Reef water*		*Offshore water*	
	Summer	*Winter*	*Summer*	*Winter*
Inorganic nitrogen	0.35 (0.09)	0.65 (0.08)	0.13 (0.03)	0.58 (0.05)
Phosphate	0.06 (0.01)	0.09 (0.01)	0.02 (0.01)	0.07 (0.01)
Silicate	1.05 (0.14)	1.78 (0.10)	0.7 (0.01)	1.43 (0.03)
Chlorophyll a	0.19 (0.02)	0.23 (0.03)	0.14 (0.02)	0.23 (0.02)

Table 1: Annual average of nutrients (μM) and chlorophyll a (μg L^{-1}) concentrations in the offshore and reef waters during summer and winter (n= 70 for summer and 28 for winter). The values between parentheses represent the standerd deviations.

Parameter	*Summer*		*Winter*	
	Mean difference	*P*	*Mean difference*	*P*
Inorganic nitrogen	0.22	< 0.0001	0.07	0.4761
Phosphate	0.04	< 0.0001	0.02	0.0057
Silicate	0.35	0.0015	0.35	0.0178
Chlorophyll a	0.05	0.0316	0.00	0.7394

Table 2: Mean differences of nutrient (μM) and chlorophyll a (μg L^{-1}) concentrations between the offshore and reef waters in summer and winter. P values obtained from ANOVA analysis at a significant level of 5% (When p < 0.05 the difference is significant).

Within the reef framework, nutrient concentrations were higher than in the free-stream waters (Fig. 3) in approximately 90% of the cases. Much higher nutrient concentrations were found in sediment pore waters compared to concentrations in the water above the sediment (factors of 21 to 80 in summer and 15 to 74 in winter: Fig. 4).

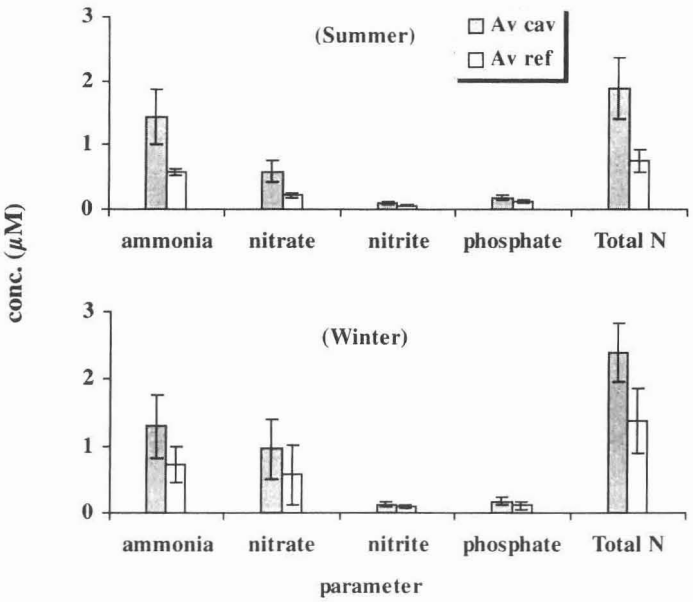
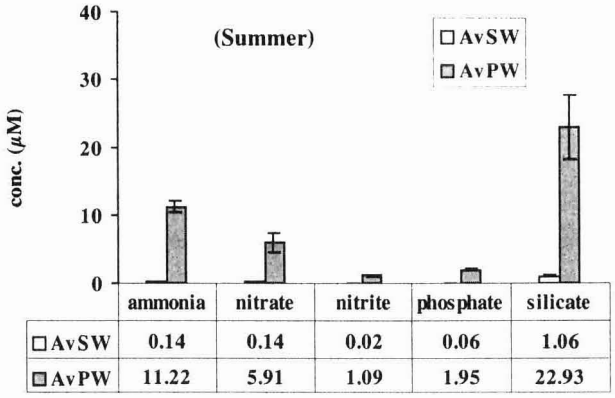
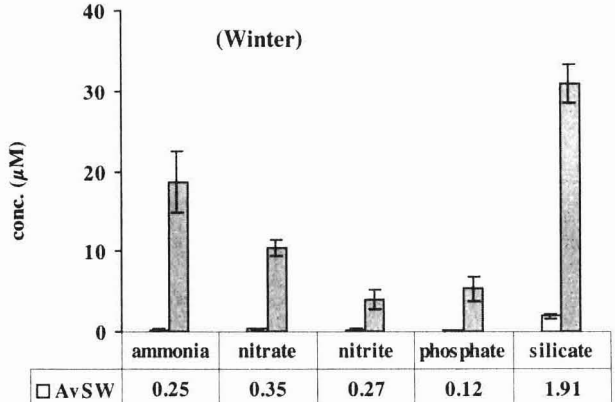


Fig. 3: Average nutrient concentrations (μM) in the framework of the coral reef (gray columns) and surrounding waters (white columns).



	ammonia	nitrate	nitrite	phosphate	silicate
AvSW	0.14	0.14	0.02	0.06	1.06
AvPW	11.22	5.91	1.09	1.95	22.93



	ammonia	nitrate	nitrite	phosphate	silicate
AvSW	0.25	0.35	0.27	0.12	1.91
AvPW	18.71	10.51	4.01	5.33	30.93

Fig. 4: Average of nutrient concentrations during the period July 99 to March 2000 in the pore water (Av PW) and sediment water interface (Av SW) of the coral reef.

Discussion

This study shows, for the first time, clear seasonal changes in nutrient and chlorophyll a in reef and offshore waters, as well as differences in these parameters between the two. Enhancement of nutrient concentrations in reef water was found particularly during summer. Higher nutrient concentrations were found in the sediment pore water and in the reef framework than in the surrounding water. This steep concentration gradient would result in fluxes of these nutrients to the surrounding water.

Seasonal pattern of nutrients in coral reef waters

According to Furnas et al. (1990), Hatcher and Hatcher (1981), and Ayukai (1993), it is difficult to detect seasonal variations in reef-water nutrient concentrations by sampling at 1 month or longer intervals because of the strong short-term variations in the reef waters. Our results demonstrate temporal and spatial changes in the nutrient concentrations in the coastal environment of the northern Gulf of Aqaba, whereas, no significant difference in current speed and direction between summer and winter were reported (Rasheed et al. unpubl. data). We have shown that the coral reef ecosystem in the Gulf of Aqaba is subjected to seasonal changes, with elevated concentrations of all measured nutrients in fall and winter. The main 2 reasons which could cause these seasonal changes are (1) deep-water column-mixing during winter increasing the nutrient concentrations in the coastal waters and boosting phytoplankton growth (Venrick et al. 1973, Souvermezoglou et al. 1989, Lindell and Post 1995), and (2) water-column stratification and increased light intensities during summer which result in a depletion of the inorganic nutrients by enhanced primary production (Olson 1981, Souvermezoglou et al. 1989).

Comparison between nutrient and chlorophyll a values in reef and offshore waters

In our study we found spatial differences in nutrient concentrations between reef water and offshore water adjacent to the reef. During the summer months, when the offshore water was nutrient-depleted, concentrations of nutrients and chlorophyll a in the reef water were higher than in the offshore water. During winter, strong vertical mixing reduced the differences in nutrient and chlorophyll a concentrations between reef and offshore waters. Vertical mixing moved deep water, rich in nutrients, up into the water

column (Venrick et al. 1973, Klinker et al. 1978, Levanon-Spanier et al. 1979, Robert and Olson 1981, Al-Najjar 2000) while diffusion caused nutrient equilibration between reef and offshore waters. Nitrogen enrichment of coral reef waters has been reported by several authors (Meyer and Shultz 1985, Blanchot et al. 1989, Tribble et al. 1990, Bell 1991), and the reef in the Gulf of Aqaba showed similar trends (Badran and Foster 1998). Enhanced primary productivity during winter months in the Gulf of Aqaba was recorded by Levanon-Spanier et al. (1979).

Possible reasons for higher nutrient concentrations in the reef waters

Increased nutrient concentrations in reef waters can be originate from anthropogenic sources such as nutrient-rich groundwater input (d'Elia et al. 1981, Lewis 1985), sewage discharge (Johannes 1975) and terrestrial runoff (Marsh 1977). However, these sources are negligible in our study area because the reef is an environmentally protected zone and there is no groundwater input (no salinity change was recorded in the study area) and very little rainfall throughout the year. The higher silicate concentrations could be attributable partly to an influx of atmospheric silicate-rich desert dust (Alfuqaha unpubl. data). We suggest that the higher nutrient concentrations in the reef are caused by the efficient trapping and decomposition of suspended particles by the reef framework, coral sands and reef biota, as well as nitrogen fixation by organisms living in the reef environment.

Framework

Our study has shown that the concentrations of nutrients in the framework water were higher than those in the free flowing water (Fig. 3), which would cause nutrient fluxes from the framework to the surrounding water. The average fluxes in summer and winter from the framework reached approximately 14.5 mmol m^{-2} d^{-1} for ammonia, 7.7 mmol m^{-2} d^{-1} for nitrate, 0.9 mmol m^{-2} d^{-1} for nitrite, and 1.3 mmol m^{-2} d^{-1} for phosphate. These fluxes have added more nutrients to the reef water, particularly during summer when the concentrations were low (Fig. 2). Three mechanisms may be responsible for the higher nutrient concentrations in the framework: (1) decomposition of organic matter enclosed in the framework carbonates that had been overgrown by corals (e.g. coral tissue, boring organisms, coralline algae), (2) suspended particulate matter, including small phytoplankton and bacteria that are efficiently trapped by the abundant suspension

feeders living within the reef framework (Gast et al. 1998, Richter and Wunsch 1999, Richter et al. 2001), and (3) remineralization of faeces from migrating invertebrates and fishes, which forage on and above the reef and use cavities as a temporary shelter (Bray et al. 1981, Meyer et al. 1983). Similar findings were reported by Ferrer and Szmant (1988), who measured increased nutrient concentrations in the cavities of the reef of Beliza Barrier and Kaneohe Bay Reef respectively, and a net flux of nutrients from the reef framework to the surrounding water. These findings indicate that the reef framework is an important site for organic matter mineralization in the reef (Andrews and Muller 1983, Szmant-Froelich 1983, Sansone 1985, Buddemeier and Oberdorfer 1986, Tribble et al. 1986, 1988) and suggest that the framework may act as a temporal nutrient source in the reef environment.

Coral sands

We measured increased nutrient concentrations in the pore water of the sediment relative to the overlying water during summer and winter (Fig. 4). This steep concentration gradient would result in a net flux of nutrients from the pore water to the overlying water (Fig. 5). Fluxes of ammonia, nitrite, nitrate and phosphate increased during the winter months (December to March: Fig. 5). The average fluxes over the whole year were 0.06 mmol m^{-2} d^{-1} for ammonia, 0.03 mmol m^{-2} d^{-1} for nitrate, 0.01 mmol m^{-2} d^{-1} for nitrite, 0.01 mmol m^{-2} d^{-1} for phosphate, and 0.07 mmol m^{-2} d^{-1} for silicate. However, the calculated fluxes only represent the diffusive fluxes from the sediment, as the calculation we used (Fick's law of diffusion) does not include fluxes caused by bioturbation and advective pore-water exchange (Clavero et al. 2000). Laboratory core incubation resulted in silicate fluxes which exceeded the calculated silicate flux by a factor of 20 (Rasheed et al. unpubl. data) suggesting that both bioturbation and advective pore-water exchange probably added to the flux.

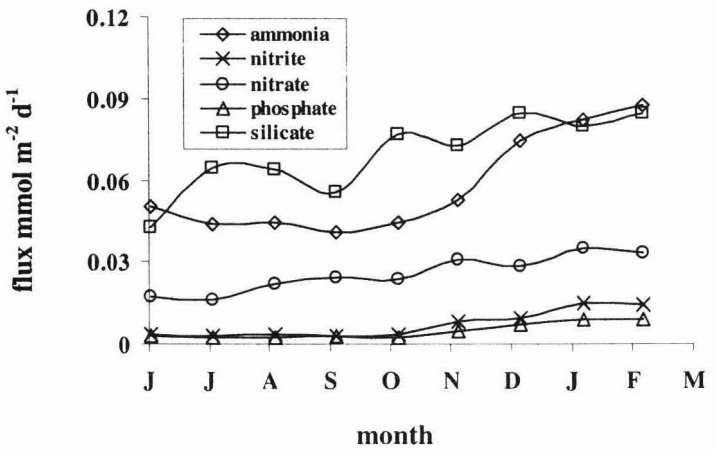


Fig. 5: Calculated nutrient fluxes from the sediment to the water column during the period July 99 to March 2000.

This indicates that the coarse-grained carbonate reef sediments may act as a biocatalytic converter (Rasheed et al. unpubl. data), similar to the porous framework. We suggest that organic matter filtered from the water column when bottom currents interact with the permeable sediment (Huettel et al. 1996, Huettel and Rusch 2000) is decomposed in the sedimentary microbial food chain. The products of the mineralization, the nutrients, are then released into the pore water and overlying water column. Increased nutrient concentrations in the pore water of reef sediments were also reported by Capone et al. (1992) for the Great Barrier Reef, Szmant and Forrester (1996) for the Florida Coral Reef, and Ciceri et al. (1999) for the northern lagoon of Venice. Nutrient release from reef pore waters to the water column was reported by several authors (e.g. Fuentes and Espino 1990, Bertuzzi et al. 1996, Charpy-Roubaud et al. 1996, and Ciceri et al. 1999). The flux of ammonium in our study (0.06 mmol m^{-2} d^{-1}) was lower than the fluxes reported by Charpy-Rouband et al. (0.16 mmol m^{-2} d^{-1}) and Bertuzzi et al. (0.3 mmol m^{-2} d^{-1}). However, phosphate flux in our study was higher compared to the previous 2 studies (0.010, 0.004, and 0.001 respectively). The differences in the flux values resulted from different nutrient concentrations in the water column and in the pore water, which might be attributable to the differences in the organic matter loading and different chemical and

physical properties of the study areas (Shum and Sundby 1996, Hulthe et al. 1998). Charpy-Roubaud et al. (1996) found that aerobic bacteria that live in coral sediment could mineralize organic compounds to mineral end-products. In most tropical shallow marine environments like the Gulf of Aqaba, the highest metabolic activity is associated with the benthos (Zieman 1982, d'Elia and Wiebe 1990).

Reef biota

Corals, mollusks, polychaetes, echinoderms and a variety of other reef-dwelling organisms can efficiently filter and digest organic particles from water in the reef and thereby also increase the concentration of nutrients in the reef water relative to the offshore water (Hatcher and Hatcher 1981, Andrews and Muller 1983, Tribble et al. 1988, Larned 1998).

Nitrogen fixation

Nitrogen fixation in the different habitats within the reef has been reported in several studies (e.g. Wiebe et al. 1975, Goldner 1980, Wilkinson et al. 1984). According to Crossland and Barnes (1976), corals themselves do not have the ability to fix nitrogen, but endolithic organisms in the coral skeleton do. Shashar et al. (1994) reported a fixation rate of 0.6 to 1.0 mmol N_2 m^{-2} d^{-1} in the Gulf of Aqaba and reported that 70% of the fixation occurred in the sand-covered lagoon.

Our study has shown seasonal changes in the nutrient concentrations in the reef and a nutrient gradient between reef water and offshore water during summer. In winter, high nutrient concentrations in the coastal zone in the Gulf of Aqaba caused by enhanced water-column mixing remove this gradient. In summer, particle trapping and biocatalytic conversion of dissolved and particulate material in framework and reef sands increase the nutrient concentrations in the reef water relative to the offshore water. This nutrient availability during summer permits a higher primary productivity in the reef environment during this period in comparison to the offshore water, as indicated by the chlorophyll a data. We conclude that the decomposition activity and buffer capacity of the coral sands and reef framework play an important role in the support of primary productivity in the coral reef ecosystem during phases of nutrient depletion in the water column. During the fall and winter months, sands and framework accumulate nutrients (due to sorption and binding processes) and particulate organic matter. This organic matter is decomposed in

the pore space of the sand and reef framework, and the resulting nutrients may be gradually released during the summer months.

Acknowledgements

This work forms part of the Red Sea Program and has been funded by the German Federal Ministry of Education and Research (BMBF grant no. 03F0245A). Thanks are due to the director and the staff members of the Marine Science Station for their support during this study. Thanks are also due to Khalid Al-Tarabeen for his assistance in the laboratory and to Tariq Al-Salman, Riyad Manasreh, Saber Al-Rousan, Britta Munkes, Iris Kötter and Mark Wunsch for their help in the field.

References

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

Al-Najjar T (2000) The seasonal dynamics and grazing control of phyto- and mesozooplankton in the northern Gulf of Aqaba. Ph D thesis, Bremen University

Arar EJ, Collins GB (1992) In vitro Determination of chlorophyll a and pheophytin a in marine and freshwater phytoplankton by fluorescence. Environmental Monitoring System Laboratory Office of Research and Development. US Environmental Protection Agencey, Cincinnati, OH

Andrews JC, Müller HR (1983) Space-time variability of nutrients in a lagoonal patch reef. Limnol Oceanogr 28:215-227

Arenas FV, de la Lanz EG (1983) Annual phosphorus budget of a coastal lagoon in the northwest of Mexico. Ecol Bull 35:431-440

Atkinson MJ, Carlson B, Crow GL (1995) Coral growth in high-nutrient, low-pH seawater: a case study of corals cultured at the Waikiki Aquarium, Hawaii. Coral Reefs 14:215-223

Ayukai T (1993) Temporal variability of the nutrient environment on Davies Reef in the Central Great Barrier Reef, Australia. Pac Sci 47 :171-179

Badran MI, Foster P (1998) Environmental quality of the Jordanian coastal waters of the Gulf of Aqaba, Red Sea. Aquat Ecosyst Health Manag 1:75-89

Beekman JW (1990) Mathmatical description of heterogeneous materials. Chem Eng Sci 45:2603-2610

Bell PRF (1991) Status of eutrophication in the Great Barrier Reef lagoon. Mar Pollut bull 23:89-93

Bertuzzi A, Faganeli J, Brambati A (1996) Annual variation of benthic nutrient fluxes in shallow coastal waters (Gulf of Trieste, Northern Adriatic Sea). PSZN I: Mar Ecol 17:261-278

Blanchot J, Charpy L, Le Borgne R (1989) Size composition of particulate organic matter in the lagoon of Tikehau atoll (Tuamotu archipelago). Mar Biol 102:329-339

Bray RN, Miller AC, Geesey GG (1981) The fish connection: a trophic link between planktonic and rocky reef communities? Science 214:204-205

Buddemeier RW, Oberdorfer JA (1986) Internal hydrology and geochemistry of coral reefs and atoll islands: key to diagenetic variations. In: Schroeder JH, Purser BH (eds) Reef diagenesis. Springer, Berlin, Heidelberg, New York, p 91-111

Callender E, Hammond DE (1982) Nutrient exchange across the sediment-water interface in the Potomac River estuary. Est Coast Shelf Sci 15:395-413

Capone DG, Dunham SE, Horrigan SG Duguay LE (1992) Microbial nitrogen transformations in unconsolidated coral reef sediments. Mar Ecol Prog Ser 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). Mar Ecol Prog Ser 132:181-190

Ciceri G, Ceradina S, Zitelli A (1999) Nutrient benthic fluxes and pore water profiles in a shallow brackish marsh of the lagoon of Venice. Annali di Chimica 89:359-375

Clavero V, Izquierdo JJ, Fernandez JA, Niell FX (2000) Seasonal fluxes of phosphate and ammonium across the sediment-water interface in a shallow small estuary (Palmones River, southern Spain). Mar Ecol Prog Ser 198:51-60

Crossland CJ, Barnes DJ (1976) Acetylene reduction by coral skeleton. Limnol Oceanogr 21:153-156

d'Elia CF, Wiebe WJ (1990) Biogeochemical nutrient cycles in coral reef ecosystems. Reprinted from: Dubinsky Z (ed) Ecosytem of the World. Coral reefs. Elsevier Science Publishers, Amsterdam, Netherlands, p 49-74

d'Elia CF, Webb KL, Porter JW (1981) Nitrate-rich groundwater input to Discovery Bay, Jamaica: a significant source of N to local coral reefs? Bull Mar Sci 31:903-910

Engvall AG (1978) The fate of nitrogen in early diagenesis of Baltic sediment. A study of the sediment-water interface. Contributions in Microbial Geochemistry, Dep Of Geology, Univ of Stockholm (2):103

Entsch B, Boto KG, Sim RG, Wellington JT (1983) Phosphorus and nitrogen in coral reef sediment. Limnol Oceanogr 28:465-476

Ferrer LM, Szmant AM (1988) Nutrient regeneration by the endolithic community in coral skeletons. Proc 6th Int Coral Reef Symp 3:1-4

Fuentes VA de le G, Espino L (1990) Metabolism as determinant of nutrient exchange in organic-rich sediments of a coastal lagoon. Cienc Mar 16:45-62

Furnas MJ (1992) The behaviour of nutrients in tropical aquatic ecosystems. In: Connell DW, Hawker DW (eds) Land use patterns and nutrient loadings of the Great Barrier Reef Region. James Cook University, Townsville, p 162-179

Furnas MJ, Mitchell AW, Gilmartin M, Revelante N (1990) Phytoplankton biomass and primary production in semi-enclosed reef lagoons of the central Great Barrier Reef, Australia. Coral Reefs 9:1-10

Furnas MJ, Mitchell AW, Skuza M (1993) Nitrogen and phosphorus budgets for the Great Barrier Reef Marine Park Authority, Aust Inst Mar Sci, Townville

Gast GJ, Wiegmann S, Wieringa E, van Duyl FC, Bak RPM (1998) Bacteria in coral reef water types: removal of cells, stimulation of growth and mineralization. Mar Ecol Prog Ser 167:37-45

Ginsberg RN (1983) Geological and biological roles of cavities in coral reefs. In: Barnes DJ (ed) Perspectives on coral reefs. Australian Institute of Marine Science, Townsville, p 148-153

Goldner LL (1980) Nitrogen fixation (acetylene reduction) in shallow water Bahamian environments. Bull Mar Sci 30:444-453

Hallock P, Muller FE, Halas JC (1993) Coral reef decline. Natl Geogr Res Explor 9:358-378

Hatcher RAI, Hatcher BG (1981) Seasonal and spatial variation in dissolved inorganic nitrogen in One Tree Reef lagoon. Proc 4th Int Coral Reef Symp 1:419-424

Hesselein RH (1976) An in situ sampler for close internal pore water studies. Limnol Oceanogr 21:912-924

Holm NG (1978) Phosphorus exchange through the sediment-water interface. Mechanism studies of dynamic processes in the Baltic Sea. Contrib Microb Geochem, Dep Geol, Univ Stockh 3:149

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

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

Hulthe G, Hulth S, Hall POJ (1998) Effect of oxygen on degradation rate of refractory and labile organic matter in continental margin sediments. Geochim Cosmochim Acta 62(8):1319-1328

Johannes RE (1975) Pollution and degredation of coral reef communities. Elsevier Oceanogr Ser 12:13-15

Kinsey DW (1977) Seasonality and zonation in coral reef productivity and calcification. Proc 3rd Int Coral Reef Symp 2:383-388

Klinker J, Reiss Z, Kropach C, Levanon I, Harpaz H, Shapiro Y (1978). Nutrients and biomas distribution in the Gulf of Aqaba (Elat), Red Sea. Mar Biol 45:53-64

Kobluk DR, van Soest RWM (1989) Cavity-dwelling sponges in a southern Caribbean coral reef and their paleontological implications. Bull Mar Sci 44:1207-1235

Larned ST (1998) Nitrogen- versus phosphorus-limited growth and sources of nutrients for coral reef macroalgae. Mar Biol 132:409-421

Lerman A (1979) Geochemical Processes, water and Sediment Environment. John Wiley and Sons, NY

Levanon-Spanier I, Padan E, Reisis Z (1979) Primary production in a desert-enclosed sea-the Gulf of Elat (Aqaba), Red Sea. Deep-Sea Res 26:673-6855

Lewis JB (1985) Groundwater discharge onto coral reefs, Barbados (West Indies). Proc 5th Int Coral Reef Symp 6:477-481

Li YH, Gregory S (1974) Diffusion of ions in sea water and in deep sea sediment. Geochim Cosmochim Acta 38:703-714

Lindell D, Post AF (1995) Ultraphytoplankton succession is triggered by deep winter mixing in the Gulf of Aqaba (Eilat), Red Sea. Limnol Oceanogr 40:1130-1141

Marsh JA (1977) Terrestrial inputs of nitrogen and phosphorus on fringing reefs of Guam. Proc 3rd Int Coral Reef Symp 1:331-336

Meyer JL, Schultz ET (1985) Tissue condition and growth rate of corals associated with schooling fish. Limnol Oceanogr 30:157-166

Meyer JL, Schultz ET, Helfman GS (1983) Fish schools: an asset to corals. Science 220:1047-1049

Nixon SW, Pilson MEQ (1983) Nitrogen in estuarine and coastal marine ecosystems. In: Carpenter ED, Carpenter DG (eds) Nitrogen in the Marine Environment. Academic Press, New York, p 565-648

Olson RJ (1981) Differential photoinhibitation of marine nitrifying bacteria: a possible mechanism for the formation of the primary nitrite maximum. J Mar Res 39:227-238

Richter C, Wunsch M (1999) Cavity-dwelling suspension feeders in coral reefs-a new link in reef trophodynamics. Mar Ecol Prog Ser 188:105-116

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

Risk MJ, Müller HR (1983) Pore water in coral heads: evidence for nutrient regeneration. Limnol Oceanogr 28:1004-1008

Robert J, Olson (1981) Differential photoinhibition of marine nitrifying bacteria: a possible mechanism for the formation of the primary nitrite maximum. J Mar Res 39:227-238

Sansone FJ (1985) Methane in the reef flat pore-waters of Davies Reef, Great Barrier Reef (Australia). Proc 5th Int Coral reef Cong 3:415-419

Schuhmacher H , Mergner H (1985) Quantitative Analyse von Korallengemeinschaften des Sanganeb-Atolls (mittleres Rotes Meer). 2. Vergleich mit einem Riffareal bei Aqaba (nördliches Rotes Meer) am Nordrande des indopazifischen Riffgürtels. Helgol Meeresunters 39:419-440

Shashar N, Feldstein T, Cohen Y, Loya Y (1994) Nitrogen fixation (acetylene reduction) on a coral reef. Coral Reefs 13:171-174

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

Smith SV, Kimmerer WJ, Laws EA, Brock RE, Walsh TW (1981) Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. Pac Sci 35:279-402

Sorokin YI (1993) Coral reef ecology. Springer-Verlag, Berlin

Souvermezoglou E, Metzl N, Poisson A (1989) Red Sea budgets of salinity, nutrients and carbon calculated in the Strait of Bab-El-Mandab during the summer and winter seasons. J Mar Res 47:441-456

Strickland JDH, Parsons TR (1972) A practical handbook of seawater analysis, 2nd edn. Bull Fish Res Board Can 167:310

Szmant-Froelich A (1983) Functional aspects of nutrient cycling in coral reefs. NOAA Symp Ser Undersea Res 1:133-139

Szmant AM, Forrester A (1996) Water column sediment nitrogen and phosphorus distribution patterns in the Florida Key, USA. Coral Reefs 15:21-41

Torrance DC (1991) Deep ecology: rescuing Florida's reef. Nat Conserv July-Aug:9-17

Tribble GW, Sansone FJ, Andrews CC, Smith SV (1986) Organic geochemistry of reef interstitial water. EOS 67:997

Tribble GW, Sansone FJ, Li YH, Smith SV, Buddemeier RW (1988) Material fluxes from a reef framework. Proc 6th Int Coral Reef Symp 2:577-582

Tribble GW, Sansone FJ, Smith SV (1990) Stoichiometric modeling of carbon diagenesis within a coral reef framework. Geochim Cosmochim Acta 54:2439-2449

Venrick El, McGowan JA, Mantyla AW (1973) Deep maximua of photosynthetic chlorophyll *a* in the Pacific Ocean. Fish Bull 71:41-52

Ward F (1990) Florida's coral reefs are imperiled. Natl Geogr 178:114-132

Wells SM (1988) Coral reefs of the world. Vol 2. Indian Oceans, Red Sea and Gulf. The IUCN Conservation Monitoring Center, Cambridge, UK

Wiebe WJ, Johannes RE, Webb KL (1975) Nitrogen fixation in a coral reef community. Science 188:257-259

Wilkinson CR,Williams DMcB, Sammarco PW, Hogg RW, Trott LA (1984) Rates of nitrogen fixation on coral reefs across the continental shelf of the central Great Barrier Reef. Mar Biol 80:255-262

Williams SL (1984) Uptake of sediment ammonium and translocation in the marine green alga *Caulerpa cupressoides*. Limnol Oceanogr 29:374-379

Williams SL, Gill IP, Yarish SM (1985) Nitrogen cycle in back reef sediments. Proc 5th Int Coral Reef Symp 3:389-394

Zieman JC (1982) The ecology of the seagrasses of South Florida: A community profile. US Fish Wildl Serv FWS/OBS-82/25 123

Chapter 3

Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges

Claudio Richter [1], Mark Wunsch [1], Mohammed Rasheed [2,3], Iris Kötter [1], Mohammed Badran[2],

[1] Zentrum für Marine Tropenökologie, Bremen, Germany

[2] Marine Science Station, University of Jordan and Yarmouk University, Aqaba Jordan

[3] Max Plank Institute for Marine Microbiology, Bremen University, 28359 Bremen, Germany

This chapter has been published in Nature

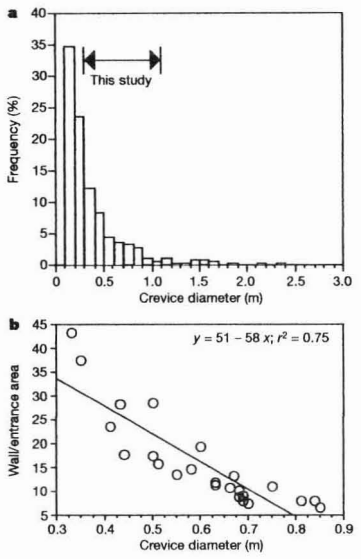


Figure 2 Physical dimensions of coral reef crevices. **a**, Length–frequency histograms of crevice opening diameters, showing the size range amenable to the endoscopic methods used in this study. Earlier studies by divers were limited to cavities with opening diameters much greater than 1 m, comprising less than 1% of the total number of crevices and much less than 1% of the total cavity area. **b**, Surface increase (ratio of crevice wall area to entrance area) as a function of cavity size, highlighting the importance of small crevices as living habitats in the coral reef framework.

as the dominance of delicate sheet-like growth forms (Fig. 3d), support the assumption that the distribution and abundance patterns of coral reef sponges are controlled by predators[12,13]. Less than 1% of the total area covered by sponges was due to erect or massive morphotypes, and less than 2% was due to boring taxa. Other filter-feeders (ascidians, bivalves, bryozoans and polychaetes) occurred regularly but at much lower densities, covering generally less than 5% of the substrate.

Qualitative wide-angle overviews with the CaveCam mounted on a flexible rod confirmed the pattern of well-flushed and densely populated crevices up to the 4 m reaches of the instrument. With a projected cover of 82 ± 55% per unit area of coral reef, coelobite sponges outweighed by far epibenthic sponges (0.2–1.2% cover[8–10]). Using an area : biomass conversion of 25.6 mg C per 10-cm^2 sponge, determined on small fragments of fresh reference material ($r^2 = 0.59$, $n = 25$), this translates into a coelobite sponge biomass of 21.1 ± 14.2 g C per m^2 coral reef (median ± MAD (median absolute deviation)).

Intense filtering by the coelobite community resulted in marked depletions of phytoplankton chlorophyll *a* (Chl*a*) towards the inner reaches of the crevices (64 ± 8% of the freestream waters; Fig. 4b; see Methods), alongside marked decreases in the ratio of Chl*a* to its degradation product phaeopigment (Fig. 4c). These findings are consistent with earlier measurements of bacteria and naked cell depletion in artificial cavities from the Caribbean[2]. Community respiration led to small but significant reductions in oxygen levels relative to freestream waters (5 ± 2%, Fig. 4d; Kruskal–Wallis test, $P < 0.0001$), reflecting the net heterotrophic nature of the cavity habitat.

Current speeds, determined by video-tracking of displaced particles and by dissolution of calibrated plaster cubes spaced over the length of the crevice, averaged between 0.9 and 5.5 cm s^{-1}. Wash-out experiments with fluorescent dyes featured half-life periods of only 75 ± 15 s, suggesting complete flushing of cavity waters within a few minutes.

Dye experiments showed that water flow through framework crevices was driven by flow speed differences across the bumpy reef surface, much like pressure-induced air flow through termite mounds, where the intake openings are located in troughs near the base and the exhaust openings in exposed position near the crest[14]. As a result, water flow was almost always directed into the crevices, leaving the framework through countless cracks and holes near the elevated parts of the reef.

The largely unidirectional flow pattern allowed us to determine the bulk filtering rate of the coelobite community using the standard flow respirometric approach[15]. Flux was calculated from the measured changes in Chl*a* and the rate of water exchange across a unit volume of cavernicolous reef, according to

$$F = \Delta\text{Chl}a \times rpk \quad (1)$$

where F is the amount of phytoplankton carbon filtered per unit volume of cavernicolous reef (g C per m^3 reef d^{-1}, or g C per m^2 reef d^{-1} normalized, for conservancy, to the upper first metre of framework); ΔChl*a* is the mean concentration difference between upstream and cavity waters (0.16 ± 0.01 mg Chl*a* per m^3 water; Table 2); r is a conservative value for the water exchange rate in the crevices (the inverse of the water residence time, as determined by fluorescent tracer experiments; 300 per day); p is a conservative value for the volume fraction of crevices per unit framework (0.3 m^3 water per m^3 reef; Table 1) and k is a carbon : Chl*a* conversion factor of 60 g C per g Chl*a* (ref. 10).

Table 2 Differences in chlorophyll *a*, phytoplankton biomass, total picoplankton and nutrient concentrations between cavity and freestream waters above the reef

	Measured					
	ΔChl*a* (μg l^{-1})	ΔNH_4^+ (μM)	ΔNO_2 (μM)	ΔNO_3 (μM)	ΔTIN (μM)	ΔPO_4^{3-} (μM)
Mean	−0.164	0.312	0.037	0.395	0.744	0.048
s.e.	0.014	0.097	0.003	0.043	0.116	0.008
n	32	64	64	64	64	64
P	<0.0001	0.1034	<0.0001	<0.0001	<0.0001	<0.0001
	Calculated					
	Phytoplankton (μg C l^{-1})	Picoplankton (μg C l^{-1})	New TIN (μM)	New PO_4^{3-} (μM)	New TIN (% of measured change)	New PO_4^{3-}
Mean	−9.84	−19.68	0.248	0.015	33.3	32.2

Picoplankton-derived new nutrients were calculated, assuming a conservative 1:1 biomass ratio between phytoplankton and other picoplankton (such as bacteria)[16] and stoichiometric conversion according to the Redfield ratio. Positive values denote enrichment, negative values denote depletion, relative to the freestream reference 2 m away from the reef. TIN, total inorganic nitrogen.

letters to nature

Phytoplankton uptake by the coelobite community amounted to $0.89 \pm 0.05\,g\,C\,m^{-2}\,d^{-1}$, equivalent to 22% of the gross community metabolism of the entire reef[15]. Total picoplankton removal, as suggested by the available biomass of bacteria in tropical waters[16], is probably more than twice this value, ranking our findings among the highest rates reported so far for marine and freshwater sponge communities[17,18]. This is corroborated by combining our biomass data ($21.1\,g\,sponge\,C\,m^{-2}$) with reported food rations in benthic filter-feeders (2–10% body $C\,d^{-1}$; ref. 16), which yields similar values ($0.4–2.1\,g\,C\,m^{-2}\,d^{-1}$).

Owing to the long doubling times of phytoplankton and bacteria (6–24 h; ref. 19) relative to the residence time of water over the narrow shelf (1–5 h; refs 5, 10), most of the picoplankton consumed in the reef originates from offshore, thus constituting a source of new material for the reef ecosystem.

Nutrient enrichments in the cavities suggest intense mineralization of the organic matter by the crevice biota (Table 2). Nutrient ratios near the Redfield ratio (N:P = 15.5; Table 2) reflect the

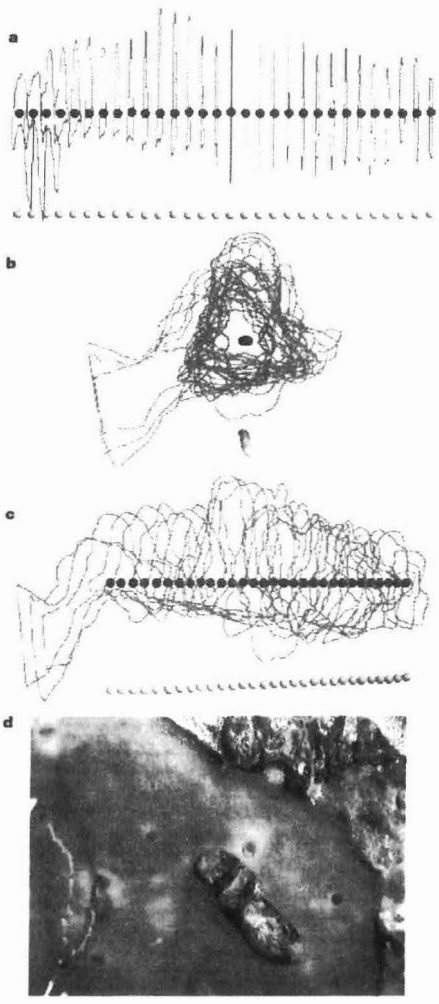


Figure 3 Endoscopic techniques for the study of crevice dimensions and coelobite communities. Wire-frame model of a framework crevice (Ras Mohammed, Egypt, 20 m depth) viewed from the side (**a**), front (**b**) and a 45° angle (**c**). Green circles, spaced 5 cm apart, mark reflection of a light sheet on crevice wall; yellow symbols mark the plumb line. **d**, Video close-up of coelobite community, including the beige sponge *Chondrilla sacciformis*, an unidentified yellow sponge (at right), solitary scleractinian polyps, the octocoral *Acabaria delicata* (below, left) and polychaete tubes (above, right). Position of the image in **d** is denoted by a square symbol in **a**–**c**.

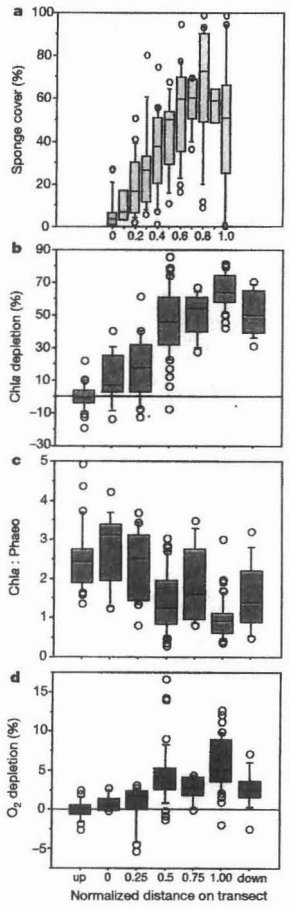


Figure 4 Small-scale distribution of coelobite sponges (**a**), Chl*a* (**b**), Chl*a*:phaeopigments (**c**) and oxygen (**d**) in Red Sea coral reef framework crevices, shown as composites of 25 (**a**) and 15 (**b**–**d**) surveys conducted within the study area (Fig. 1). Boxes and whiskers encompass 50% and 95% of the data, respectively; centre lines denote the median. In **a**, per cent cover is relative to total coelobite living area ($2.8 \pm 0.9\,m^2$ per projected m^2 reef). In **b**, **d**, depletions are relative to freestream waters (up) about 2 m above the reef. Downstream exits (down) of tunnel crevices show mixing with freestream waters.

planktonic source of the mineralized material[16], contrasting the higher values reported for intrinsic reef material, for example in lagoonal patch reefs (N:P = 20; ref. 20), pore waters (N:P = 21; ref. 21) or benthic producers (N:P = 30; ref. 22). Stoichiometric conversion of picoplanktonic organic matter to inorganic nutrients (assuming 100% of the ingested food is respired) shows that allochthonous N and P may contribute one-third of the total nutrient flux emanating from the cavities (Table 2), in readily assimilable form (such as ammonia, 42% of N; Table 2) for corals and algae[16].

On the basis of the measured concentration differences and flushing rates, we estimate that 22.3 and 1.4 mmol $m^{-2} d^{-1}$ of allochthonous N and P, respectively, are channelled into the coral reef system by coelobite filter-feeders, which exceeds the known import pathways through cross-shore advection of dissolved nutrients (1.9 and 0.3 mmol $m^{-2} d^{-1}$, respectively[23]), nitrogen fixation (0.6–1.0 mmol N $m^{-2} d^{-1}$; ref. 24) or migrating fish (2.4–7.2 mmol N $m^{-2} d^{-1}$; ref. 25).

The accrual of picoplankton by coelobite sponges and the associated enrichment of crevice waters with offshore nutrients may be a widespread phenomenon, as suggested by the occurrence of phyto- and bacterioplankton depletions near coral reefs throughout the tropics[4,5,10,26,27]. Our findings may therefore provide a general answer to Darwin's question[28] of how coral reefs manage to thrive in oligotrophic waters. □

Methods

Crevice numbers and sizes

We performed dive surveys to determine the total number and size distribution of crevices riddling the coral reef framework in Aqaba and Ras Mohammed (Fig. 1). Measuring tapes (50 m) were laid out at random, parallel to the 3-, 10-, 12- and 20-m depth lines (Table 1). Numbers and lengths of crevices intercepting the tape were recorded to the nearest 0.1 m.

Crevice morphology and dimensions

An endoscopic video system was used to assess the cross-sectional and wall area of 25 framework crevices in Aqaba, Eilat and Ras Mohammed (Fig. 1), at depths of 2–5 m (n = 9), 12–14 m (n = 8) and 19–20 m (n = 8). The system consisted of two parts: a camera head fitted with a 3-mm wide-angle lens, connected by a 3.8-m cable to its control (Panasonic KS-162) and video recording unit (Sony TRV-91E)[6]; and a modified 50-W halogen light mounted 60 cm in front of the lens, emitting a plane of light perpendicular to the axis of the camera. This configuration produced a highlighted contour at the intersection of the light sheet with the crevice wall. Moving the set-up in known increments (5 or 10 cm) on a rail along the axis of each crevice yielded a sequence of light rings outlining its shape in three dimensions (Fig. 3a–c). Video-images were digitized, and wall and cross-sectional areas were determined from the stack of scaled images for each crevice using Object-Image 1.62 software written by N. Vischer (ftp://simon.bio.uva.nl/pub). After correction of barrel distortion using Panorama Tools 1.7.2 by H. Dersch (http:// www.fh-furtwangen.de/~dersch), three dimensional wire-frame models of the crevices were obtained for visualization (Fig. 3a–c) using Rotater 3.5 by C. Kloeden (ftp://raru.adelaide.edu.au/ rotater/).

From the frontal aspect of a given framework crevice, it is obvious that the projected cross-section (Fig. 3b, white area around centre) is only a fraction of the cross-sectional area at the entrance. Given the limited air time underwater, it was not possible to customize the straight track of our system to the winding axis of each crevice, which limits the operational range of the quantitative surveys to 2.5 m. For consistency, the same margin was also applied to the quantitative investigation of the coelobite communities (below).

Coelobite cover

The CaveCam was used with a 7.5-mm close-up lens, 20-W headlights, a 45° mirror and spacers[4] to assess the corresponding community composition and living cover of coelobites. The walls of each of the 25 crevices were probed in 25-cm increments, taking sets of five 60×45-mm video frames of the sides, roof and bottom, respectively. The images were digitized and scaled, and the area covered by each taxon outlined manually with a digitizing pen for image analysis (NIH-Image; http://rsb.info.nih.gov/nih-image). Specimens were determined to the lowest taxonomic level possible and ground-truthed by taxonomic experts on the basis of reference material collected in the field.

Sponge biomass

Sponge material was obtained from small fragments of rock chiselled off the crevice walls. Tissue was scraped off the substrate using a dissecting knife. We obtained 25 samples of coelobite sponges ranging from 11 to 43 cm^2 in area cover for gravimetric determination of dry mass (24 h at 90 °C) and ash-free dry mass (AFDM; 5 h at 450 °C). Organic carbon was calculated using a C : AFDM conversion of 0.5 (ref. 16). Each specimen was photographed *in situ* before extraction to relate area cover (image analysis, above) to sponge biomass.

Currents and flushing

We determined water exchange through framework crevices by the dissolution over 24 h of plaster cards[29] spaced along the length of the crevices, and by short-term video-tracking of displaced particles using the CaveCam[6]. Additional dye experiments were carried out by injecting fluorescein into the centre of randomly selected cavities, halfway from the entrance, stirring, and measuring the decay of the fluorescence signal in syringe samples taken 0.5, 1, 2, 4, 8 and 16 min after initiation of the experiment. Regression of the log relative fluorescence versus time (seconds) yielded the relationship $y = 1.866 - 0.004t$ ($r^2 = 0.46$; $n = 240$).

Nutrients, oxygen and phytoplankton pigments

Triplicate samples for nutrient, oxygen and chlorophyll determinations were collected by an eight-channel peristaltic pump (Aqaba), which sampled simultaneously in crevice and freestream waters above the reef over a diel period alongside measurements of water exchange. Alternatively, samples were collected by divers (Fig. 1, other sites) drawing water through 100-μm screened silicone tubing into 100-ml polyethylene syringes. Intakes were spaced along the axis of crevices, and additional samples were collected from the downstream ends of tunnel cavities (Fig. 4, right). Cooled and shaded samples were processed within 2 h of collection. Oxygen was measured by Winkler titration[30], and Chla and phaeopigments by fluorometry using the acidification method[30] (100-ml sample, 25-mm Whatman GF/F filters, 24 h of dark 90% acetone extraction at 4 °C). Filtrate ammonia, nitrite, nitrate and phosphate were determined spectrophotometrically[30].

Received 13 March; accepted 21 August 2001.

1. Ginsburg, R. N. in *Perspectives on Coral Reefs* (ed. Barnes, D. J.) 148–153 (Australian Institute of Marine Science, Townsville, 1983).
2. Buss, L. W. & Jackson, J. B. C. Planktonic food availability and suspension-feeder abundance: evidence of *in situ* depletion. *J. Exp. Mar. Biol. Ecol.* **49,** 151–161 (1981).
3. Kobluk, D. R. Cryptic faunas in reefs: ecology and geologic importance. *Palaios* **3,** 379–390 (1988).
4. Gast, G. J., Wiegmann, S., Wieringa, E., van Duyl, F. C. & Bak, R. P. M. Bacteria in coral reef water types: removal of cells, stimulation of growth and mineralization. *Mar. Ecol. Prog. Ser.* **167,** 37–45 (1998).
5. Richter, C. & Wunsch, M. Cavity-dwelling suspension feeders in coral reefs - a new link in reef trophodynamics. *Mar. Ecol. Prog. Ser.* **188,** 105–116 (1999).
6. Wunsch, M. & Richter, C. The CaveCam—an endoscopic underwater videosystem for the exploration of cryptic habitats. *Mar. Ecol. Prog. Ser.* **169,** 277–282 (1998).
7. Jackson, J. B. C., Goreau, T. F. & Hartman, W. D. Recent brachiopod-coralline sponge communities and their paleoecological significance. *Science* **173,** 623–625 (1971).
8. Mergner, H. in *Proc. Symp. Coastal Marine Environ. Red Sea, Gulf of Aden and Tropical Western Indian Ocean* 39–76 (ALECSO Red Sea and Gulf of Aden Environmental Programme, Jeddah (Saudi Arabia), Khartoum, Sudan, 1980).
9. Mergner, H. & Schuhmacher, H. in *Proc. 5th Int. Coral Reef Symp.* Vol. 6 (eds Gabrie, C. & Harmelin-Vivien, M.) 243–248 (Antenne Mus., EPHE, Moorea, 1985).
10. Yahel, G. *et al.* Phytoplankton distribution and grazing near coral reefs. *Limnol. Oceanogr.* **43,** 551–563 (1998).
11. Erez, J. in *Coral Reefs* (ed. Dubinsky, Z.) 411–418 (Elsevier Science, New York, 1990).
12. Pawlik, J. R. Coral reef sponges: Do predatory fishes affect their distribution? *Limnol. Oceanogr.* **43,** 1396–1399 (1998).
13. Wulff, J. L. Parrotfish predation on cryptic sponges of Caribbean coral reefs. *Mar. Biol.* **129,** 41–52 (1997).
14. Vogel, S. *Life in Moving Fluids—the Physical Biology of Flow* 1–467 (Princeton Univ. Press, Princeton, 1994).
15. D'Elia, C. F. in *Concepts of Ecosystem Ecology* (eds Pomeroy, L. R. & Alberts, J. J.) 195–230 (Springer, New York, 1988).
16. Sorokin, Y. I. *Coral Reef Ecology* (Springer, Berlin, 1995).
17. Pile, A. J., Patterson, M. R., Savarese, M., Chernykh, V. I. & Fialkov, V. A. Trophic effects of sponge feeding within Lake Baikal's littoral zone. 2. Sponge abundance, diet, feeding efficiency, and carbon flux. *Limnol. Oceanogr.* **42,** 178–184 (1997).
18. Reiswig, H. M. Particle feeding in natural populations of three marine demosponges. *Biol. Bull.* **141,** 568–591 (1971).
19. Ferrier-Pagès, C. & Gattuso, J.-P. Biomass, production and grazing rates of pico- and nanoplankton in coral reef waters (Miyako Island, Japan). *Microb. Ecol.* **35,** 46–57 (1998).
20. Andrews, J. C. & Müller, H. Space–time variability of nutrients in a lagoonal patch reef. *Limnol. Oceanogr.* **28,** 215–227 (1983).
21. Tribble, G. W., Sansone, F. J., Li, Y.-H., Smith, S. V. & Buddemeier, R. W. in *Proc. 6th Int. Coral Reef Symp.* (eds Choat, J. H. *et al.*) 577–582 (Townsville, 1988).
22. Atkinson, M. J. & Smith, S. V. C:N:P ratios of benthic marine plants. *Limnol. Oceanogr.* **28,** 568–574 (1983).
23. Rougérie, F. Nature et fonctionnement des atolls des Tuamotu (Polynésie Française). *Oceanol. Acta* **18,** 61–78 (1995).
24. Shashar, N., Feldstein, T., Cohen, Y. & Loya, Y. Nitrogen fixation (acetylene reduction) on a coral reef. *Coral Reefs* **13,** 171–174 (1994).
25. Meyer, J. L., Schultz, E. T. & Helfman, G. S. Fish schools: an asset to corals. *Science* **220,** 1047–1049 (1983).
26. Ayukai, T. Retention of phytoplankton and planktonic microbes on coral reefs within the Great Barrier Reef, Australia. *Coral Reefs* **14,** 141–147 (1995).
27. Glynn, P. W. Ecology of a Caribbean coral reef, the *Porites* reef flat biotope. Part II. Plankton community with evidence for depletion. *Mar. Biol.* **22,** 1–22 (1973).

letters to nature

28. Darwin, C. *The Structure and Distribution of Coral Reefs* (Smith, Elder & Company, London, 1842).
29. Jokiel, P. L. & Morrissey, J. I. Water motion on coral reefs: evaluation of the 'clod card' technique. *Mar. Ecol. Prog. Ser.* **93,** 175–181 (1993).
30. Parsons, T. R., Maita, Y. & Lalli, C. M. *A Manual of Chemical and Biological Methods for Seawater Analysis* (Pergamon, Oxford, 1984).

Acknowledgements

We thank G. Hempel and the participants of the Red Sea Programme for support; the Egyptian, Israeli and Jordanian authorities for sampling permission; A. Abu-Hilal, the staff of the Aqaba Marine Science Station, G. Yahel, R. Yahel, B. Munkes and E. Saadalla for field and laboratory support; U. Diez, I. and J. Zainer for assistance; K. Fabricius, A. Genin, B. Lazar and G. Yahel for discussions; R. van Soest for sponge determinations; and V. Ittekkot and M. Huettel for improving the manuscript. This study was funded by the German Federal Ministry of Education and Research (BMBF).

Correspondence and requests for materials should be addressed to C.R. (e-mail: crichter@uni-bremen.de).

Chapter 4

Particulate Matter Filtration and Seasonal Nutrient Dynamics in Permeable Carbonate and Silicate Sands of the Gulf of Aqaba, Red Sea

Mohammed Rasheed [1,2], Mohammed Badran[2], Markus Huettel[1]

[1] Max Plank Institute for Marine Microbiology, Bremen University, 28359 Bremen, Germany

[2] Marine Science Station, University of Jordan and Yarmouk University, Aqaba Jordan

This chapter has been submitted to Coral Reefs

Particulate Matter Filtration and Seasonal Nutrient Dynamics in Permeable Carbonate and Silicate Sands of the Gulf of Aqaba, Red Sea

Summary

This study compares mineralization in permeable silicate and carbonate sands in the shallow shelf of the Gulf of Aqaba. From July-1999 to March-2000 we monitored concentrations of inorganic nutrients in water and pore water at two neighbouring sites, one of which was dominated by silicate, the other by carbonate sand. Although the carbonate was coarser than the quartz sand, organic matter, DIN and ortho-phosphate concentrations in the biogenic carbonate sediment always exceeded those in the terrigenic silicate sands (factor 1.5-2.0 for organic matter, 1.7-14.0 for nutrients). Higher nutrient concentrations in the water column during winter months caused increases in pore water nutrient concentrations in both sediments down to 10 cm depth with no significant delay, emphasising the effect of advective transport of solutes and particles into permeable sands. An experiment was conducted where sieved clean quartz and carbonate sands of same grain size (250-500 µm) were incubated in-situ. Although exposed to the same water and boundary current conditions, the sieved carbonate sand accumulated more organic matter and developed higher nutrient concentrations than the incubated silicate sediment. We conclude that the mineralogical characteristics of the carbonate sand (higher porosity, sorption capacity and pH buffer capacity) enhance the filtration capacity and the biocatalytic conversion efficiency relative to the smooth crystalline quartz grains.

Introduction

In the shallow shelf, the sediment is an important site for the mineralization of organic detritus (Charpy-Roubaud et al. 1989, Ciceri et al. 1999). The degradation process occurs mainly within the uppermost sediment layers, where bioturbation, advection and diffusion cause rapid exchange of solutes and particles with the overlying water (Jørgensen et al. 1990, Ziebis et al. 1996, Macintyre et al. 1996, Furukawa et al. 2000, Huettel and Rusch 2000). Transport rates, temperature and the physical and chemical characteristics of the sediment are the main factors that control the rates of biological and chemical transformation (Berner 1980).

Where coral reefs grow on terrigenous sediments, carbonate and silicate (quartz) sands can be found in close proximity. Silicate and carbonate sands do not only differ in their mineral composition but also in their surface structure, sorption and desorption characteristics and dissolution kinetics (Schroeder and Purser 1986). Carbonate sediments are amongst the most abundant reactive minerals near the earth surface and they dissolve at faster rate than the rate for silicate mineral dissolution (Banfield and Nealson 1998). CO_2, HCO_3 produced during the sedimentary organic matter decomposition affects the dissolution and precipitation reactions of the carbonate grains.

Pore water nutrient profiles provide hints on the mineralization intensity and decomposition pathways in the sediment (Froelich et al. 1979, Emerson et al. 1980, Corredor and Morell 1985, Santschi et al. 1990, Mortimer et al. 1998, Tuominen et al. 1999), and the transport processes and interfacial solute fluxes (Corredor and Capone 1985, Hansen and Kristensen 1997, Burdige and Zheng 1998). In medium to coarse sands, such as the silicate and carbonate sediments that occur in the coastal zones of the Gulf of Aqaba, pore water flows can transport substances into and out of the bed, thereby affecting the sedimentary biogeochemical transformations of matter (Huettel and Gust 1992, Huettel et al. 1996). Elevated nutrient concentrations reported in the pore water of highly permeable carbonate sediments (Sansone 1985, Buddemeier and Oberdorfer 1986, Sansone et al. 1988, Sansone et al. 1993) indicate efficient filtration of particulate organic matter. Due to the rapid fluid exchange between sediment and overlying water, seasonal changes of the chemical properties of the water column may be transmitted effectively to the pore water and affect the diagenetic processes (Bertuzzi et al. 1996, Ciceri et al. 1999).

In order to elucidate the influence of the mineral sediment matrix on the sedimentary decomposition process, we compare sedimentary profiles of particulate organic carbon and nutrients of two adjacent sites in the Gulf of Aqaba, one dominated by carbonate sands, the other by quartz sands. A time series demonstrates the tight coupling of the pore water concentrations to the seasonal changes in the water column and shows different responses in carbonate and quartz sands. The results of an in-situ experiment suggest that the different mineral characteristics of the two sediments are responsible for these different responses.

Study site and Methods

The study was carried out in a fringing reef in the Gulf of Aqaba situated on the Jordanian coast (lat. 29°27′, long. 34°58′ Fig. 1a). Mean water depth at the two sampling sites was 5 m, the average tidal range 0.7 m. Site # 1 was located in an area where the sediment consisted mainly of calcareous biogenic sands composed of coral (ca. 35% of dw), and shell fragments (ca. 15%), remains of forminiferans, calcareous red algae, and sea urchins (ca. 30%) and ca 20% silicate grains (Fig. 1b). At site # 2, the sediment was of terrigeneous origin and mainly composed of crystalline quartz derived from weathered rock. However, approximately 2% of the sand consisted of biogenic materials, mostly shells and forminiferan tests (Fig. 1c). The distance between the two sites was approximately 200 m.

The physical and chemical characteristics of the carbonate and silicate sediments are summarised in Table 1. The coarser carbonate sand was less well sorted and had a higher porosity and permeability than the quartz sand. A set of calibrated analytical sieves was used to assess the grain size distributions. Sediment porosities were calculated from weight loss of wet sediment slices after drying at 60°C for 24 h. The hydraulic conductivities of the silicate and carbonate sediments were measured with a constant head permeameter as described by Klute and Dirksen (1986). The concentration of calcium carbonate in the sediment was determined by complexometric titration of calcium carbonate with 0.1 N of HCL according to Muller (1967). Organic carbon contents in the sediments were measured following the method of Gaudette and Flight (1974). In this method, 0.2 g of the sediment were treated with H_2SO_4 (12 M) and potassium dichromate and then titrated with ferrous ammonium sulphate solution.

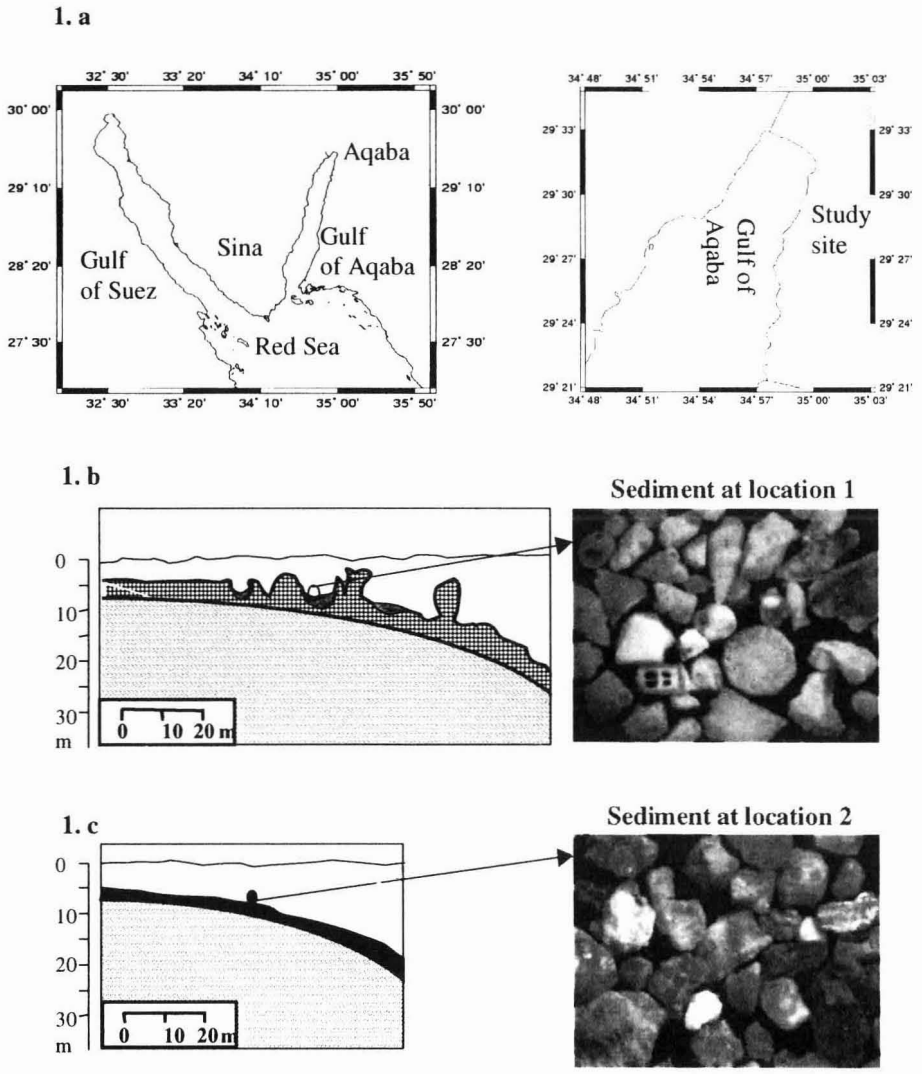


Fig. 1: (a) Study site in the Gulf of Aqaba (b) Left: ○ Location of the carbonate sand sampling site (dotted area reef, grey area: sediment). Right: carbonate sands from the sampling site. (c) Left: ● Location of the silicate sand sampling site (grey area: sediment). Right: silicate sands from sampling site. The distance between carbonate and silicate sites was 200 m.

	Natural sediment		sieved sediment	
Characters	Carbonate	**Silicate**	**Carbonate**	**Silicate**
$CaCO_3$ content	75-85%	4-6%	82%	2%
Median grain size (µm)	624	206		
Q1 grain size (µm)	1149	323		
Q2 grain size (µm)	272	163		
Mean grain size (µm)	559	229	375	375
Sorting	1.3	0.9		
Skewness	0.6	-2.0		
Porosity %	47	33	41	40
Permeability m^2	$143*10^{-12}$	$18.5*10^{-12}$	$43.8*10^{-12}$	$22.6*10^{-12}$
Chlorophyll a ($\mu g\ g^{-1}$)	0.719	0.625		
Organic carbon %	0.36	0.24	0.10	0.07
Shells numbers m^{-2}	560	310	0	0
Snails numbers m^{-2}	1720	310	0	0

Table 1: Sedimentological properties of the natural carbonate and silicate sands at the study sites and the sieved sediments that have been used in the in-situ incubation.

Seasonal study

From July 1999 until April 2000, sediment samples were collected monthly (2 cores for each sediment type) by divers using cylindrical acrylic pipes (25 cm high, 9.5 cm inner diameter) that could be closed on both sides with rubber stoppers. The length of the retrieved sediment cores was usually about 15 cm. Immediately after sampling, the sediment cores were cut into horizontal slices (upper 6 cm: 1 cm slices, below 2 cm thick slices). 50 cm^3 of each sediment slice was used for pore water extraction, another 2 cm^3 for the assessment of the content of carbonate and organic carbon. In order to extract the pore water, the sediment subsamples were centrifuged at 12500 g and 4°C for 15 minutes and the pore water then was filtered through 0.45 µm syringe filters. The pore water samples were analysed directly. For nutrient analysis, 5 ml of the filtered water were diluted to 50 ml with deionized distilled water.

During the study period, we recorded temperature, salinity, current speed and current direction of the water at about 0.5 m above the sediment at a station half-way between

the two sampling sites (initial samples have shown that there were no significant differences in the water current and temperatures above the two adjacent sampling sites). Current speed and direction at 0.5 m above the sediment were measured using a Sd-6000 mini current meter; temperature and salinity with Ocean sensors OS200 CTD.

Water samples for nutrients and chlorophyll a were collected by divers at about 0.5 m above the sediment. The nutrient samples were analysed spectrophotometrically according to Strickland and Parson (1972), and chlorophyll a was measured fluorometrically using the method of Arar and Collins (1992) using acetone (95%) as the extraction agent.

In-situ experiment

The in-situ experiment was conducted in December 1999 and designed to investigate whether silicate and carbonate sands of the same grain size have the same trapping efficiency for suspended material. Carbonate and silicate sands for this experiment were collected at the two study sites by divers. The collected sediments were washed with fresh water, dried, and sieved to extract the fraction of 250-500 μm grains. Although these sand fractions had a very similar grain size, the permeability of the sieved carbonate sand (43.8×10^{-12}) was twice as large as that of the quartz sand (22.6×10^{-12} m^2). The organic carbon contents prior to the start of the experiment were 0.11±0.03 and 0.06±0.02% for carbonate and silicate sediments, respectively.

For the incubation, 12 cylindrical pipes (24 cm inner diameter, 20 cm length) were filled with the cleaned sands, saturated with 0.2 μm filtered see water and covered with tough plastic foils secured with rubber bands at the top and the bottom. At the selected sublittoral site, close to the Marine Science Station (at about 5 m water depth, half way between sampling sites 1 and 2), 12 holes were made in the sea bed and 12 cylindrical acrylic pipes (28 cm inner diameter, 40 cm length) were inserted to 35 cm length into these holes. The sediments enclosed in the cylinders with foil covers then were inserted in the cylinders that had been embedded in the sea bed. Afterwards, the lower foil covers were removed carefully from the sediment cylinders. The upper surfaces of the embedded sediments were slightly above the sea bed surface. The outer cylinders then were removed. After 20 hours of temperature equilibration, the upper covers and the inner cylinders were removed and the surface of the embedded cores adjusted to the level

of sea bed. The 12 embedded sediments were aligned in two rows, each row had 6 incubated cores of the same sediment type (silicate or carbonate sediments).

After 10 days of incubation, we sampled 6 of the embedded sediment cores (3 carbonate and 3 silicate). 1 core (10 cm diameter, 20 cm long) was taken from the central part of each of the embedded sediments. The cores were cut into slices (upper 6 cm: 1 cm slices, below that 2 cm thick slices). The sediment slices were analysed as described for the seasonal study. After 22 days of incubation, a second set of subcores was collected in the same manner and the same measurements were done. Dissection of the cores at the end of the incubation revealed that no macrofauna organisms were present in the experimental sediments.

Results

Seasonal study

The water temperature 0.5 m above the sediment showed a clear seasonal trend. Temperatures were high from July until September (maximum 25.7 °C) and started to decrease in October (-0.9 °C $month^{-1}$) reaching a minimum in March (minimum 20.9°C) (Fig. 2a). However, salinity did not show strong variations or a clear trend during the study period (Fig. 2a) and ranged from 40.23 to 40.43 ppt. Boundary layer current velocities at 0.5 m above the sediment fluctuated between 2.1 and 9.2 cm s^{-1} (average 4.99 cm s^{-1}) and the direction was predominantly from south-west in summer shifting to more south-eastern directions in winter (average 170°) (Fig. 2b).

Nutrient and chlorophyll a concentrations in the boundary current also showed seasonal variation with low concentrations during summer and higher concentrations during winter months (Fig. 3). The concentrations began to increase in October (rates listed in Table 2a), when temperature also started to decrease indicating the intrusion of water from deeper layers of the Gulf. The data in Fig. 3 demonstrate that there was no significant difference between the nutrient or chlorophyll a concentrations of the water above silicate and carbonate sediment.

Despite its larger grain size, the organic carbon content in the carbonate sand was always higher than in the quartz sand (Table 3, average 1.7 fold). The concentration profiles (Fig. 4) show that there was an increase of organic carbon content in the surface sediments (1-3 cm) during the winter months, while in the deeper sediment layers the concentrations remained almost constant.

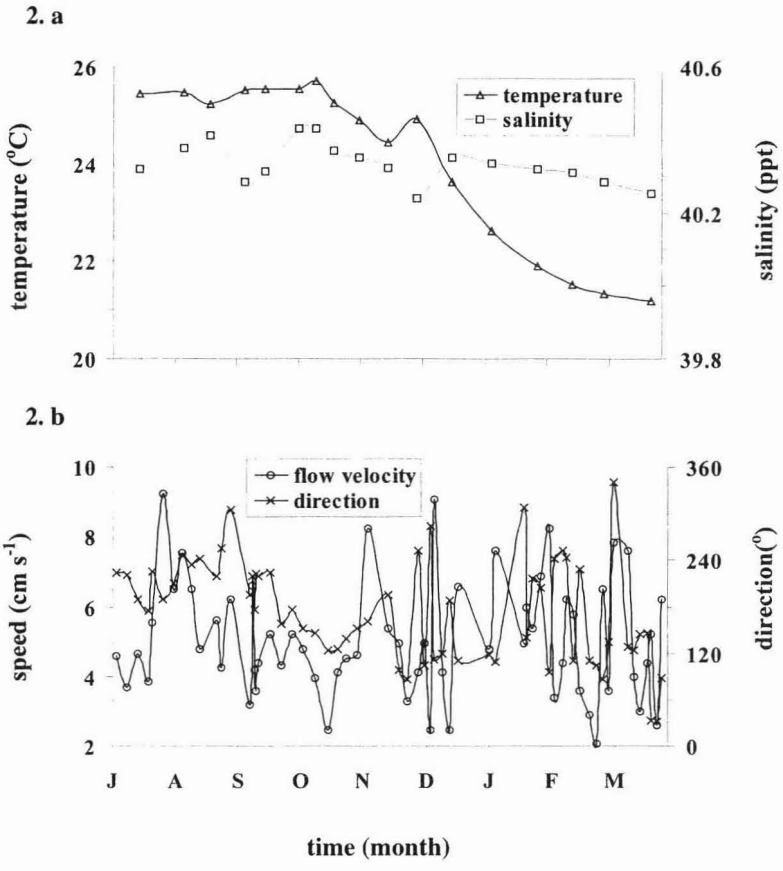


Fig. 2: (a) Temperature °C (triangles) and salinity ppt (squares) (b) Current velocities (circles) and directions (crosses) at 0.5 m above the sediment during the study period July/1999 to March/2000.

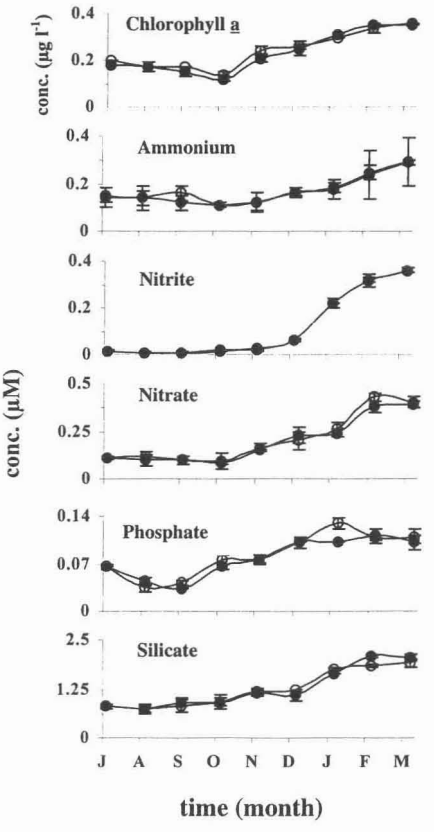


Fig. 3: Chlorophyll a (µg l^{-1}) and nutrient concentrations (µM) in the water column, 0.5 m above silicate (closed circles) and carbonate (opened circles) sediments during the period July/1999 to March/2000.

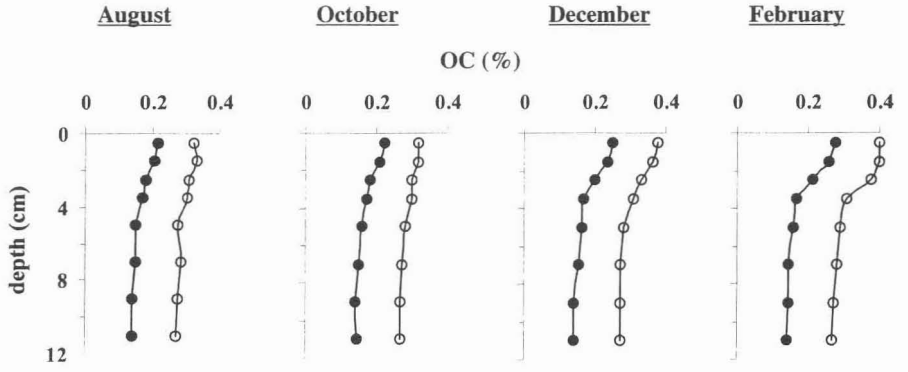


Fig. 4: Organic carbon (%) profiles in silicate (closed circles) and carbonate (opened circles) sediments in August, October, December of 1999 and February of 2000.

Content in 12 dm^3 of sediment	October			February		
	Si	*C*	*Ratio*	*Si*	*C*	*Ratio*
OC (g)	2.57	4.31	1.70	2.79	4.77	1.70
Ammonium (µmol)	69.16	144.22	2.08	79.30	166.50	2.09
Nitrite (µmol)	1.41	12.45	8.83	2.33	13.45	5.78
Nitrate (µmol)	5.95	43.20	7.26	5.18	61.18	11.81
DIN (µmol)	76.52	199.86	2.61	86.10	241.10	2.8
DIP (µmol)	6.20	16.99	2.74	6.95	22.55	3.24
Silicate (µmol)	150.14	245.49	1.64	160.93	293.46	1.82

Table 3: Organic carbon and nutrient contents in the silicate and carbonate sediment in October/1999 and February/2000 and the ratio between the contents in the two sediment types.

In both, carbonate and quartz sands, the concentrations of all nutrients in the upper sediment layers were higher in winter than in summer (Fig. 5). Below 10 cm sediment depth, the concentrations did not vary between seasons. Ammonium and silicate concentrations in both sediments increased gradually from the surface downwards (Fig. 5). In the surface layer, ammonium concentrations were higher in the carbonate than in the quartz throughout the study period, however, below that layer the concentrations did not vary between both sediments (Fig. 5). In all depth layers, the nitrate and nitrite concentrations of the carbonate sediment were always higher than in the silicate. Phosphate and silicate concentration profiles showed no clear differences between the two sediments. However, when taking the higher porosity of the carbonate into account, the contents of all nutrients were obviously higher in the carbonate sand than in the quartz sand (factors 1.64 to11.81, Table 3). Figure 6 depicts integrated nutrient contents of the frequently resuspended surface layer (0-2 cm), the intermediate layer that can be affected by bioturbation (2-8 cm, Boudreau 1998) and the deeper sediment (8-12 cm), where the biogeochemical processes are governed mostly by diffusion. In all three depths layers, the nutrient contents were on average 2 to 10 times higher in the carbonate with highest differences in the nitrate contents.

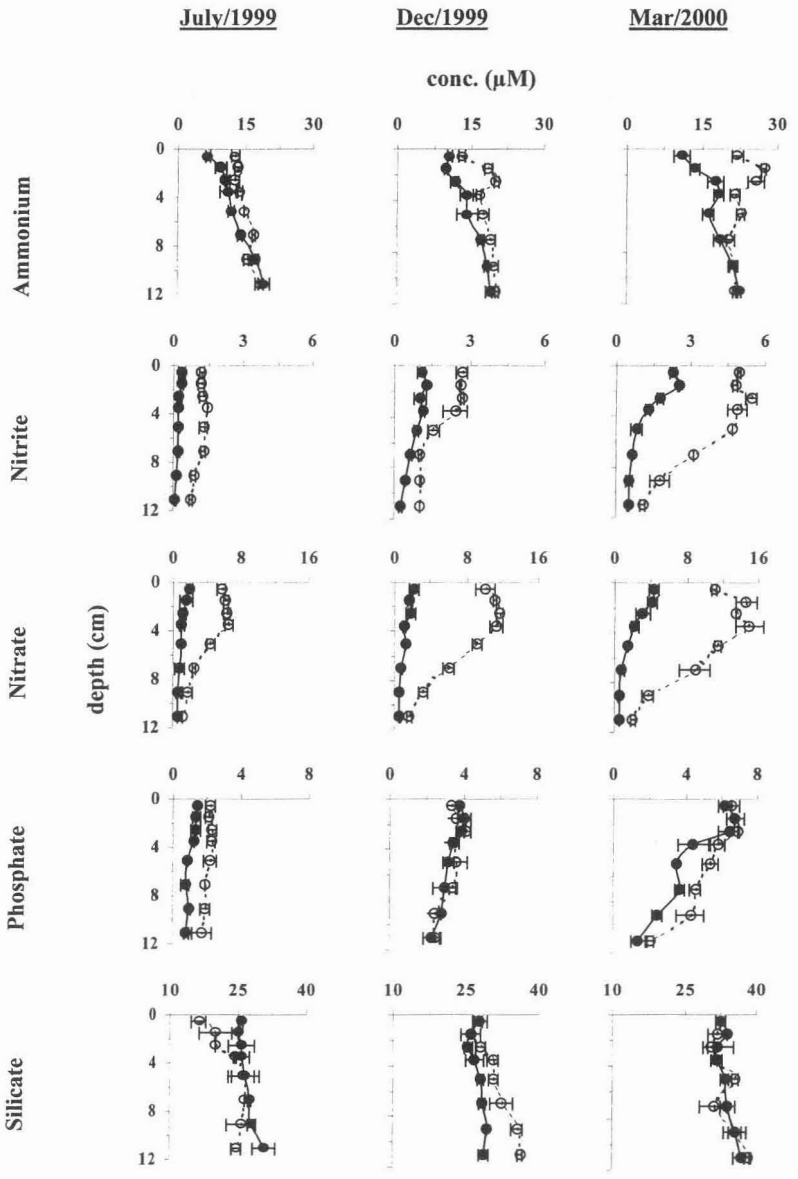


Fig. 5: Nutrient concentrations profiles (µM) in carbonate (opened circles and dotted lines) and silicate (closed circles and solid lines) sediments in July and December of 1999 and March of 2000. Each point represents the average of two pore water samples extracted from two different cores. Error bars reflect the differences between these two samples. Complete data sets including the period July/1999 to March/2000 are available from the authors.

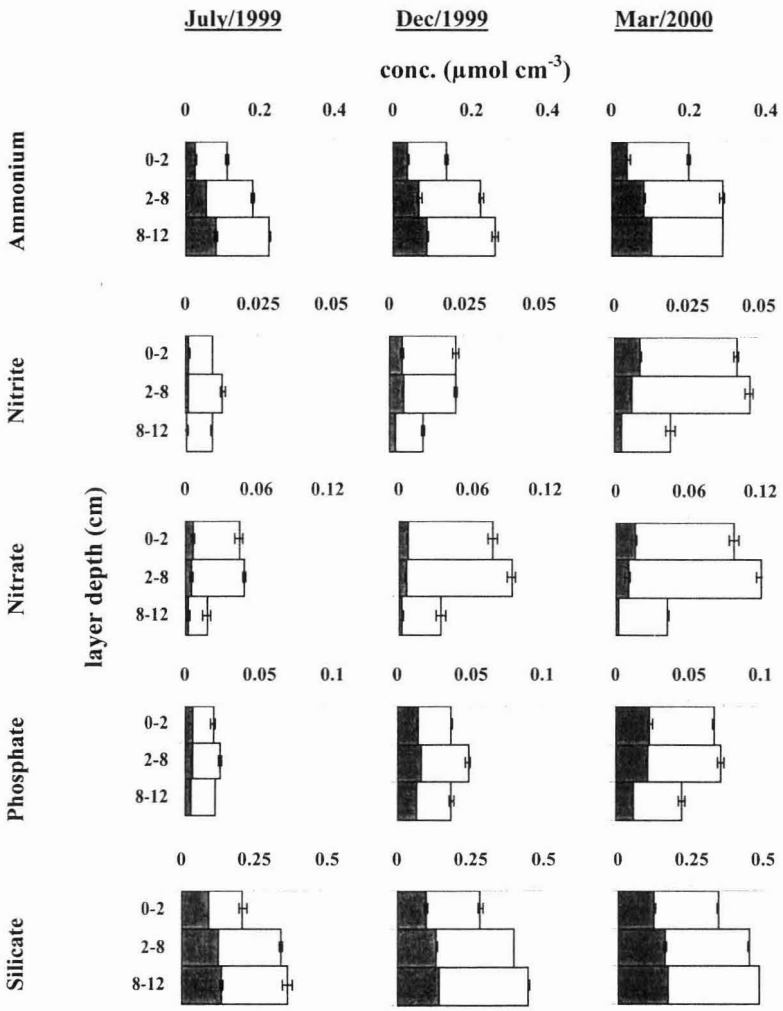


Fig. 6: Contents of nutrients at 0-2, 2-8, 8-12 cm depth of silicate (grey bar) and carbonate (white bar) sediments in July and December of 1999 and March of 2000. The error bars reflect the differences in concentrations between two samples extracted from two cores.

In- situ incubation experiment

The incubated sands accumulated particulate organic matter during the in-situ experiment, and the carbonate trapped more organic matter than the silicate (0.28 vs. 0.17 g $m^{-2}d^{-1}$, factor 1.65). Ten days into the incubation, the organic carbon contents had reached 0.15% and 0.09% in the surface layer of the carbonate and silicate, respectively, corresponding to increases by 36% and 50% relative to the initial concentrations. After 22 days, these values had increased to 0.17% and 0.11% (Fig. 7, 13% and 22% increase after day 10). Figure 7 shows that the organic matter accumulation was restricted to the upper 3 centimetres in the silicate and the upper 5 centimetres in the carbonate sand. Pore water nutrient concentrations increased in both sediments during the incubation and were always significantly higher than the nutrient concentrations in the overlying water column (Fig. 3 and 8). In the carbonate sand, these increases exceeded those in the quartz sand, except for dissolved silicate that after 22 days showed higher concentrations in the quartz sands in the layers deeper than 4 cm. Phosphate concentrations in the upper 5 cm of the carbonate exceeded those in the quartz sand by factor 2.

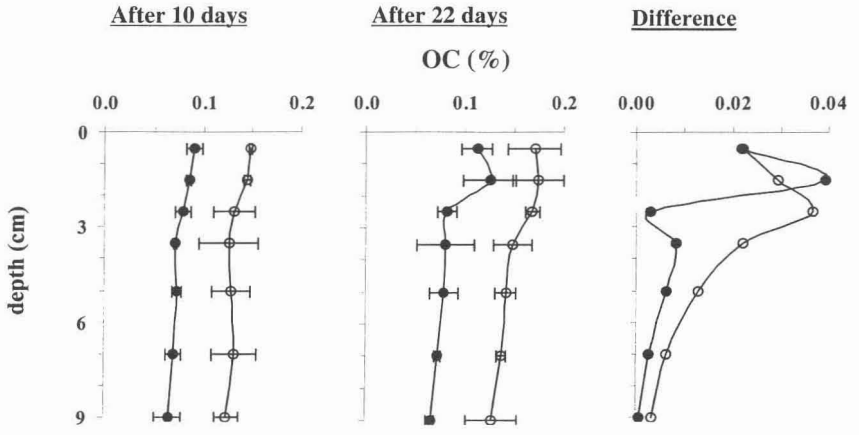


Fig. 7: Pore water organic carbon (%) profiles in silicate (open circles) and carbonate (closed circles) sediments during the in-situ incubation experiment. After 10 days of incubation, after 22 days of incubation, and differences between the two measurements. Each point represents the average of two sediment samples taken from two different cores. Error bars indicate the difference between these two samples.

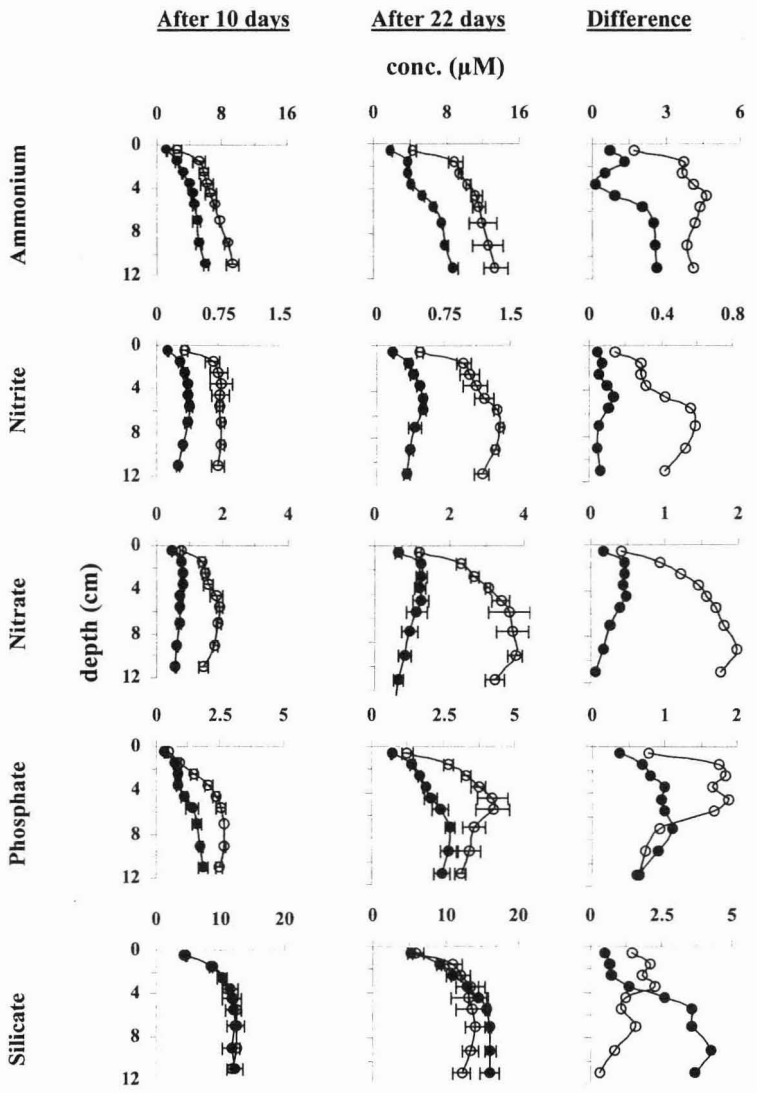


Fig. 8: Nutrient pore water profiles in silicate (closed circles) and carbonate (open circles) sediments after the in-situ incubation. After 10 days of incubation, after 22 days of incubation, and the difference in concentrations between the two measurements. Each point from a and b represents the average of three porewater samples extracted from three different cores. Error bars show the standard deviations for these three samples.

Discussion

Over the whole study period of 8 months, the organic matter and nutrient contents in the carbonate sediment were higher than those in the silicate sand (Figs. 4, 5 and table 3), although the characteristics of the water columns overlying the two sites were almost identical (Fig. 3). These results were unexpected considering the larger median grain size of the carbonate (600 vs. 300 µm median) that suggests a lower specific surface area and, due to the fact the most organic material in sands is attached to the grain surfaces (Mayer 1994a, 1994b), also a lower organic content (Capone et al. 1992).
Potential causes for the concentration differences between the two sediment types are 1) other sources for organic matter than the overlying water, 2) differences in biogenic sources 3) differences in the transport between water and sediment.

1) Sources of organic matter and nutrients other than the water column are atmospheric and groundwater input (D'Elia et al.1981, Lewis 1985) and biogenic input by benthic phototrophs or heterotrophs (e.g. polychaetes, molluscs, echinoderms, and vertebrates). Due to the close proximity of the two study sites, eolian input is unlikely to cause a pronounced difference between the two sites. Groundwater input can be excluded as well because the Gulf of Aqaba is situated in an extremely dry desert region, and none of the pore water samples showed any salinity anomalies.

2) Biogenic sources were more likely to contribute to the organic carbon and nutrient differences between the two sediments. Shallow carbonate sands can support a dense population of benthic phototrophs e.g. cyanobacteria (Blanchot et al. 1989), microphytobenthos (Smith 1981), multicellular algae (Bell 1992, Larned 1998), and higher plants (Darke 1996, Limpus and Limpus 2000). The latter two were no factor at our study sites but at both sites, cyanobacteria and diatoms were abundant. However, sedimentary chlorophyll a analyses (Table 1) indicated that the populations of benthic phototrophs were similar at the two sites. In contrast, the benthic fauna that was present at the two sites in early spring, the most productive season, was different between the two sites and, thus, also influenced the concentrations of organic matter and nutrients differently (Table 1). Molluscs were the dominant macrofauna organisms at both sites, and in the carbonate sand, snails were 3-times as abundant as in the quartz sand.

3) Transport of solutes and particles through bioirrigation and bioturbation (e.g. Aller 1988, Kristensen 1988), thus, may have been stronger in the carbonate and may have increased the concentration of organic carbon in the carbonate sediment. Mechanical mixing and oxygenation of the sediment by infauna activity is known to increase the mineralization and nutrient release from the bed (Aller 1988, Hansen and Kristensen 1997, Mortimer et al. 1999). Although the benthic fauna may have contributed to the difference in organic matter and nutrient concentrations, the results of our in-situ experiment suggest that the mineralogical characteristics of the two sand types were the main reason for the observed differences in organic matter and nutrient content.

In the carbonate sand, the grains represent a large pool of carbonate that can buffer pore water pH when CO_2 is released during oxidation of organic matter (Buddemeier and Oberdorfer 1986). The stabilisation of the pH may be advantageous for some bacterial strains but microbial decomposition occurs over a much wider pH-range than found in our marine sediments (Madigan et al. 1997) and, thus, can hardly explain the pronounced differences in organic matter and nutrient concentrations between the two sediments.

The coarser carbonate sand had a much higher permeability than the silicate sand. In sands with permeabilities like those we measured for our sediments, bottom currents as observed at our study site (Fig. 2) cause advective exchange of water between the sea bed and the boundary layer flows (Savant et al. 1987, Huettel and Gust 1992). Flume experiments showed that the ensuing advective pore water flows could transport solutes and particulate matter up to 10 centimetres into the bed within 12 hours (Huettel et al. 1996, 1998, Huettel and Rusch 2000). Advective interfacial exchange, thus, converts such sand beds into large filter systems, and the carbonate sand may have been a more efficient filter than the silicate sand.

This hypothesis was tested in the in-situ experiment. Although the carbonate and silicate sands used for this experiment originated from the same sieved fraction (250-500 µm), the permeability of the carbonate was twice as large as that of the silicate sand, which can be attributed to the effect of grain porosity. The skeletal remains of corals, foraminifers and sea urchins that form the carbonate sands are perforated by many small pores that were occupied by organic tissue in the living animal. After incubation at the study site, the carbonate trapped more organic matter than the silicate (6.2 g m^{-2} vs. 3.8 g m^{-2}, factor 1.63), and the depth distribution (Fig. 7) shows that in the carbonate sand the organic matter was transported deeper and also accumulated deeper in the sediment

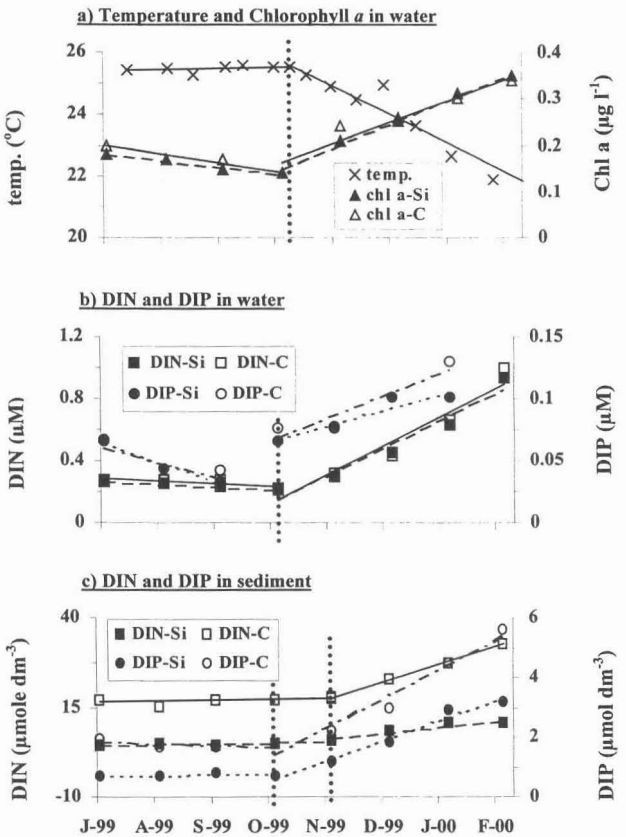
(silicate at 1.5 cm depth, carbonate at 2.5 cm depth). Because no fauna was present in the cores, this particle transport and accumulation at depth can be attributed to advective pore water flows (Huettel and Rusch 2000). The higher permeability in the carbonate permitted stronger and deeper-reaching pore water flows, thus, particles accumulated in a deeper sediment layer. At the end of the in-situ experiment, the organic matter contents in the incubated cores were still approximately 50% lower than in the natural sediment (Fig. 4, 7). However, the comparison shows that the ratio of carbon contents (experimental sediments: 1.65, natural sediments: 1.62 (50.3 g m^{-2} vs. 31.1 g m^{-2})) and distributions of the carbon in experimental and natural sediments were similar indicating that the same transport mechanism, advection, dominated in the upper layers of both sediment types.

Through the supply of electron acceptors and the removal of decomposition products, the advective pore water flows enhance the microbial decomposition activities in the upper sediment layer and especially in the particle accumulation layer (Huettel and Rusch, 2000). In the more permeable carbonate, this effect was more pronounced than in the quartz sand, resulting in higher nutrient release to the pore water that caused higher nutrient contents in the carbonate sediment despite stronger advective exchange (Fig. 6). The distributions of the nutrients support the hypothesis that the advective pore water flows were more effective in the carbonate sand. Maximum concentration increases of nitrite and nitrate in the carbonate were recorded deeper in the sediment than in the silicate (nitrite: 7 cm vs. 5 cm, nitrate: 9 cm vs. 7 cm, Fig. 8). In both sediments, the pore water concentrations of nitrite and nitrate exceeded those in the overlying water column by more than one order of magnitude, disclosing that sedimentary nitrification produced these nutrients (Capone et al. 1992, Mortimer et al. 1998, Barelson et al. 1998, Tuominen et al 1999). The deeper nitrate maxima demonstrate that oxygen-carrying advective pore water flows reached deeper into the carbonate sand. Falter and Sansone (2000) showed that nitrate and nitrite concentration in the pore water reach their maximum where dissolved oxygen is still abundant. Bioirrigation can be excluded and diffusion alone could not transport oxygen to these depth within the duration of the experiment. The depth oxygen could reach by diffusion can be estimated using $t = z^2/2Ds$ (Crank 1983) where t is time, z is sediment depth and Ds is the effective diffusion coefficient for oxygen in the carbonate sediment ($3.6x10^{-6}$ cm^2 s^{-1}). Even without consumption in the sediment, oxygen could not diffuse deeper than 3.7 cm into the sediment within the 22

days of experimental duration. During the in-situ experiment, ammonium, phosphate and silicate concentrations also increased within the upper 8 cm of the carbonate sand; in the quartz sand, these increases were less pronounced.

The seasonal changes in organic carbon and nutrient inventories in water column and carbonate and quartz sands demonstrate the impact of the different filtration efficiencies of the two sediments investigated. In the Gulf of Aqaba, two main seasonal patterns can be distinguished that are reflected in the physical and chemical properties of the coastal water: the winter pattern that includes the months from October until April, and the summer pattern that ranges from July to September. In October, the main wind direction changes from 220° to 150° (Fig. 2) and causes upwelling of deep nutrient-rich water to the surface and into the reefs (Levanon-Spanier et al. 1979, Al-najjar 2000). In May, the input of the offshore water decreases and the nutrient concentrations in the reef drop. The summer pattern is characterised by low but relatively constant nutrient concentrations in the water column.

This study covers the period July-1999 to March-2000 and, thus, also includes the transition between the two seasonal patterns. Our temperature, salinity and wind data (Fig. 2) mark this transition in October 1999. The intrusion of nutrient-rich water into the reef is reflected by an increase in the phosphate concentrations in the water column at both study sites (Fig. 9). Inorganic nitrogen (DIN) increases simultaneously but the increase seems less salient. Chlorophyll a in the water column follows the trend of the nutrients and increases as soon as the upwelling starts (marked in Fig. 9 by the drop in water temperature). Enhanced primary productivity during winter (November-March) in the Gulf of Aqaba was also recorded by Levanon-Spanier et al. (1979), who also observed high diatom concentrations in the water column in February. Yahel et al. (1998) found relatively high content of Synochoccus in February at 0.5 m above the reef sediment. The nutrient inventory of the upper sediment layer (0-2 cm) mirrors the concentration changes in the water column and demonstrates the tight coupling due to the advective exchange processes. Such tight coupling between seasonal changes in the water column and the sediment were also reported by Sugai 1987 and Lohse et al. 1995.



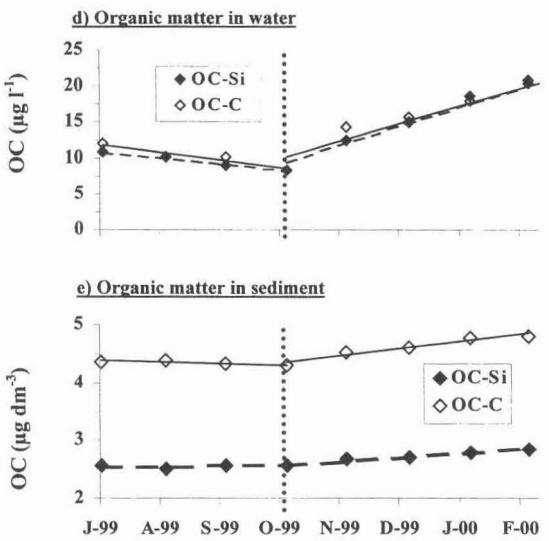


Fig. 9: (a, b and d): Time series data of temperature, chlorophyll a, dissolved inorganic nitrogen (DIN), dissolved inorganic phosphate (DIP), and integrated organic carbon content (OC) in the water of the silicate and carbonate sediments. c and e: Time series data of dissolved inorganic nitrogen (DIN) dissolved inorganic phosphate (DIP), and organic carbon in the surface sediment (0-2cm). The dotted lines represent the time, when the water from deeper layers of the Gulf intruded the reef environment.

The phosphate concentrations in the pore water increased with the onset of the upwelling (0.66 µM and 0.99 µM $month^{-1}$ for silicate and carbonate sediment respectively, Table 2b). The increase in pore water DIN shows a delay that lasts about one month, which likely is caused by nitrogen starvation of the reef environment (Larned 1998), initially causing a rapid consumption of the intruding DIN. However, the rates of nutrient increase in water column and sediment (Table 2) show, that the nutrient concentrations in the sediment increased much faster (factor 10 to 50) than in the water column, indicating a simultaneous increase of decomposition activities in the sediments. With the increase of the POC content in the water column, the deposition of organic matter increased (Fig. 9), causing higher mineralization and nutrient release to the pore water.

In the carbonate sand, the organic matter concentrations increased more rapidly than in the quartz sediment (Table 2, Fig. 9). We suggest that the additional deposition necessary to account for this difference is caused by a higher filtration rate of the carbonate sand. Pilditch and Grant (1999) and Huettel and Rusch (2000) demonstrated in flume experiments that permeable sand beds could filter phytoplankton from the boundary layer. Horizontal pressure gradients, generated when the boundary flows interact with small sediment topography (sand ripples, biogenic structures, shells) cause water intrusion into the bed that can transport suspended planktonic algae into the sediment. Because the sediment permeabilities of the quartz and carbonate sands and the boundary current velocities measured at the study sites permit such advective pore water flows, it is probable that in the Aqaba sediments a significant fraction of the POC deposition takes place through filtration.

We conclude that in biogenic carbonate sand the coupling between water column and sediment is tighter relative to crystalline quartz sand due to the mineralogical characteristics of the sand. The porous carbonate grains increase the permeability of the sediment and also provide a large surface area for sorption processes and bacterial colonization. These characteristics cause higher filtration efficiency and mineralization rates in the carbonate sand. Carbonate sands in coral reefs and on tropical beaches, thus, are sites of rapid mineralization that in its intensity may exceed that of similar environments dominated by quartz sands.

Acknowledgements

This work was done in the framework of the Red Sea Program and has been funded by the German Federal Ministry of Education and Research (BMBF grants no. 03F0245A) and the Max Plank Institute for Marine Microbiology in Bremen, Germany. Thanks are due to the director and the staff members of the Marine Science Station for their full support and help during the whole period of this study. Special thanks are due to Tariq Al-Salman and Khalid Al-Sokhni for assisting in diving and for Ali-Hammad and Khalid Al-Sane for helping in the lab.

References

Aller RC (1988) Benthic fauna and biogeochemical processes in marine sediments: the role of burrow structures. In Nitrogen Cycling in Coastal Marine Environments (Blackburn TH and Sorensen J eds). John Wiley and Sons Ltd, Chichester, p 301-338

Al-Najjar T (2000) The seasonal dynamics and grazing control of phyto- and mesozooplankton in the northern Gulf of Aqaba. Ph D Thesis, Bremen University, Bremen-Germany

Arar EJ, Collins GB (1992) In vitro Determination of chlorophyll a and pheophytin a in marine and freshwater phytoplankton by fluorescence. Environmental Monitoring System Laboratory Office of Research and Development. US Environmental Protection Agency Cincinnata Oh 45268

Banfield JF, Nealson KH (1998) Geomicrobiology: Interactions between microbes and minerals. In Ribbe H (ed) Review in Mineralogy vol 35

Barelson WM, Heggie D, Longmore A, Kilgore T, Nicholson G, Skyring G (1998) Benthic nutrient recycling in Port Phillip Bay, Australia. Est Coast Shelf Sci 46:917-934

Bell PRF (1992) Eutrophication and coral reef-some examples in the Great Barrier Reef Lagoon. Wat Res 26(5):553-568

Bertuzzi A, Faganeli J, Brambati A (1996) Annual variation of benthic nutrient fluxes in shallow coastal waters (Gulf of Trieste, Northern Adriatic Sea). Mar Ecol 17 (1-3):261-278

Blanchot J, Charry L, Leborgne R (1989) Size composition of particulate organic matter in the lagoon of Tikehau atoll (Tuamotu Archipelago). Mar Biol 102:329-339

Boudreau BP (1998) Mean mixed depth of sediments: The wherefore and the why. Limnol Oceanogr 43(3):524-536

Berner R (1980) Early Diagenesis: A Theoritical Approach. Princeton Univ. Press, Princeton, New Jersy, p 241

Buddemeier RW, Oberdorfer JA (1986) Internal hydrology and geochemistry of coral reefs and atoll islands: key to diagenetic variations. In: Schroeder JH, Purser BH (eds). Reef diagenesis. Springer, Berlin, Heidelberg, New York, pp 91-111

Burdige D, Zheng S (1998) The biogeochemical cycling of dissolved organic nitrogen in estuarine sediments. Limnol Oceanogr 43(8):1796-1813

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

Charpy-Roubaud C, Charpy L, Lemasson L (1989) Benthic and plaktonic primary production of an open atoll lagoon (Tikehau, Taumotu archipelago, French Polynesia). Proceeding of the Sixth International Coral Reef Congress, Townsville, 1988 2:551-556

Ciceri G, Ceradina S, Zitelli A (1999) Nutrient benthic fluxes and pore water profiles in a shallow brackish marsh of the lagoon of Venice. Annali di Chimica 89:359-375

Correder JE, Capone DG (1985) Studies on nitrogen diagenesis in coral reef sands. Proc Fifth int Coral Reef Symp 3:395-399

Corredor JE, Morell J (1985) Inorganic nitrogen in coral reef sediments. Mar Chem 16:379-384

Crank J (1983) The Mathematics of Diffusion. Clarendon Press, Oxford

Darke SF (1996) The international coral reef initiative: A strategy for the sustainable management of coral reefs and related ecosystems. Coast Manag 24(4): 279-299

D'Elia CF, Webb KL, Porter JW (1981) Nitrate-rich groungwater input to Discovery Bay, Jamaica: A significant source of N to Local coral reefs?? Bull Mar Sci 31:903-910

Emerson S, Janker R, Bender M, Froelich P, Klinkhammer G, Bowser G, Setlock G (1980) Early diagenesis in sediments from the eastern equatorial Pacific. 1. Pore water nutrient and carbonate results. Earth Planet Sci Lett 49:57-80

Falter L, Sansone FJ (2000) Hydraulic control of pore water geochemistry within the oxic-suboxic zone of a permeable sediment. Limnol Oceanogr 45(3): 550-557

Froelich P, Klinkhammer G, Bender M, Luetke N, Heath G, Cullen D, Dauphin P, Hammond D, Hartman B, Maynard V (1979) Early oxidation of organic matter in pelagic sediments of the eastern equatorial Atlantic: sub-oxic diagenesis. Geochim Cosmochim Acta 43:1075-1091

Furukawa Y, Bentley SJ, Shiller AM, Lavoie DL, van Cappellen P (2000) The role of biologically-enhanced pore water transport in early diagenesis: An example from carbonate sediment in the vicinity of North Key Harbor, Dry Tortugas National Park, Florida. J Mar Res 58:493-522

Gaudette HE, Flight WR (1974) An inexpensive titration method for the determination of organic carbon in recent sediments. J Sediment Petrol 44(1):249-253

Hansen K, Kristensen E (1997) Impact of macrofaunal recolonization on benthic metabolism and nutrient fluxes in a shallow marine sediment previously overgrown with macroalgal mats. Est Coast Shelf Sci 45:613-628

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

Huettel M, Ziebis WS, Forster S (1996) Flow-induced uptake of particulate matter in permeable sediments. Limnol Oceanogr 41(2):309-322

Huettel M, Ziebis WS., Forster S, Luther GW (1998) Advective transport affecting metal and nutrient distributions and interfacial fluxes in permeable sediments. Geochim Cosmochim Acta. 62(4):613-631

Huettel M, Rusch A (2000) Transport and degradation of phytoplankton in permeable sediment. Limnol Oceanogr 45(3):534-549

Jørgensen BB, Bang M, Blackburn T (1990) Anaerobic mineralization in marine sediments from the Baltic Sea-North Sea transition. Mar Ecol prog ser 59:39-54

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

Kristensen E (1988) Benthic fauna and biogeochemical processes in marine sediments: microbial activities and fluxes. In Blackburn TH and Sorensen J (eds) Nitrogen Cycling in Coastal Marine Environments. John Wiley and Sons Ltd, Chichester, pp 275-299

Larned ST (1998) Nitrogen- versus phosphorous-limited growth and sources of nutrients for coral reef macroalgae. Mar Bio (Berlin) 132(3):409-421

Levanon-Spanier I, Padan E, Reisis Z (1979) Primary production in a desert-enclosed sea - the Gulf of Elat (Aqaba), Red Sea. Deep-Sea Res 26:673-685

Lewis JB (1985) Groundwater discharge onto coral reefs, Barbados (West Indies). Pro Fifth Int Coral Reef Symp 6:477-481

Limpus CJ, Limpus DJ (2000) Mangroves in the diet of Chelonia mydas in Queensland, Australia. Mar Turtle Newsl 89:13-15

Lohse L, Malschaert JFP, Slomp CP, Helder W, van Raaphorst W (1995) Sediment-water fluxes of inorganic nitrogen compounds along the transport route of organic matter in the North Sea. Ophelia. 41:173-197

Macintyre HL, Geider RJ, Miller DC (1996) Microphytobenthos: The ecological role of the "Secret Garden" of unvegetated, shallow-water marine habitats, 1. Distribution, abundance and primary production. Estuaries. 19(2a):186-201

Madigan MT, Martinko JM, Parker L (1997) Biology of microorganisms. 8th ed Prentice Hall International, Inc

Mayer LM (1994a) Relationships between mineral surfaces and organic carbon concentrations in soils and sediments. Chem Geol 114:347-363

Mayer LM (1994b) Surface area control of organic carbon accumulation in continental shelf sediments. Geochim Cosmochim Acta. 58(4):1271-1284

Mortimer R, Krom M, Watson P, Frickers P, Davey J, Clifton R (1998) Sediment-water exchange of nutrients in the intertidal zone of the Humber Estuary, UK. Mar Poll Bull 37(3-7):261-279

Mortimer R, Davey J, Krom M, Watson P, Frickers P, Clifton R (1999) The effect of macroauna on porewater profiles and nutrient fluxes in the intertidal zone of the Humber Estuary. Est Coast Shelf Sci 48:683-699

Muller G (1967) Method in sedimentary petrology. J Sed Petrol Part 1, Gebruder Ran2, Dietenheim

Pilditch CA, Grant J (1999) Effect of variations in flow velocity and phytoplankton concentration on sea scallop (Placopecten magellanicus) grazing rates. J Exp Mar Biol Ecol 240(1):111-136

Sansone FJ (1985) Methane in the reef flat porewaters of Davies Reef, Great Barrier Reef, Australia. Proc. Fifth Int. Coral Reef Congress, Tahiti 3:415-419

Sansone FJ, Andrews CC, Buddemeier RW, Tribble GW (1988) Well point sampling of reef interstitial water. Coral Reefs 7:19-22

Sansone FJ, Chanton JP, Haberstroh PR, Bozeat. R (1993) Methane cycling in coral reef frameworks. In: Guerrero R and Pedros-Alio C (eds.) Trends in Microbial Ecology,. Spanish Soc. Microbiol. pp. 157-162

Santaschi P, Hohener P, Benoit G, Buchholtz-ten Brink M (1990) Chemical processes at the sediment-water interface. Mar Chem 30:269-315

Savant SA, Reible DD, Thibodeaux LJ (1987) Convective transport within stable river sediments. Water Resour Res 23:1763-1768

Schroeder JH, Purser BH (1986) Reef diagenesis. Berlin (Springer), p 450

Smith SV (1981) Marine macrophytes as a global carbon sink. Science 211:838-840

Strickland JDH, Parsons TR (1972) A Particular Handbook of Seawater Analysis. Fish Research Board of Canada Bull, Ottawa, p 311

Sugai SF (1987) Temporal changes in the sediment geochemistry of two southeast Alaskan fjords. Deep-Sea Res 34(5-6):913-925

Tuominen L, Maekelae K, Haahti H, Lehtonen K, Hietanen S, Kuparinen J (1999) Denitrification, pore water profiles and nitrogen fluxes in the sediment of the northern Baltic Sea (Extended abstract). ICES J Mar Sci, 56 Supp:150-152

Yahel G, Post A, Fabricius K, Vaulot D, Genin A (1998) Phytoplankton distribution and grazing near coral reef. Limnol Oceanogr 43:551-563

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

Chapter 5

Influence of sediment permeability and mineral composition on organic matter decomposition in three sediments from the Gulf of Aqaba, Red Sea

Mohammed Rasheed [1,2], Mohammed Badran[2], Markus Huettel[1]

[1] Max Plank Institute for Marine Microbiology, Bremen University, 28359 Bremen, Germany

[2] Marine Science Station, University of Jordan and Yarmouk University, Aqaba Jordan

This chapter has been submitted to Estuarine, Coastal and Shelf Science

Influence of sediment permeability and mineral composition on organic matter decomposition in three sediments from the Gulf of Aqaba, Red Sea

Summary

In order to investigate the influence of sediment physical and chemical characteristics on the degradation of deposited organic matter, we compared decomposition in three sediments from the Gulf of Aqaba (Red Sea) that differ in permeability and mineral composition. Freeze-dried *Spirulina* was added to coarse carbonate and silicate sands from a shallow nearshore region and silt-clay sediment from the deeper center region of the Gulf incubated in laboratory chambers. The stirring in the chambers caused higher solute exchange in the coarse permeable sands relative to the fine less permeable silt due to the generation of advective fluid exchange between the sediment and overlaying water. This enhanced exchange increased the decomposition rates of organic matter in the incubated sands. The decomposition rates of total organic carbon in the permeable carbonate (3.0 mg C m^{-2} d^{-1}) and silicate sands (2.0 mg C m^{-2} d^{-1}) exceeded that in the fine-grained sediment (1.4 mg C m^{-2} d^{-1}). Oxygen consumption in the coarse sands was 3-fold higher than in the silt-clay sediment with highest rates in the carbonate sand. In carbonate and silicate sands of the same grain size, the carbonate sediment was more permeable than the silicate, resulting in 1.4-fold higher fluid exchange rates and 1.4-fold larger sedimentary organic matter mineralization rates. An *in-situ* experiment comparing trapping efficiencies in carbonate and silicate sands showed that the higher fluid exchange rate in the carbonate sand results in larger filtration rates and a faster accumulation of particulate organic matter from the boundary layer. Our experiments demonstrate that with respect to sedimentary mineralization rates, higher transport rates in permeable coarse sediments can outweigh the effect of a higher specific surface area in fine-grained silt sediments. In permeable sands, however, the higher specific surface area and fluid exchange in biogenic carbonate sands result in higher mineralization rates than in silicate sands of the same grain size.

Introduction

The decomposition of organic matter in marine sediments is controlled by a number of physical, chemical and biological parameters of which mixing intensity, temperature, availability of electron acceptors and activity of benthic organisms are some of the most important ones (Aller 1980, Holmer 1996, Knoblauch 1999, Canfield 1993). In this contribution we investigate the importance of sediment permeability and the sediment mineral matrix characteristics on the decomposition process by contrasting mineralization in coarse and fine sediments from the Gulf of Aqaba including carbonate and silicate sands.

Permeability controls whether diffusive or advective transport dominates in the upper sediment layer and, thus, is a key parameter affecting the exchange of metabolites between the sea bed and the overlying water (Rusch and Huettel 2000). The permeability of marine sediments depends on their grain size distribution and sorting and normally increases with decreasing water depths (Huettel & Rusch, 2000). In the deep ocean, water currents above the sediment are usually weak permitting the deposition of fine material (Boudreau and Guinasso 1982). The ensuing bottom sediments are relatively impermeable, and diffusion is the most important mechanism for transport of solutes in the seabed (Revsbech and Jorgensen 1986). In the shallow coastal environment, stronger bottom currents and wave orbital motion reaching the sea bed winnow the sediment from fine materials resulting in coarser sediments with relatively high permeabilities (Jahnke et al. 2000, Marinelli et al. 1998). Huettel and Gust (1992) and Huettel et al. (1996) have shown that in sediments with permeabilities exceeding 10^{-12} m^2 advective pore water flows enhance the transport of dissolved and particulate matter into and out of the sea bed. In permeable sediments organic matter can penetrate deeper and the degradation rates in the flushed layers are accelerated (Shum and Sundby 1996, Huettel and Rusch 2000). In laboratory flume experiments, Forster et al. (1996) compared oxygen consumption in sediments with different permeabilities and found that oxygen consumption in the coarse sediment was up to 91±23% higher than in the fine-grained sediment.

Because most of the sedimentary organic matter and bacteria are attached to the sediment grains (Rusch et al. 2001), the size, morphology and physical and chemical characteristics of these grains should be important factors determining the mineralization

potential of the respective sediment. Biogenic carbonate sands that are composed of fragments of corals, shells, foraminifera and coralline algae etc. differ fundamentally in their sedimentological characteristics from terrigenic quartz sands that are frequently found in temperate and boreal coastal environments. Oxygen consumption rates in coarse reef sediments (e.g. 13.8 to 24.1 mmol m^{-2} d^{-1}, Knoppers et al. 1996), that are mainly composed of carbonate sands indicate high mineralization potential in these sediments, although they have a relatively low organic content (0.15-1%, Sorkin 1995).

The aim of this study was to investigate the effect of the mineral composition of the sediments grains on the decomposition process and to contrast this effect to the effect of grain size. To this end, we evaluate decomposition in permeable carbonate and silicate sands from the Gulf of Aqaba (Red Sea) and compare mineralization in Gulf sediments with different permeabilities.

Materials and methods

Our study combines three laboratory chamber incubation experiments and one *in-situ* incubation experiment addressing filtration and degradation in sediments of different permeabilities and mineral composition. The results are used to interpret measurements obtained from natural sediments immediately after retrieval (Table 1).

Sampling sites

Sediment samples were collected from two shallow near shore sites (Fig. 1, A, B, ca. 5 m water depth) and one deeper site (Fig. 1, C, ca. 825 m water depth), all situated in the Northern Gulf of Aqaba (Fig. 1). The shallow sites A and B were located in the marine preserve close to the Marine Science Station on the Jordanian coast (29°27′ N, 34°58′ E, Fig. 1). The sediment at site A was mainly biogenic carbonate sand composed of coral and shell fragments, remains of foraminiferans, calcareous red algae and sea urchins.

Experiment	*Sediment used for incubation*	*Added material*	*No. of incubated cores*	*Measured parameters*
Lab incubation # 1	Natural shallow-water silicate and carbonate sands and slit-clay sediments	0.1 g of Spirulina were added to the overlying water. Controls without addition	2 with Spirulina and 2 controls for each sediment type	Nutrients, oxygen and sediment parameters
Lab incubation # 2	Sieved silicate and carbonate sands (250-500 µm)	3 g of Spirulina were mixed with the sediment. Controls without Spirulina	4 with Spirulina and 2 controls for each sediment type	Nutrients, oxygen and sediment parameters
Lab incubation #3	Sieved silicate and carbonate sands (250-500 µm)	Fluoresceine added to the overlying water	2 for each sediment type	Fluoresceine and sediment parameters
In-situ incubation	Sieved silicate and carbonate sands (250-500 µm)	Natural sedimentation and filtration added organic matter to cores	6 for each sediment type	Pigments, oxygen consumption for retrieved sub-cores of sediment

Table1: Experiments that were carried out in this study.

The sediment at site B was terrigeneous, composed primarily of quartz sand. The distance between sites A and B was 200 m. The sediment cores at site A and B were collected by divers using acrylic cylinders with 9.5 cm inner diameter and 40 cm height. Site C was located at 29°25′ N, 34°55′ E, (Fig. 1), halfway across the Gulf of Aqaba. The sediment at this site was silt-clay. Cores were collected using a multicorer system during the Meteor Cruise (GeoB 5801-2, Paetzold et al. 2000) that took place during January-May 1999. The core samples were frozen, until experimental incubation.

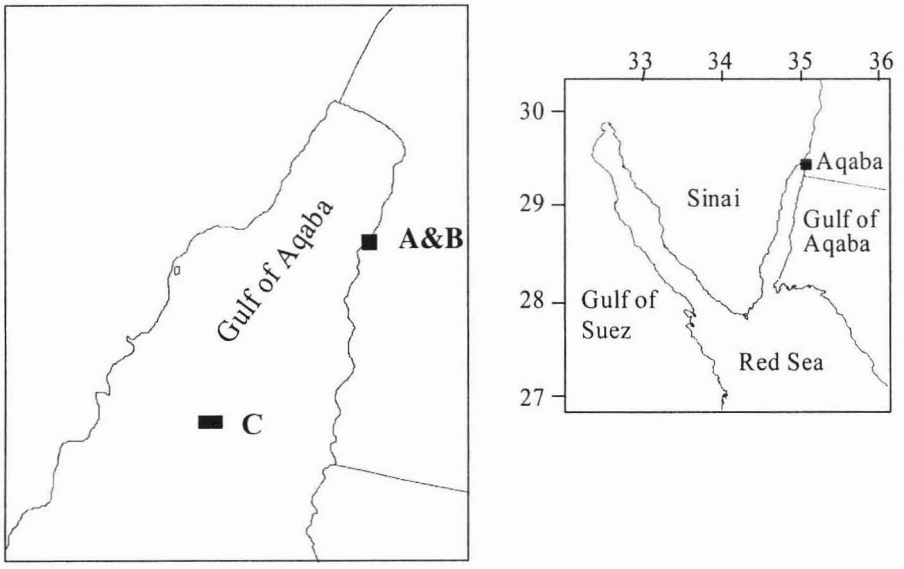


Fig. 1: Shallow (A&B) and deep sediment (C) sites.

Physical and chemical properties of the sediments are summarised in Table 2. The permeabilities of the silicate and carbonate sediments were measured using a constant head permeameter as described by Klute and Dirksen (1986). With permeabilities $k<10^{-12}$ m^2 the fine-grained deep sediment was relatively impermeable, while both nearshore carbonate and silicate sands were highly permeable ($k>10^{-11}$ m^2). Sediment porosities were calculated from weight loss of wet sediment after drying at 60°C for 24 h. Specific surface areas for the sieved sediment were assessed after drying at 80°C for 30 minutes by measuring the nitrogen absorbed to the grain surfaces using a Quantachrome Quantasorb instrument. In order to demonstrate the grain surface characteristics of carbonate and silicate sands, we took pictures of selected grains using Electronic Scanning Microscopy (Fig. 2).

	Shallow sediment		*Deep sediment*	*Sieved sediment*	
Character	*Carbonate*	*Silicate*	*Silt-clay*	*Carbonate*	*Silicate*
$CaCO_3$ content	75-85%	4-6%	30%	82%	2%
Mean grain size (µm)	559	229	45	375	375
Porosity %	47	33	58	41	40
Permeability m^2	$143*10^{-12}$	$18.5*10^{-12}$	$< 1*10^{-12}$	$43.8*10^{-12}$	$22.6*10^{-12}$
Organic carbon %	0.36	0.24	0.4	0.10	0.07
Surface area (m^2 g^{-1})			6.95	0.41	0.27

Table 2: Some physical and chemical characteristics of the investigated sediments

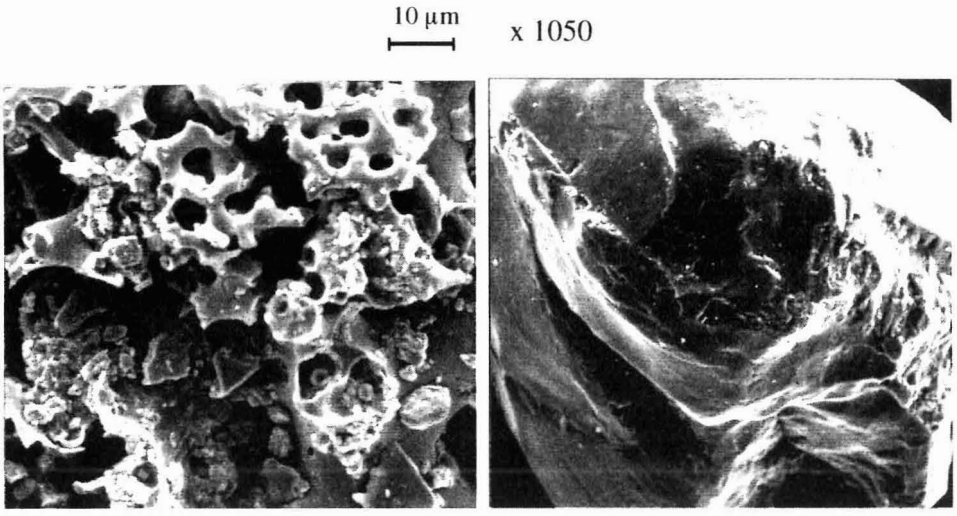


Fig. 2 Pictures for carbonate (left) and silicate (right) grains taken by Electronic Scanning Microscopy.

Measurements in natural sediments

In the sediment cores collected from deep site C in March, we measured concentration profiles of oxygen immediately after retrieval using a micro-manipulator operated microelectrode (Revsbech 1989). In addition, two cores (9.5 cm diameter, 15 cm length) were cut into 1 cm (first 6 cm) and 2 cm slices (6 to 12 cm) for pore water extraction and subsequent nutrient analyses.

Sediment cores from the nearshore sites A and B collected also in March were approximately 15 cm long. 50 cm^3 of each sediment slice were used for pore water extraction and nutrient analysis. 2 cm^3 sediment were kept at -80°C for pigment analysis.

Analytical procedures

Pore water was extracted by centrifugation (12500 g, 4°C, 15 minutes) and filtered through 0.45µm syringe filters. Nutrient analyses were made spectrophotometrically in duplicates following the methods of Strickland and Parson (1972). Pigments were analysed by HPLC using the method described by Rusch et al. (2001). According to this

method, chlorophyll a, chlorophyll b, fucoxanthine and peridinin were analysed using 90% acetone as extraction agent. Calcium carbonate content of the sediment was measured by complexometric titration of calcium carbonate with 0.1 N of hydrochloric acid according to Muller (1967). The Spirulina powder used for the laboratory experiments and the investigated sediments were analysed for particulate carbon (PC) and particulate nitrogen (PN) contents using a Fisons NA1500N elemental analyser with sulphanilamide as a calibration standard. The phosphorus content of the Spirulina powder was determined using the ignition method for particulate phosphate (PP) analysis (Andersen 1976). Following this method, 0.2 g of *Spirulina* was combusted in a furnace (450°C) and the ash was boiled in 1N HCL for 15 minutes. The sample was diluted to 100 ml with distilled water. Phosphate was then measured spectrophotometrically following the method of Strickland and Parson (1972).

Incubation experiments

Laboratory Incubation #1 with natural sediments

This experiment investigated the degradation of deposited organic matter in natural sediments from the Gulf of Aqaba with different mineral composition and permeabilities. Sediment cores retrieved from the shallow-water sites (4 carbonate and 4 silicate sand) as well as the 4 sediment cores collected at the deep site were incubated in acrylic flux chambers with 9.5 cm inner diameter and 40 cm height. The lengths of sediment cores were about 23 cm and the depth of the water column above the sediments was approximately 15 cm. The chambers were covered with gas-tight plastic lids with two sampling ports such that no air was enclosed in the chambers. To avoid stratification, the water above all sediments was stirred (18 rpm) using a rotating disk of 7 cm diameter placed 5 cm above the sediment surface.

At the beginning of the experiment, 0.1 g of freeze-dried *Spirulina* (containing 715 µmol N and 25 µmol P) was added to the water of chambers of each sediment type. The other 4 chambers were used as controls and remained without *Spirulina*. After initiating stirring, dissolved oxygen was measured in the water above each core at different time intervals (shown in Fig. 6) using a Clarke type microelectrode (Revsbech 1989). For

nutrient analyses, 50 ml of the overlaying water were withdrawn at different time intervals (shown in Fig. 6) using a 50 ml syringe, and replaced by 50 ml of sea water originating from the location where the sediments cores were collected. The duration of the experiment was 390 h.

Fluxes of solutes were calculated from linear regressions of solute concentrations over time for the initial (0 to 76 h for nutrients and 0 to 44 h for oxygen) and final period of the incubation (76 to 336 h for nutrients and 44 to 390 for oxygen). Diffusive flux of nutrients was calculated from concentration gradients at the sediment water interface from the nutrient profiles in March using Fick's first law of diffusion according to Rasheed *et al.* (in press).

Laboratory Incubation #2 with sieved sediments

This experiment investigated the degradation of organic matter in silicate and carbonate sands of the same grain size. Carbonate and silicate sediments were collected at the shallow sites in the Gulf of Aqaba by divers. The collected sediments were washed, dried, and the fraction of 250-500 µm grains was extracted by sieving. The sieved carbonate sand had a permeability of 43.8×10^{-12} m^2 and the sieved silicate of 22.6×10^{-12} m^2. The experiment and measurements were performed as described for Laboratory Incubation #1 except that here we used six chambers for each sediment type. In four of these six chambers, 3 g of *Spirulina* powder were mixed thoroughly with the sediment before incubation, corresponding to an addition of 21.6 mmol N and 0.7 mmol P. The remaining two chambers were used as controls. This experiment was designed to compare the decomposition of organic matter within the two sediment types, no *Spirulina* was mixed to the water column of the chambers. The duration of the experiment was 390 h.

Laboratory Incubation #3 with sieved sediments and tracer

In this experiment we compared the fluid exchange rates between overlaying water and sieved silicate and carbonate sediments (250-500µm), using an inert solute tracer. The experimental set-up was identical to that described for Laboratory Incubation #1 except that only four chambers were used, two for each sediment type. Instead of organic

matter, fluoresceine was added to the water of each chamber to a final concentration of 1µg l^{-1}. During the experiment, 5 ml of water were withdrawn at different time intervals (shown in Fig. 8) and replaced by the same volume of unstained water. The fluoresceine concentration in the samples was measured spectrofluorometrically. The duration of the experiment was 48 h.

In-situ incubation with sieved sediments

This experiment compared filtration and mineralization rates in sieved carbonate and silicate sands under field conditions. The carbonate and silicate sands for this experiment were collected and treated in the same manner as in laboratory incubation #2. The organic carbon contents prior to the experiment were 0.11 ± 0.03 and 0.06 ± 0.02% for the carbonate and silicate sediments, respectively.

Six cylinders (24 cm inner diameter, 20 cm length) were filled with the sieved carbonate sand, another six with the sieved silicate and sealed at the top and bottom with tough plastic foils secured by rubber bands. The sands were saturated with 0.2 µm filtered see water. At the selected sublittoral site (at about 5 m water depth, Fig. 1), 12 acrylic pipes (28 cm inner diameter, 40 cm length) were inserted to 35 cm length into the sea bed and the sediment inside the pipes was removed to approximately 19 cm depth. The cylinders containing the sieved sediments then were inserted into these pipes. Afterwards, the lower foil covers were removed from the sediment cylinders by pulling strings attached to the rubber bands and plastic foils. The gaps between pipes and cylinders were filled with sediment. The upper surfaces of the embedded sediments extended slightly above the sea bed. Then the pipes were removed. After 20 hours for temperature equilibration, first the upper foils and then the cylinders were removed leaving the sieved sands embedded in the seabed. Finally, the surfaces of the embedded sand cores were adjusted to the elevation of the surrounding sediment.

After 10 days, we sampled 6 of the embedded sediment cores (3 carbonate and 3 silicate). One large sub-core (9.5 cm i.diam., 20 cm long) and 4 small sub-cores (3.6 cm i.diam, 20 cm long) were taken from the central part of each of the 6 embedded sediments. The large sub-cores were sliced (upper 6 cm: 1 cm slices, and below that 2 cm slices). 50 cm^3 of each sediment slice were used for pore water extraction, another 2 cm^3 for the assessment of organic carbon content. 3 carbonate and 3 silicate sub-cores

(from the retrieved small cores) were immediately tested for oxygen consumption. The cores were cut into 3 layers (0-5, 5-10, and 10-15 cm). The sediment layers were homogenised and 25 cm^3 of each layer were incubated individually in gas tight bottles (250ml) with seawater (ca. 225 ml, filtered through 0.2µm filter). For the controls we incubated the cleaned sieved silicate and carbonate sediments. Before the bottles were tightly closed, the oxygen concentration in the water of each bottle was measured using a microelectrode. The oxygen measurements were repeated after 12 and 24 hours of incubation. For the pigment analysis, two of the small sub-cores (1 of each sediment type) were sliced (1 cm in the upper 6 cm and 2 cm downward to 10 cm). 2 cm^3 of sediment from each layer were removed using cut-off syringes and frozen at -80°C until analysis. After 22 days, a second set of subcores was collected in the same manner from the sieved sediments incubated in the seabed, and the same measurements were performed.

Results

Concentration profiles in natural silicate and carbonate sediments

The pore water profiles in the permeable sands from the shallow sites showed higher concentrations of all measured nutrients in the upper sediment layer (0-2 cm) relative to the profiles measured in the sediment from the deep site (Fig. 3).

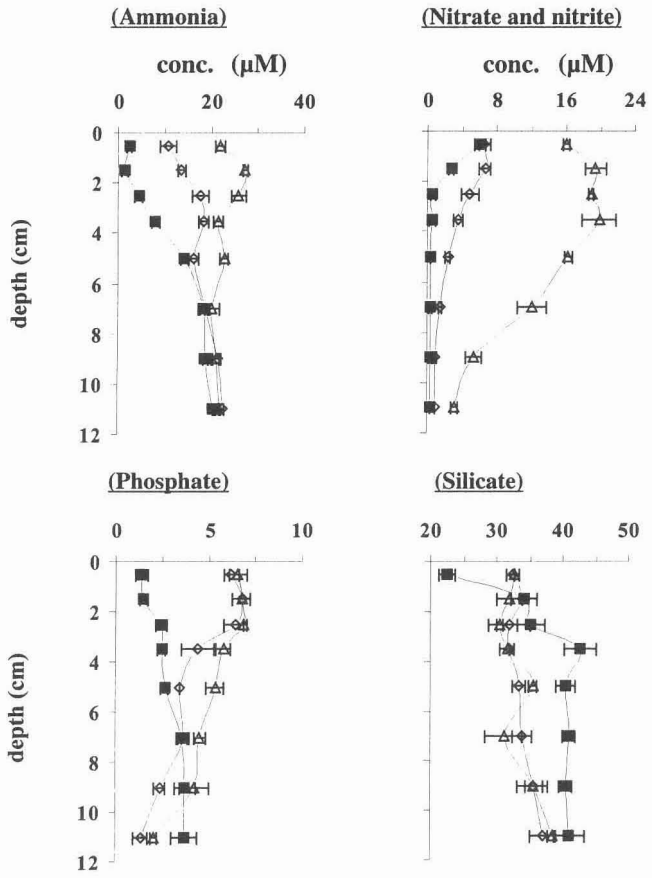


Fig. 3: Nutrient concentration (μM) profiles in carbonate (triangles), silicate (diamonds) and silt-clay (solid squares) sediments in March. Error bars represent the differences between two measured profiles.

This difference was most pronounced in the ammonium and phosphate profiles, in the silicate profiles the higher concentrations were restricted to the uppermost centimetres of the sediment. Below 5 cm depth, nutrient concentrations in all tested sediments were similar except nitrate and nitrite, where relatively high concentrations were recorded in the carbonate sand down to 8 cm depth. In the fine-grained sediment from the deep site, nitrate and nitrite was limited to the upper 2 cm and free oxygen could not penetrate deeper than 1.5 mm (Fig. 4).

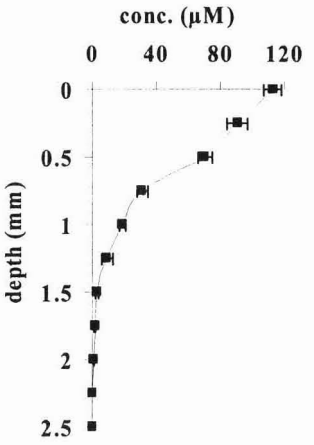


Fig. 4: Oxygen profile (µM) in the silt-clay sediment. Error bars represent the difference between two measured profiles.

Pigment profiles in carbonate and silicate sands from the shallow sites showed higher concentrations in the carbonate sediment (factors 2.0, 2.7, 2.6 for chl a, chl b, and fucoxanthine, respectively, for the whole sediment depth Fig. 5). These differences were most pronounced in chlorophyll b and fucoxanthine in the upper 2 cm of the sediments.

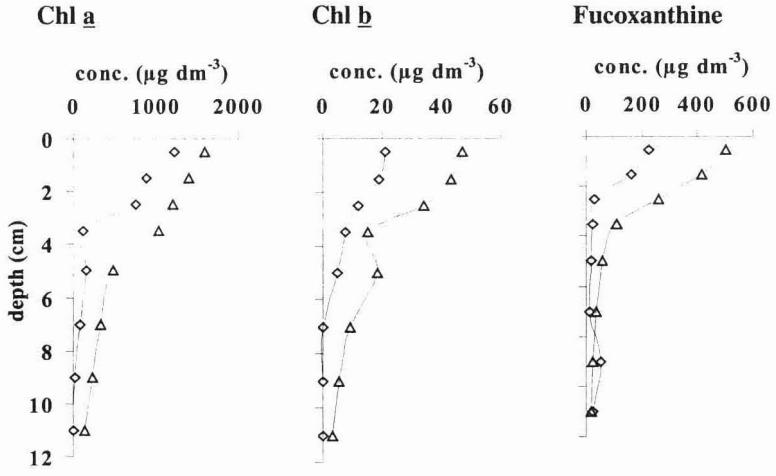


Fig. 5: pigment profiles (µg dm^{-3}) in carbonate (triangles) and silicate (diamonds) sediments in March.

Laboratory Incubation #1 with natural sediments, effect of permeability

After closing the lids, the oxygen concentrations in the water of all chambers immediately started to decrease, with highest consumption rates in the chambers with permeable sands (Figs. 6, 7). Maximum consumption rates were recorded in the chambers with *Spirulina*, reaching a peak value of 15.5 mmol m^{-2} d^{-1} in the carbonate sand chamber, 12.1 mmol m^{-2} d^{-1} in the silicate sand chamber, and 11.3 mmol m^{-2} d^{-1} in the silt chamber. 44 h into the experiment, the oxygen in the chambers with *Spirulina* had dropped below 35% of the start concentration, while in the control chambers more than 60% were still available. After this initial 44 h period, the changes in the oxygen concentrations in all chambers were relatively small (< 1.5 mmol m^{-2} d^{-1}), and in Fig. 7 we contrast the fluxes calculated for the initial period and the remaining time period.

In all chambers, concentrations of ammonium, phosphate and silicate concentrations grew throughout the incubation period, with strongest increases within the first 76 h (Fig. 7). The only exception was ammonium in the control chamber with silt that showed a concentration decrease during the last 72 h of the incubation. Nitrate and nitrite initially increased for a period of about 18 hours, and then dropped until the end of the incubation. Ammonium fluxes from the permeable control sands were 1.4 (silicate) to 2.0 (carbonate) times higher than that from the silt, while silicate and phosphate fluxes were higher in the chamber with the silt.

In all chambers with *Spirulina*, ammonium and phosphate concentrations increased faster than in the control chambers all through the incubation (Fig. 6, 7). Highest fluxes in ammonium (10.4 mmol m^{-2} d^{-1}) and phosphate (0.54 mmol m^{-2} d^{-1}) were recorded in the chambers with carbonate sand exceeding the fluxes in the chamber with silt (4.7 mmol NH_4^+ m^{-2} d^{-1}, 0.23 mmol PO_4 m^{-2} d^{-1}) by factor 2.2 and 2.3, respectively. Ammonium and phosphate fluxes in the silicate sand (7.3 mmol NH_4^+ m^{-2} d^{-1}, 0.28 mmol PO_4 m^{-2} d^{-1}) ranged between the fluxes recorded for the carbonate sand and the silt. Silicate fluxes again were highest in the chambers with silt (0.68 mmol m^{-2} d^{-1}).

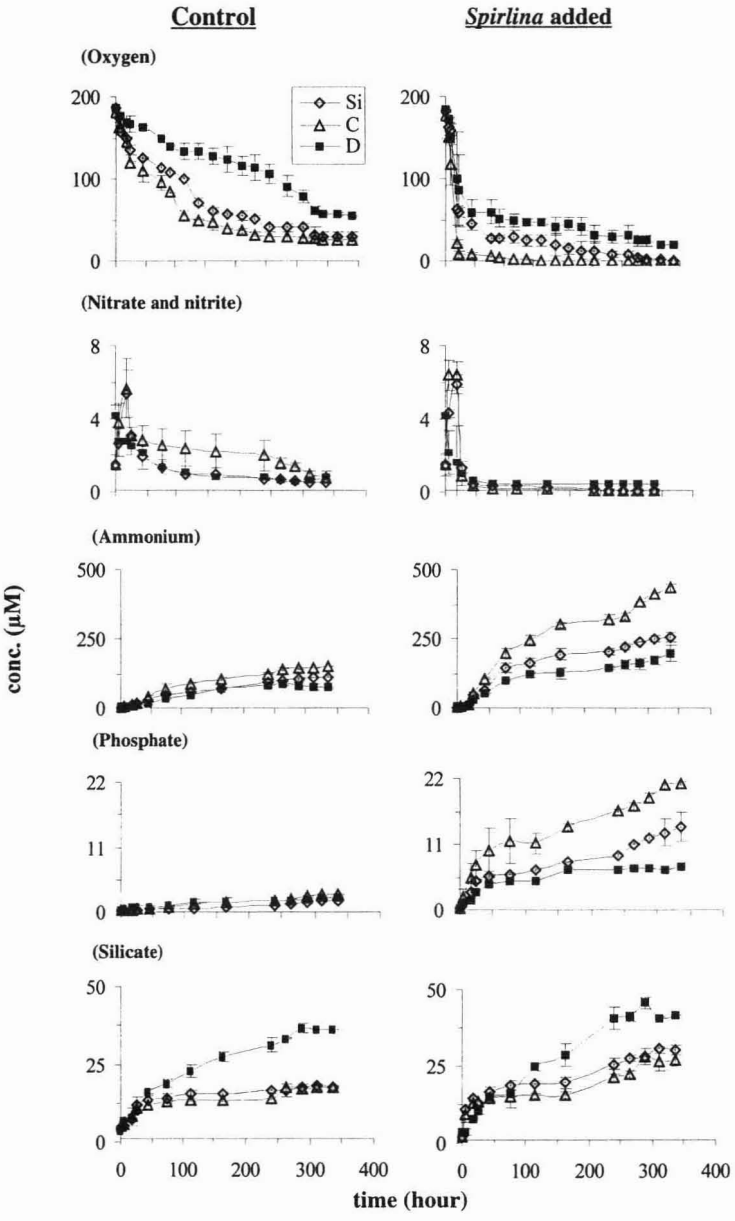


Fig. 6: Time course of nutrient and oxygen concentrations (µM) during the incubation of natural carbonate (triangles), silicate (diamonds) and silt-clay deep site (sequares) sediments. Number of incubation chambers 2 for control and 4 with *Spirulina*. Error bars represent the standard deviations of the concentrations from different chambers.

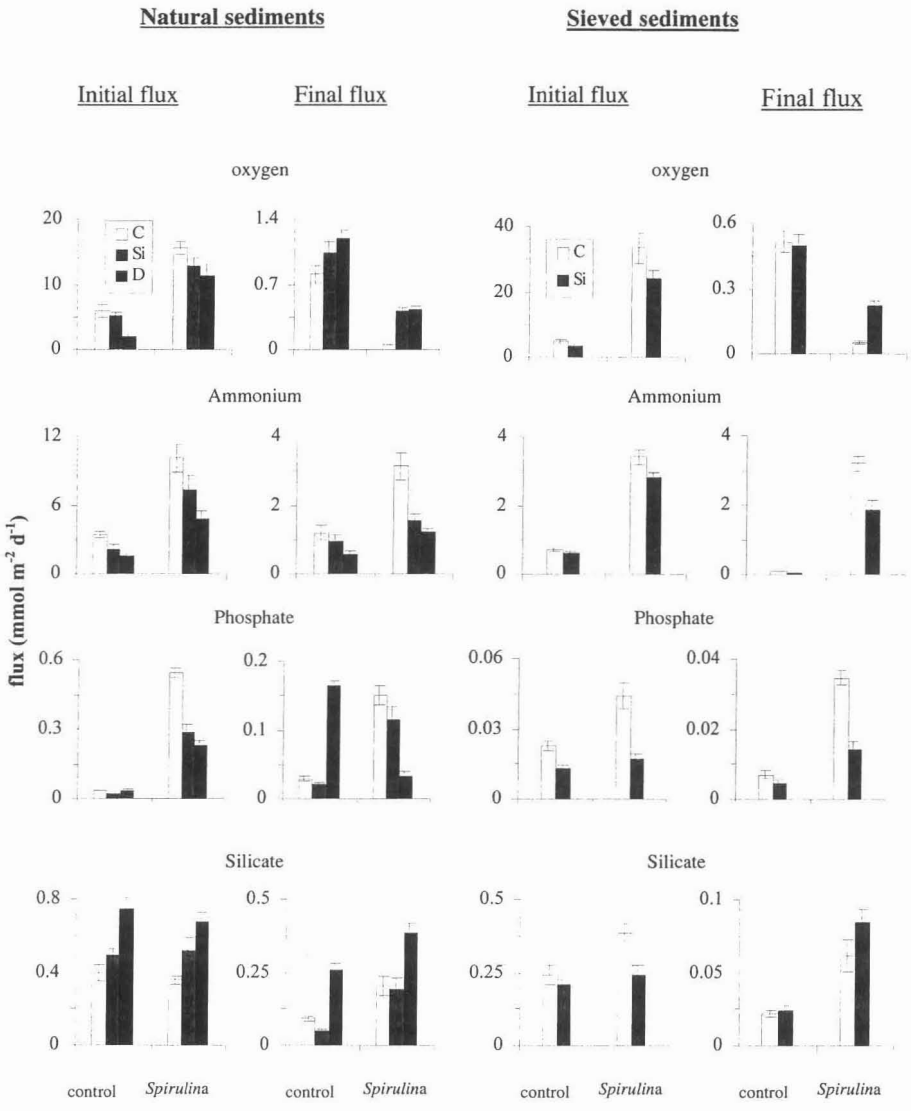


Fig. 7: Oxygen consumptions and nutrient fluxes (mmol m^{-2} d^{-1}) from carbonate (white), silicate (grey) and silt-clay (black) sediments calculated from the incubation of natural and sieved sediment in control chambers and chambers with added *Spirulina*.

Laboratory Incubation #2 with sieved sands, effect of mineral composition

Due to the cleaning and sieving of the sediments, the control chambers nutrient concentrations in this incubation were in general lower in the control chambers than in the previous experiment. Analogous to the incubations with natural sediments, oxygen concentrations decreased and nutrient concentrations increased (except for nitrate and nitrite) during the incubation of the sieved sands. In the control chambers, oxygen consumption rates and ammonium and silicate fluxes in the two sediment types were not significantly different, while the phosphate flux in the chamber with carbonate was higher than in the chamber with silicate sand (0.02 vs. 0.01 mmol m^{-2} d^{-1}, Fig. 7). However, the carbonate sand showed a stronger reaction to the addition of organic matter (*Spirulina*) relative to the silicate sand. Oxygen fluxes into the carbonate sediments were higher than into the silicate (33.4 vs 24.3 mmol m^{-2} d^{-1}). In the chambers with carbonate sand, flux of ammonium and phosphate were 1.4, 1.9 times higher than in the chambers with silicate sands, and the final concentrations of ammonium and phosphate in the carbonate sand reached 368.9 and 5.3 µM respectively, while in the silicate sands only 247.8 and 2.1 µM were recorded.

Laboratory Incubation #3 with sieved sands, effect of mineral composition

With values exceeding 10^{-12} m^2, the permeabilities of silicate and carbonate sands permitted advective pore water exchange. The radial pressure gradient generated by the rotating water column forced chamber water with solute tracer into, and pore water without tracer out of the sands. The curves depicted in Fig. 8.a reflect the gradual dilution of the fluoresceine-stained chamber water with clear pore water. Fluoresceine influx was higher in the carbonate sediment than in the silicate (initial flux: factor 1.4 Fig 8.b). For the chamber geometry and water volume used in the experiments, 8.3 and 11.1 ml h^{-1} water were flushed through the silicate and carbonate sand, respectively.

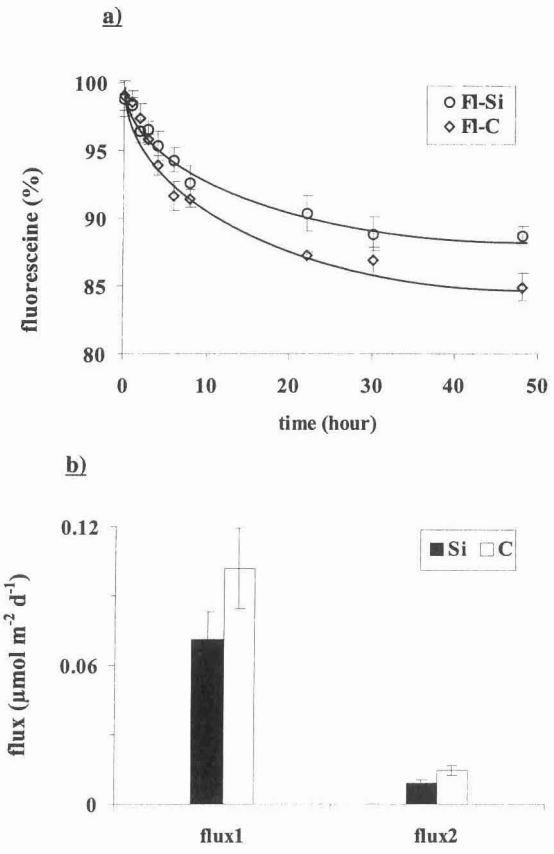


Fig. 8: a) Time course of fluoresceine (%) during the incubation of sieved carbonate and silicate sediments. Error bars represent the standard deviations of 3 chamber incubations. b) fluoreceine fluxes (µmol m^{-2} d^{-1}) calculated from the incubation.

In-situ sediment incubation

The pigment analyses in the dissected subcores revealed that the carbonate sands accumulated higher amounts of particulate organic matter during the *in-situ* incubation than the silicate sands (Fig. 9). After 10 days incubation, the profiles of chlorophyll a, chlorophyll b, and fucoxanthine showed higher concentrations down to 6 cm sediment depth, and after 22 days the differences between the pigment profiles in the two sediments had further increased. The calculated fluxes indicate a 2 to 3 fold higher accumulation rate in the carbonate sand (4.7 vs. 2.3, 0.3 vs 0.1, 2.1 vs 0.8 mg m^{-2} d^{-1} for

chl a, chl b, and fucoxanthine respectively). The differences in the concentration profiles between the two samplings (Fig. 9) show that the accumulation of chl a, chl b and fucoxanthine occurred deeper in the carbonate sand relative to the silicate. The accumulation rate in the carbonate sand had a subsurface maximum between 2 and 2.5 cm depth, while in the silicate sands, this rate peaked in the surface layer.

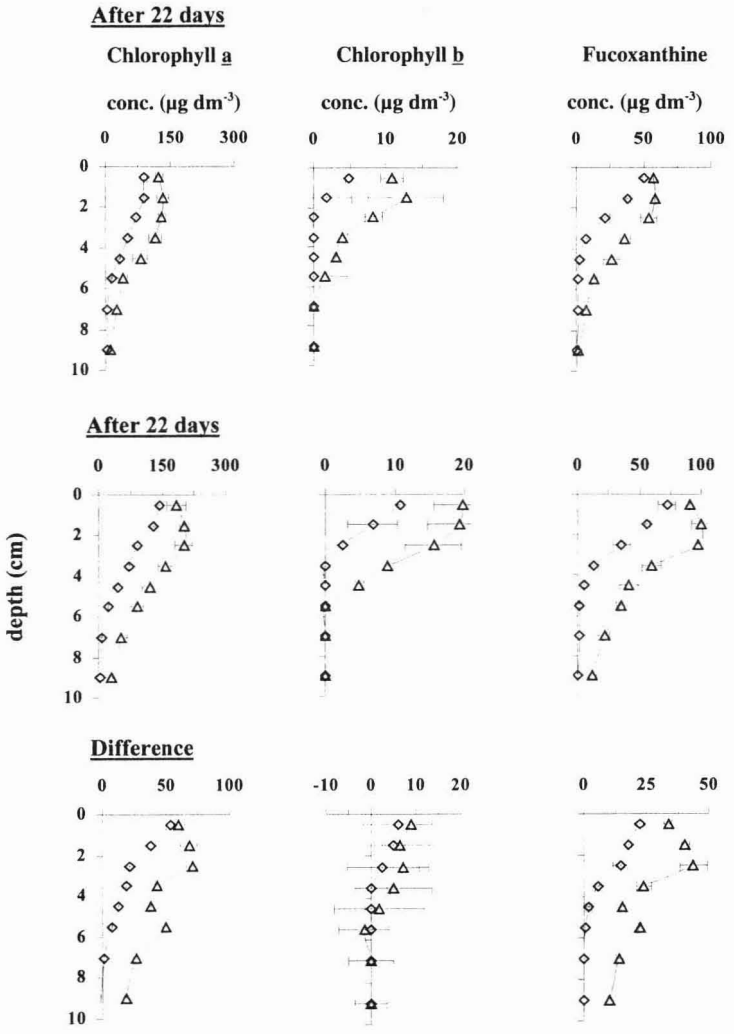


Fig. 9: Pigment profiles (µg dm^{-3} sediment) in silicate (diamonds) and carbonate (triangles) sediments after 10 and 22 day of *in-situ* incubation.

Oxygen consumption rates in the incubated carbonate and silicate sands decreased with sediment depth, (Fig. 10). At the end of incubation, the consumption rates of the two upper layers (0-5 cm: 2.3 µmol cm^{-3} d^{-1}, 5-10 cm: 2.0 µmol cm^{-3} d^{-1}) of the carbonate sand were 1.5 and 1.7 times higher than those of the respective layers in the silicate sand (0-5 cm: 1.6 mmol cm^{-3} d^{-1}, 5-10 cm: 1.4 mmol cm^{-3} d^{-1}). Below 10 cm depth the rates were lower and similar in both sediments. Between the first and second sampling, the consumption rates in the two upper layers increased by more than 40%, below these layers, the rates did not change significantly.

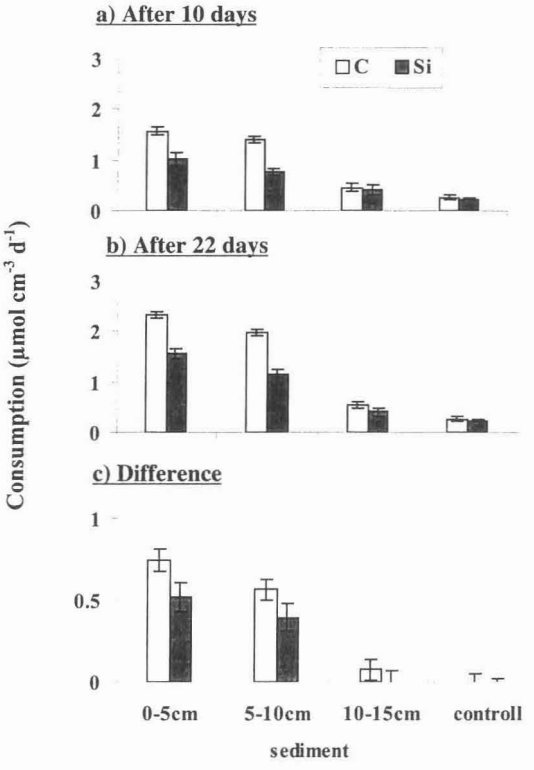


Fig. 10: Oxygen consumption (µmol cm^{-3} d^{-1}) for different layers of the incubated sieved carbonate (white column) and silicate (grey column) and for control (sieved sediments without incubation), a) after 10, b) 22 days of *in-situ* incubation and c) the differences between the two incubation times.

Discussion

Our findings highlight the differences in degradation rates of organic material in shallow coarse and deep site silt sediments with different permeabilities and mineral compositions. *In-situ* measurements of nutrient profiles showed higher concentrations in coarse permeable sediment compared to the silt, which indicate different degradation rates of organic matter. Nutrient and pigment profiles in shallow site carbonate and silicate sands reveal also higher decomposition activity in the biogenic sediments. In the following paragraphs, we elucidate first the main difference between the three sediments and then try to discuss the processes that cause these differences.

In-situ measurements

The concentrations of DIN and DIP of shallow coarse sand were higher than in the silt-clay (2.3 and 1.8 fold for the whole sediment column, respectively Fig. 3) and the concentration in carbonate sand were higher than those in the silicate sand (1.8, 1.2 fold). Pigment concentrations were also higher in carbonate sediments compared to silicate (Fig. 5). These differences can be an indication of different organic matter mineralization rates and decomposition pathways, that we link to the different properties of these sediments, i.e. the permeability, specific surface area and mineral composition. The effect of high sediment permeability on biogeochemical processes was demonstrated by Falter and Sansone (2000) who studied DIN and oxygen distribution in permeable sediments. Through the measurement of nutrients and oxygen profiles, they found different metabolic rates and decomposition pathways depending on sediment permeability. However, from in-situ results alone we could not make solid conclusions about the important factors which cause these differences because numerous factors might play a role in these differences including all ecological parameters, such as temperature, current velocity and anthropological input. To exclude these factors from the possible reasons, lab incubations under controlled conditions were carried out to study the effect of permeability, mineralogical characteristics, and grain surface area.

Benthic nutrient fluxes

Fluxes of nutrients in the laboratory control cores (Fig. 7) were comparable to fluxes reported in the literature for carbonate, silicate and silt-clay sediments (Table 3). Oxygen consumption rates in our sediments were relatively low compared to rates reported for coastal sediments in the literature. For example Reay et al. (1995) found higher oxygen consumption rates and higher ammonium and phosphate fluxes in Chesapeake Bay sediments, however, these sediments also had higher organic matter content (0.7 and 4.7 % respectively) than our sediments (0.1 and 0.4 respectively, Table 2). Clavero et al. (2000) also reported high nutrient fluxes and high oxygen consumption rates from Palmones Estuary and attributed the high values to high organic content in the silt clay sediment that they investigated (8 %). It is clear that besides organic content, many other factors affect the solute fluxes in marine sediments. Friedl et al. (1998) and Clavero et al. (2000) demonstrated the dependence of fluxes on temperature and reported higher flux values with higher temperature, which caused high diffusion rates and biological activity. Abundance of benthic microalgae has been found to affect fluxes of nutrients (Bertuzzi et al. 1996). Shum and Sundby (1996) emphasised the importance of different physical properties of the sediments for the oxygen uptake.

Diffusive fluxes are usually inferred from pore water profiles and Fick's first law of diffusion (Berelson et al. 1987, Ciceri et al. 1999, Clavero et al. 2000). To compare fluxes calculated by this method to the total fluxes calculated from concentration changes in the water of our incubation chambers, pore water profiles for carbonate and silicate sediments previously measured at the same study sites (Rasheed et al. sub.) were used to calculate diffusive fluxes for ammonium, phosphate and silicate. Total fluxes were always at least 3-fold higher than the calculated diffusive fluxes (Table. 4). The higher total fluxes resulted either from bioturbation (Kelley et al. 1990, Barbanti et al. 1992) or from advective pore water exchange, which occurs mainly in coarse permeable sediment (Huettel et al. 1996, Huettel & Rusch 2000). In our case, we can exclude the effect of bioturbation, since no macrofauna was present in the incubated sediment. This suggests that stronger advective transport was responsible for higher fluxes in the carbonate sediment (Rasheed et al. sub.).

Location	Sediment type	Ammonium	phosphate	Oxygen	Ref.
Davies Reef Great Barrier Reef, Australia	Sandy carbonate			9.32 ± 0.79	Hansen et al. (1992)
Araruama Lagoon Brazil	Sandy carbonate	0.62 ± 0.32	0.01 ± 0.01	-18.95 ± 4.85	Knoppers et al. (1996)
Kanoeohe Bay Hawaii	Sandy carbonate	0.47	0.03		Stimson and Larned (2000)
Chesapeake Bay	Sandy silicate	-1.06 - 8.59	-0.13-1.008	-20.93	Reay et al. (1995)
USA	Silt clay	-0.72 - 14.76	-0.08-0.86	-53.28	
Palmones Estuary	Silt clay	3.2 - 9.6	0.27 - 1.6	-62.5 - -87.4	Clavero et al. (2000)
This study (Gulf of Aqaba)	Sandy carbonate	3.41 ± 0.3	0.03 ± 0.002	-5.92 ± 0.05	
	Sandy silicate	2.15 ± 0.3	0.02 ± 0.002	-5.07 ± 0.05	
	Silt clay	1.57 ± 0.3	0.04 ± 0.002	-1.89 ± 0.05	

Table 3: Fluxes of the Gulf of Aqaba compared with fluxes from other areas (in mmol m^{-2} d^{-1}). Positive values are efflux out of the sediment and negative values are influx into the sediment.

Paramete	*Silicate*	*Carbonate*
Ammonium	88.5	114.2
Phosphate	3.5	7.8
Silicate	14.4	11.6

Table 4: Ratios between fluxes calculated from chamber experiment and diffusive fluxes for carbonate and silicate sediment.

Mineralization rates of Spirulina in different sediment under oxic and anoxic conditions

The laboratory experiments with addition of Spirulina showed the same general trends. The mineralization rates of *Spirulina* were depending on the type of the incubated sediment and its permeability (Fig. 7). In order to get an estimate of the mineralization rates of *Spirulina* in different sediments under oxic and suboxic/ anoxic conditions (oxygen less than 5 % of saturation) , we calculated the mineralized carbon using the fluxes of DIP, DIN and oxygen in the spiked chambers assuming a Redfield ratio of C:N:P (106:16:1) and a ratio of 1 for CO_2:O_2 (e.g. Berelson et al. 1998) after subtraction the fluxes recorded in the control chambers. The mineralization rate under oxic condition were estimated from the initial fluxes because these fluxes were recorded when oxygen concentrations in all chambers were still higher than 5% oxygen air saturation. The initial mineralization activity in the chambers and the resulting DIP and DIN fluxes (Fig. 6) were considered to correspond to the mineralization activity taking place under oxic conditions with more than 5% oxygen air saturation. Analogously, the late fluxes (Fig. 7) were used to estimate the rates under suboxic/anoxic conditions. The mineralization rates of *Spirulina* in coarse sediments estimated from DIP and DIN were approximately 2 times higher than those estimated for the fine silt sediments, and the coarse carbonate sand showed a higher degradation rate than the coarse silicate sediment (~ 1.5 fold, Table 5 and 6). In the natural sediments, the mineralization rates estimated from DIP and DIN were always higher than the rates estimated from oxygen consumption, which indicated the importance of anerobic mineralization of organic matter in these sediments.

conditions		*Oxic*			*Anoxic*	
parameter	*DIN*	*DIP*	*Oxygen*	*DIN*	*DIP*	*Oxygen*
carbonate	3.7	4.5	0.8	1.1	1.1	-0.1
silicate	2.8	2.4	0.7	0.3	0.8	-0.1
silt	1.8	1.7	0.8	0.3	0.0	-0.1

Table 5: Spirulina mineralization rate (mg C m^{-2} d^{-1}) calculated from DIN and DIP fluxes and oxygen consumptions in natural carbonate, silicate and silt-clay sediments under oxic and suboxic/anoxic conditions (calculations can be found in the text). The negative values indicate higher fluxes or consumptions in control chamber than the chambers with Spirulina.

conditions		*Oxic*			*Anoxic*	
parameter	*DIN*	*DIP*	*Oxygen*	*DIN*	*DIP*	*Oxygen*
carbonate	1.5	0.2	2.4	1.7	0.2	0.0
silicate	1.2	0.1	1.7	1.0	0.1	0.0

Table 6: Spirulina mineralization rate (mg C m^{-2} d^{-1}) calculated from DIN and DIP fluxes and oxygen consumptions in sieved carbonate, and silicate sediments under oxic and suboxic/anoxic conditions (calculations can be found in the text).

The degradation rates under oxic conditions were higher than the rate under suboxic/anoxic conditions for all sediment types (>2.5 fold) except the mineralization estimated from DIP and DIN in sieved sediment (Table. 5 and 6). Several studies compared organic matter decomposition rates in oxic and suboxic/anoxic conditions. Some authors demonstrated that the rates were not significantly different (e.g. Westrich and Berner 1984, Lee 1992). Others found that anoxic mineralization was greater than under oxic conditions (Sun et al. 1993), unless macrofauna were present (Kristensen and Blackburn 1987). Our study, however, showed that the oxic degradation rates of organic matter were higher than the suboxic/anoxic degradation rates, which agrees with some other studies (e.g. Benner et al. 1984, Henrichs and Reeburgh 1987, Sun et al. 1997). Several theories have been suggested to explain the lower decomposition rates under anoxic conditions. Some of the decomposition pathways could not be catalysed under anoxic conditions or inhibitory metabolites may build up and reduce degradation rates in anoxic sediment (Schink 1988).

In lab incubation #1, specific amounts of *Spirulina* were added to the water column above the sediment, and most of the added *Spirulina* were deposited on the sediment surface shortly after start of the experiment. In the case of the silt sediment, most of the organic matter degraded on the surface of the sediment. Due to the high permeabilities of the coarse sands, which allowed some organic matter to penetrate into the sediment (Huettel and Rusch 2000), degradation in these coarse sands occurred on the surface and within the upper sediment layer The degradation rate then depends also on how deep the organic matter penetrated into the sediment. Under same stirring conditions, the permeability of the sediment was the controlling factor that determined the penetration depth as has been shown in similar experiments by Huettel and Rusch (2000).

In lab incubation #2, we mixed *Spirulina* with the sieved sediment trying to minimize the effect of permeability and to study the effect of mineral composition and grain surface area on the mineralization of organic materials. In this experiment, carbonate and silicate sediment of same grain sizes were used to compare mineralization of organic matter in the two sand types. Despite the similarity of the size distribution, permeability of the carbonate sediment was twice as high as that of the silicate sediment (Table. 2). The grain surface area of the carbonate sediment was also higher than that of the silicate sediment (factor 1.5, Table. 2) and the grains of the carbonate were more porous and rough compared to the less porous and smooth silicate grains (Fig. 2). Also in this experiment, the degradation rate of *Spirulina* in the carbonate sediments were always higher than in the silicate sediments under both, oxic and suboxic/anoxic conditions (factor at least > 1.2 Table. 6). In the study of Marinelli et al. (2000) using sediments with the same median grain size (250-500), they emphasised the importance of the permeability as a key factor for enhancing nutrient fluxes as a result of pore water advection in such sediments. Further discussion of the impact of the permeability and the surface area on organic matter degradation are in the following suctions.

Lab experiment #3 with fluoresceine showed that in the carbonate sediment, which was more permeable than the silicate (2 fold, Table. 1), the fluoresceine flux into the sediment was higher (factor 1.4, Fig. 8). This implied a stronger advective transport in the carbonate sediment compared to the less permeable silicate sediment. This finding is in agreement with Forster et al. (1996) who found in a flume experiment with rhodamine as a tracer, stronger and deeper flux in permeable sediments. This experiment with an

inert tracer demonstrates that in sand with the same grain size, interfacial water flows are higher in the biogenic carbonate sands than in the terrigenic silicate sands (factor 1.3). Pores within the individual grains, a less rounded shape with very rough grain surfaces are the main factors for the higher permeability in the carbonate (Fig.2). These interfacial water flows carry dissolved and particulate organic matter into the sediment (Pilditch et al. 1998, Huettel and Rusch 2000, Jahnke et al. 2000, Rusch & Huettel 2000) and thus could be responsible for the higher fluxes and mineralization rates observed in the carbonate sand.

The in situ incubation experiment tested the trapping efficiency of organic particles in the sieved carbonate and silicate sediments. During incubation, more pigments (chl a, chl b and fucoxanthine) were trapped in the carbonate sediment than in the silicate (average factor of 2 for all measured pigments). Moreover, the pigments penetrated deeper into the carbonate sediment (average of 6 cm and 4 cm, respectively). This increase in pigment content in the sediments during the incubation can be attributed mainly to the filtration of water through the permeable sediments. To calculate trapping rates of PON, we converted Chl a to POC assuming a conversion factor of 60 for the Chl a : POC ratio as reported in Yahel et al. (1998). A factor of 0.15 was used to convert POC to PON according to Redfield ratio. With these conservative calculations we arrived at trapping rates of 21 and 42 mg m^{-2} d^{-1} PON in silicate and carbonate sediments, respectively. These values are comparable to other values reported in tropical region (e.g. Charpy and Charpy-Roubaud 1991 (36 mg m^{-2} d^{-1}), Clavier et al. 1995 (23-35 mg m^{-2} d^{-1})). In order to estimate the difference in filtration rates between silicate and carbonate sands, we also calculated how much seawater would have to be filtered (100% filtration efficiency) through the upper sediment layer to account for the increase of organic matter in both sediments during the incubation period. In these calculation, the trapping rates of Chl a in 9 cm (Fig. 9) of the carbonate and silicate sediments after 22 days (2.3 and 4.7 mg m^{-2} d^{-1} respectively) and Chl a value in seawater (0.22 µg l^{-1}, Rasheed et al. in press.) were used. According to these calculations, we arrived at flushing rates of 348 and 712 l m^{-2} $month^{-1}$ for silicate and carbonate sediment respectively. The higher carbonate filtration capacity (2 fold) can be expected due to the 2 fold higher permeability of the carbonate sediment (Table. 2). The oxygen consumption measurements of the sliced sediment cores emphasised these findings. The rates of oxygen consumption were higher in the carbonate sediment than in the silicate (factor 1.5 in all layers, Fig. 10) indicating higher

organic matter trapping rate in the carbonate. A decrease of consumption with increasing depth in both sediments indicated that more organic material was trapped in the surface sediment layers.

What controls organic matter decomposition in sediments

We found significant differences in organic matter mineralization and consequently re-emission of inorganic nutrients to the water column in the three different sediment types of the study. The different experiments carried out have pinpointed some possible reasons for these differences. Amongst these are permeability, grain surface area and mineralogical characteristics.

(i) Permeability

Different permeabilities of the three sediment types (Table. 2), cause different oxygen transport rates and penetration depths that lead to different degradation rates under oxic conditions. Oxygen penetration depth of the silt-clay was 1.5 mm (Fig. 3), compared with a penetration depth of more than 5 mm for permeable sands (Huettel and Rusch 2000). Ziebis et al. (1996) have reported even higher oxygen penetration in more permeable sediments. Increased oxygen consumption related to increased organic matter degradation with increasing sediment permeability (Table 2. and Fig. 10) was reported by several authors (Forster et al. 1996, Marinelli et al. 1998, Dauwe et al. 2001). In silt-clay, the transport of electron acceptors for the degradation of organic matter, is limited by diffusion (Froelich et al. 1979) while in permeable sands, advection co-acts on transport of electron acceptors in addition to diffusion (Huettel and Gust 1992, Forster and Graf 1995) promoting higher organic matter degradation rates.

Our experiments with sieved carbonate and silicate sediment of the same grain size demonstrated how differently the two sediments controlled organic material trapping and degradation, fluoresceine penetration, oxygen consumptions and nutrient fluxes. The findings of these experiments are in good agreement with Huettel and Rusch (2000), who reported an increase in organic matter penetration depth and degradation rates with increasing sediment permeability. These authors suggest that the enhanced supply of electron acceptors and increased removal of decomposition products by pore water advection causes the higher mineralization activity in permeable sediment. Huettel and

Gust (1992) determined the critical permeability required for advective interfacial fluxes of water and microalgae as 1×10^{-12} m^2. The permeability of the silicate sediments of the present study is 22.6×10^{-12} m^2, well above the critical value. Therefore, advective flux of material cannot be ruled out.

(ii) Grain surface area of the sediment

The grain size of the deep sediment was much smaller than that of the shallow sediment (8 fold, Table 2). Consequently, the specific surface area of the silt-clay was much higher than that of the sieved carbonate and silicate sediments of the shallow site (17 and 26 fold, Table 2). Inverse correlation between grain size and organic carbon content was reported by (Anderson 1988, Oades 1988) and direct correlation between grain surface area and organic matter content was reported by several authors (Mayer 1994, Ransom et al. 1998, Adams and Bustin 2001). Mayer et al. (1993) pointed out that most organic matter in sediments is adsorbed to the mineral surfaces. Small pores and large surface area in fine sediments protect organic matter against digestive attack (Marshman and Marshall 1981, Mayer et al. 1993, Hedges and Keil 1995). The fine sediments from the deep site had higher organic content than the carbonate and silicate sediment from the shallow site (9 fold, Table 2) and lower nutrient concentrations in the sediment surface layer(Fig. 3), which in agreement with the mentioned findings. Our incubation experiment of the sieved carbonate and silicate sediments with fluoresceine and the in situ sediment incubation demonstrated that more water was flushed (factor 1.3 Fig. 8) and more organic matter accumulated in the carbonate sediments (factor 1.5, Fig. 9), which had a higher grain surface area than the silicate sediments (1.5 fold, Table 2). In the incubation experiments with sieved sands, the carbonate sediments were more reactive than the silicate sediments. These results reveal that organic matter mineralization was faster and went further in the carbonate sediment than the silicate sediment. This implies that protection of the organic matter was not efficient in this case. A likely explanation to that is higher transport velocity in the carbonate sediment, resulting in high advective processes that accelerate mineralization of the organic material (Rusch and Huettel 2000).

(iii) Mineralogical characteristics

Carbonate sediments contain mainly $CaCO_3$ (ca. 80%, Table. 2), while silicate and silicous silt-clay sediments may contain a low percentage of $CaCO_3$ (ca. 5%, 20%, Table. 2). In carbonate sediment, pore water is automatically buffered upon release of CO_2 during the oxidation of organic matter (Buddemeier and Oberdorfer 1986) which has a direct impact on the degradation process. Ransom et al. (1998) confirmed that sediment mineralogy was the primary factor for organic carbon accumulation. Carbonate sediments contain many small pores resulting from the skeletal remains of corals and sea urchins etc., which produce these sediments (Fig. 2). These pores increase the surface area of the carbonate grains and surface roughness which in turn increase the ability of the sediment to accumulate more organic matter (Mayer 1994). A conclusion can be made that different mineralogical composition of the three investigated sediments is an added reason for differences in the accumulation and degradation of organic particles.

Conclusion; consequences for natural environments

The present investigation shows that organic matter is mineralized at a higher rate in the coarse shallow sediments, including carbonate and silicate, in comparison with silt-clay bottom sediments due to different chemical and physical properties. Our study then shows the importance of the shelf sediments, which comprise 8% of the total ocean area (Ott 1988) in the mineralization of organic matter and sustaining the primary productivity of the ocean. Our result suggest that relatively large volumes of water are flushed through the silicate and carbonate sediments (348 and 712 l m^{-2} $month^{-1}$) which implies an important role of shallow sediments in filtration of organic matter and subsequent mineralization and nutrient release. Coarse permeable shelf sands, thus, can be important nutrient regenerators for primary production. This emphasises the finding of several authors that the importance of the bottom sediment to organic matter mineralization is inversely related to the water column depth (e.g. Jorgensen 1983) and that continental shelves are as important as the deep see in carbon and nitrogen biogeochemical cycles (Walsh 1991, Jorgensen 1996).

Acknowledgements:

This work was a part of the Red Sea Program and has been funded by the German Federal Ministry of Education and Research (BMBF grants no. 03F0245A) and Max Plank Institute for Marine Microbiology in Bremen, Germany. Thanks are due to Dr. Martin Kölling from Geology Department, Bremen University for his assistance in the determination of sediment surface area. Thanks are due to the staff members of the Marine Science Station in Aqaba, Jordan for their full support and help during the study, especially to Al-salamn, Al-trabeen, Al-sokhni, Mansreh, and Hammad.

References

Adams RS, Bustin RM (2001) The effects of surface area, grain size and mineralogy on organic matter sedimentation and preservation across the modern Squamish Delta, British Columbia: the potential role of sediment surface area in the formation of petroleum source rocks. Int J Coal Geol 46:93-112

Aller RC (1980) Diagenetic processes near the sediment-water interface of Long Island Sound: II. Fe and Mn. Advances in Geoph, 1980, 22: 351-415

Andersen JM (1976) An ignition method for determination of total phosphorus in lake sediments. Water Research 10:329-331

Anderson DW (1988) The effect of parent material and soil development on nutrient cycling in temperate ecosystems. biogeochem 5:71-97

Barbanti A, Ceccherelli VU, Frascari F, Reggiani G, Rosso G (1992) Nutrient regeneration processes in bottom sediments in a Po Delta Lagoon (Italy) and the role of bioturbation in determining the fluxes at the sediment water interface. Hydrobiologia 228:1-21

Benner R, Maccubbin AE, Hodson RE (1984) Anaerobic biodegradation of the lignin and polysaccharide components of lignocellulose and synthetic lignin by sediment microflora. Appl Environ Microbiol 47:998-1004

Berelson WM, Hammond DE, Johnson KS (1987) Benthic fluxes and the cycling of biogenic silica and carbon in 2 Southern-California borderland basins. Geochim Cosmochim Acta 51:1345-1363

Berelson WM, Heggie D, Longmore A, Kilgore T, Nicholson G, Skyring G (1998) Benthic nutrient recycling in Port Phillip Bay, Australia. Est Coast Shelf Sci 46:917-934

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

Boudreau BP, Guinasso NL (1982) The influence of a diffusive sublayer on accretion, dissolution, and diagenesis at the sea floor. In: Fanning KA, Manheim FT (eds) The dynamic environment at the ocean floor. Lexinton, Massachusetts, pp 115-145

Buddemeier RW, Oberdorfer JA (1986) Internal hydrology and geochemistry of coral reefs and atoll islands: key to diagenetic variations. In: Schroeder JH and Purse BH (eds) Reef Diagenesis. Springer, Berlin, pp 91-112

Canfield DE (1993) Organic matter oxidation in marine sediments. In: Wollast R, Chou L, Mackenzie F (eds) Interactions of C, N, P, and S in Biogeochemical Cycles. Nato ASI Ser. Springer, Berlin, pp 333-363

Charpy L, Charpy-Roubaud CJ (1991) Particulate Organic-Matter Fluxes in a Tuamotu Atoll Lagoon (French-Polynesia). Mar Ecol Prog Ser 71:53-63

Charpy-Roubaud CJ, 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

Ciceri G, Ceradini S, Zitelli A (1999) Nutrient benthic fluxes and pore water profiles in a shallow brackish marsh of the lagoon of Venice. Annali Di Chimica 89:359-375

Clavero V, Izquierdo JJ, Fernandez JA, Niell FX (2000) Seasonal fluxes of phosphate and ammonium across the sediment- water interface in a shallow small estuary (Palmones River, southern Spain). Mar Ecol Prog Ser 198:51-60

Clavier J, Chardy P, Chevillon C (1995) Sedimentation of particulate matter in the south-west lagoon of New-Caledonia - spatial and temporal patterns. Est Coast Shelf Sci 40:281-294

Dauwe B, Middelburg JJ, Herman PMJ (2001) 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

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

Forster S, Graf G (1995) Impact of irrigation on oxygen flux into the sediment: Intermittent pumping by Callianassa subterranea and "piston-pumping" by Lanice conchilega. Mar Biol 123:335-346

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

Friedl G, Dinkel C, Wehrli B (1998) Benthic fluxes of nutrients in the northwestern Black Sea. Mar Chem 62:77-88

Froelich PN, Klinkhammer GP, Bender ML, Luedtke NA, Heath GR, Cullen D, Dauphin P, Hammond D, Hartman B, Maynard V (1979) Early oxydation of organic matter in pelagic sediments of the eastern equatorial Atlantic suboxic diagenesis. Geochim Cosmochim Acta 43:1075-1090

Hedges JI, Keil RG (1995) Sedimentary organic matter preservation: an assessment and speculative synthesis - authors closing comments. Mar Chem 49:137-139

Henrichs SM, Reeburgh WS (1987) Anaerobic mineralization of marine sediment organic-matter -rates and the role of anaerobic processes in the oceanic carbon economy. Geomicrobiol J 5:191-237

Holmer M (1996) Composition and fate of dissolved organic carbon derived from phytoplankton detritus in coastal marine sediments. Mar Ecol Prog Ser 141:217-228

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

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

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

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. Continental Shelf Res 20:109-127

Jorgensen BB (1983) Processes at the sediment-water interface. In: Bolin B, Cook RB. (eds) The Major biochemical cycles and their interactions, vol 21. John Wiley, New York, pp 477-515

Jorgensen BB (1996) Material flux in the sediment. In: Jorgensen BB, Richardson K (eds) Eutrophication in Coastal Marine Ecosystems, vol 52. American Geophysical Union, pp 115-135

Kelley CA, Martens CS, Chanton JP (1990) Variations in sedimentary carbon remineralization rates in the White-Oak River Estuary, North-Carolina. Limnol Oceanog 35:372-383

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. Amer Soc of Agronomy

Knoblauch C (1999) Isolation and characterization of psychrophilic sulfate-reducing bacteria from permanently cold arctic sediments. Bremen University

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, Blackburn TH (1987) The fate of organic-carbon and nitrogen in experimental marine sediment systems - influence of bioturbation and anoxia. J Mar Res 45:231-257

Lee C (1992) Controls on organic-carbon preservation - the use of stratified water bodies to compare intrinsic rates of decomposition in oxic and anoxicsystems. Geochim Cosmochim Acta 56:3323-3335

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

Marshman NA, Marshall KC (1981) Bacterial-growth on proteins in the presence of clay-minerals. Soil Biol Biochem 13:127-134

Mayer LM, Jumars PA, Taghon GL, Macko SA, Trumbore S (1993) Low-density particles as potential nitrogenous foods for benthos. J Mar Res 51:373-389

Mayer LM (1994) Surface-area control of organic-carbon accumulation in continental-shelf sediments. Geochim Cosmochim Acta 58:1271-1284

Muller G (1967) Methods in sedimentary petrology. Hafner Pub. Co., New York

Oades JM (1988) The retention of organic-matter in soils. biogeochem 5:35-70

Ott J (1988) Meereskunde. Verlag Eugen Ulmer, Stuttgart

Pätzold J, Halbach PE, Hempel G, Weikert H (2000) Östliches Mittelmeer-Nördlches Rotes Meer 1999. Cruise No. 44 22 January-16 May 1999, Universität Hamburg 240pp

Pilditch CA, Emerson CW, Grant J (1998) Effect of scallop shells and sediment grain size on phytoplankton flux to the bed. Continent Shelf Res 17:1869-1885

Ransom B, Kim D, Kastner M, Wainwright S (1998) Organic matter preservation on continental slopes: Importance of mineralogy and surface area. Geochim Cosmochim Acta 62:1329-1345

Rasheed M, Badran MI, Richter C, Huettel M (in press.) 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

Reay WG, Gallagher DL, Simmons GM (1995) Sediment-water column oxygen and nutrient fluxes in nearshore environments of the lower Delmarva Peninsula, USA. Mar Ecol Prog Ser 118:215-227

Revsbech NP, Jorgensen BB (1986) Microelectrodes - their use in microbial ecology. Advances Microb Ecol 9:293-352

Revsbech NP (1989) An oxygen microsensor with a guard cathode. Limnol Oceanogr 34:474-478

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

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

Schink B (1988) Principle and limits of anaerobic degradation: Environmental and technological aspects. In: Zehnder AJB (ed) Biology of Anaerobic Microorganisms. Wiley, Interscience, pp 771-846

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

Sorkin YI (1995) Coral reef ecology. Ecological studies, vol 192. Springer-Verlag, Berlin

Stimson J, Larned ST (2000) Nitrogen efflux from the sediments of a subtropical bay and the potential contribution to macroalgal nutrient requirements. J Exp Mar Biol Ecol 252:159-180

Strickland JD, Parsons TR (1972) A practical handbook of seawater analysis. Bull. Fish. Res. Board. Can.

Sun MY, Lee C, Aller RC (1993) Laboratory studies of oxic and anoxic Degradation of chlorophyll-a in Long-Island Sound sediments. Geochim Cosmochim Acta 57:147-157

Sun MY, Wakeham SG, Lee C (1997) Rates and mechanisms of fatty acid degradation in oxic and anoxic coastal marine sediments of Long Island Sound, New York, USA. Geochim Cosmochim Acta 61:341-355

Walsh JJ (1991) Importance of continental margins in the marine miogeochemical cycling of carbon and nitrogen. Nature 350:53-55

Westrich JT, Berner RA (1984) The role of sedimentary organic-matter in bacterial sulfate reduction - the G model tested. Limnol Oceanogr 29:236-249

Yahel G, Post AF, Fabricius K, Marie D, Vaulot D, Genin A (1998) Phytoplankton distribution and grazing near coral reefs. Limnol Oceanogr 43:551-563

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 6

Benthic respiration in permeable carbonate lagoon sediments from the Heron Island atoll, Great Barrier Reef, Australia

Mohammed Rasheed [1,2], Christian Wild[1], Markus Huettel[1]

[1] Max Plank Institute for Marine Microbiology, Bremen University, 28359 Bremen, Germany

[2] Marine Science Station, University of Jordan and Yarmouk University, Aqaba Jordan

This chapter will be submitted to Estuarine, Coastal and Shelf Science

Benthic respiration in permeable carbonate lagoon sediments from the Heron Island atoll, Great Barrier Reef, Australia

Summary

Oxygen, dissolved inorganic carbon (DIC), and nutrient fluxes were measured in a shallow water carbonate sediment of Heron Island, Great Barrier Reef. Benthic respiration in these permeable sands was relatively high (54 mmol m^{-2} d^{-1}) and DIN and DIP fluxes reached 0.34 and 0.10 mmol m^{-2} d^{-1}, respectively. In order to investigate the impact of benthic boundary layer flow and sediment permeability on organic matter mineralization, in-situ and laboratory chamber experiments were carried out applying different stirring speeds (20, 10 and 0 rpm) to sediments of different permeabilities. 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 of the incubated sediment core and, thus, simulates sediment percolation as generated by boundary flow-topography interaction. Oxygen consumption rates in the chamber with fast (20 rpm, 1.2 Pa pressure gradient, 0.6 cm s^{-1} friction velocity u_*) stirring were approximately 2-fold higher than in the chambers with slow (10 rpm, 0.2 Pa pressure gradient, 0.3 cm s^{-1} friction velocity u_*) stirring. In the lab chamber experiments with stagnant water column (no stirring), oxygen consumption was 8 times lower than in the chamber with fast stirring. Lab chamber experiments with Br^- as a solute tracer revealed flushing rates of 311, 247 and 82 ml h^{-1} due to the stirring at 20, 10, and 0 rpm respectively. In a laboratory experiment investigating the effect of sediment permeability on sedimentary organic matter mineralization rate, 3-fold higher permeability resulted in 2 to 3 fold higher oxygen consumption and DIC production rates. Our experiments demonstrate the importance of boundary flow induced flushing of the upper layer of permeable carbonate sediment on organic matter degradation in the coral sands. The high filtration and degradation rates of organic matter in the sup-tropical permeable carbonate sediments and the subsequent release of nutrients may explain the high productivity in these Great Barrier Reef sediments.

Introduction

Permeable sediments cover approximately 70% of the continental shelves, which comprise 7.5% of the ocean floor (Menard and Smith 1996, Ott 1988). In the shelves, 20-30% of the oceanic primary production takes places (Walsh 1988, Jorgensen 1996) and more than 50% of the pelagic organic matter production is deposited at the sea floor (Gibbs 1981). Therefore, shallow sediments are expected to have high biogeochemical activity that supports the high primary productivity in the shelf seas. Advective transport is an important transport process in permeable sediments (Huettel and Gust 1992) in addition to molecular diffusion, which is the dominant transport process in cohesive sediments (Aller 1983, Jorgensen and Revsbech 1985). Pore water can flow through permeable sand as a result of pressure gradients at the sediment water interface. Advective transport can enhance the rate of organic matter mineralization (e.g. Forster et al. 1996, Shum and Sundby 1996) and may make sandy sediments more reactive than cohesive sediments (Reay et al. 1995). Hence, this transport may be an important process for the cycling of matter in the shelf (Rutgers Van Der Loeff 1981, Huettel and Gust 1992, Rhoads and Hecker 1994).

Carbonate sediments are common in tropical and subtropical shelves where coral reefs grow. These sediments, which consist mainly of coral and mollusc fragments, cover about 10% of the continental shelves. Due to their high permeabilties and porosities, advective transport is particularly important in carbonate sediments (Rasheed et al. in press). Through their highly porous structures and high specific surface area, they are a suitable substrate for the settlement of microorganisms (Schroeder and 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 in the coral reefs (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 a common sediment in subtropical and tropical shallow water environments, 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 that are flushed by bottom currents and waves. The coarse carbonate sands may filter organic particles from the water column and, thus, may be important for the recycling of nutrients in the oligotrophic reef environment. In this contribution we set out to investigate oxygen consumption and nutrient release in permeable carbonate sands originating from an oligotrophic reef environment off 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 favourable 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 and Hinga 1983). A common method for the assessment of solute fluxes is the laboratory or in-situ chamber incubation of sediment with measurements of the temporal variation of different solutes, O_2, and dissolved inorganic carbon (DIC) in the water enclosed in the chamber (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 lab incubations. The latter suffer from artefacts 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. However, some researchers have shown comparable fluxes measured from lab and in-situ incubations (Chanton et al. 1987, Bertuzzi et al. 1996). In this study, we measured O_2, DIC, inorganic nutrients and NaBr tracer fluxes in carbonate sands of different permeabilities using laboratory and in-situ chamber incubations. The goals of our study were to assess benthic respiration and nutrient production of 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 on 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 circular coral atoll. The atoll 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 lab experiments were also collected from Shark bay. The finer sands were collected from a site (ca. 3 m deep) in the central area of the reef lagoon.

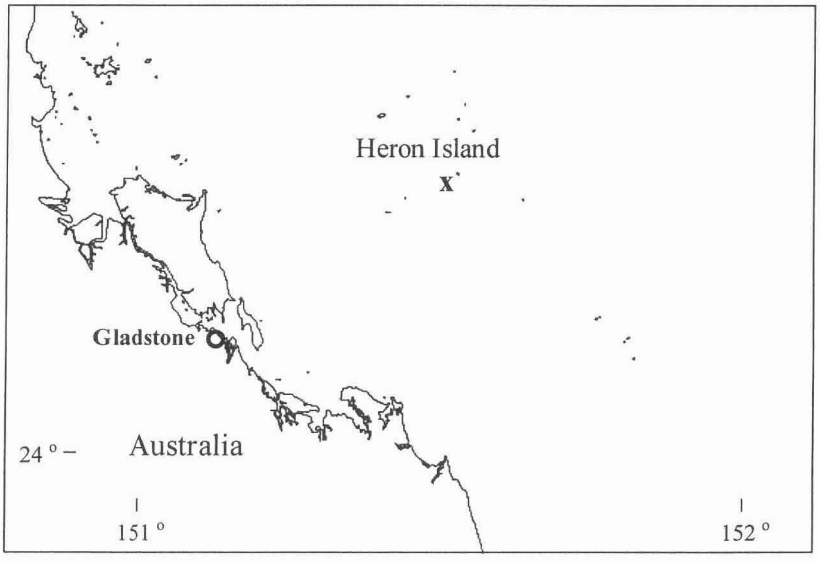


Fig. 1: Map location of Heron Island and Glad stone

Sediment characteristics

Shark Bay (SB) sediments for lab incubation were sieved into two size fractions; coarse (larger than 500 μm) and medium sands (smaller – 500 μm). From the lagoon site, finer grained sediments with ca 220 μm median grain size were collected. Some physical and chemical properties of the sediments that we used in this study are shown in Table 1. The permeabilities of the sediments were measured using a constant head permeameter as described by Klute and Dirksen (1986). All sediments used in our study 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 adsorbed at the grain surface using a Quantachrome Quantasorb instrument. Prior to analysis, the samples were dried at 80 °C for 30 minutes. The Quantasorb instrument specific surface area is measured by nitrogen sorption from a helium/nitrogen gas mixture (70% He, 30% N_2) at liquid nitrogen temperature in a flow through cell. Particulate organic carbon (POC) and nitrogen (PON) content were measured using a 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.

sediment	*surface area* (m^2g^{-1})	*Permeability* (m^2)	*Porosity* % (wt/wt)	*Median grain size* (μm)	*POC* (%)	*PON* (%)
SB	0.29	1.22×10^{-10}	30.0	838	0.24	0.042
coarse	0.18	3.75×10^{-10}	29.6	829	0.18	0.038
medium	0.31	1.17×10^{-10}	30.0	536	0.21	0.040
fine	0.74	1.37×10^{-11}	31.6	221	0.37	0.048

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

Incubation experiments

Oxygen, DIC, NaBr and nutrient fluxes were assessed from in-situ and lab incubations of different sediment types (natural and sieved) and applying different light and stirring conditions. An overview of the incubation experiments carried out in this study is shown in Table 2.

In-situ incubations

Two in-situ incubations were carried out in Shark Bay to estimate DIC, O_2 and nutrient fluxes from the natural permeable sediments under different light and stirring conditions (Table 2).

The incubation chambers were transparent cylindrical acrylic containers (19 cm 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 syringe holder for water samples and another port to replace the sampled water. Another opening in the lid contained an oxygen optode. 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. 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 fitted to the chambers and fixed by the clips. Chambers used for dark incubations were covered with tough opaque black plastic foils secured with rubber bands at the top and the bottom. The waters inside the chambers were stirred either at 20 rpm (fast stirring) or 10 rpm (slow stirring). At defined time intervals, dissolved oxygen was measured in the chamber water using the optodes (Presens) and 100 ml water were removed for DIC, nutrient and bromide analyses and replaced by local sea water. The total durations of the incubations were about 500 minutes for the first in-situ incubation and 300 minutes 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 evaluated from linear regressions of solute concentrations over time.

Experiment Process investigated	*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, 1.2 Pa & 0.6 cm s^{-1}) slow (10rpm, 0.2 Pa & 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

Table 2: Summary of the incubation experiments and measurements carried out in these incubations. u_* is the friction velocity. The data of friction velocities and pressure gradients are from Huettel and Gust (1992).

Laboratory chamber incubations

Three laboratory chamber incubations were carried out to estimate O_2, DIC, and bromide fluxes from permeable carbonate sediments (Table. 2). The first lab incubation was done with cores collected from Shark Bay directly after collection. The incubation was done in a big container flushed by natural sea water, which kept the temperature of the incubation at in-situ temperature. For this incubation, 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 covered 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 remove concentration gradient and homogenize the water. 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 were withdrawn at different time intervals using a syringe and replaced by 10 ml of sea water. The duration of the incubation was approximately 17 hours.

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 carried out in the container used for the first lab incubation, and was done using the same chambers that were used for the in-situ incubations with fast stirring (20 rpm). The height of the sediment columns in the chambers was 16cm. 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, which 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 (1.5 mM final concentration). Water samples (5ml) were withdrawn at different time intervals for bromide analysis. The duration of the experiment was 6 hours

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); SB sediments, coarse and medium sediments from SB, and fine sediments. 15 cm^3 of each sediment were incubated in gas tight bottles (60 ml) with filtered (0.2 µm) sea water (ca. 45 ml). 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 hours of incubation.

Chemical Analysis

Inorganic nutrients (DIP and DIN) were analysed spectrophotometically following the method of Grasshoff et al. (1999). Bromide concentrations were determined by ion chromatography using Water Cation column (flow rate 1ml min^{-1}, injection volume 100µl) and NaBr as standard for calibration. Dissolved inorganic carbon (DIC) concentrations in the water samples were determined using a flow injection system (Hall and 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). Oxygen was produced and CO_2 consumed by benthic primary producers. 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 and reflect the effect of light on O_2 and DIC consumptions. 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, 2.2 fold respectively, Table 3). The differences in DIC fluxes between slow and fast stirring, however, were not that pronounced (Fig. 2 and Table 3).

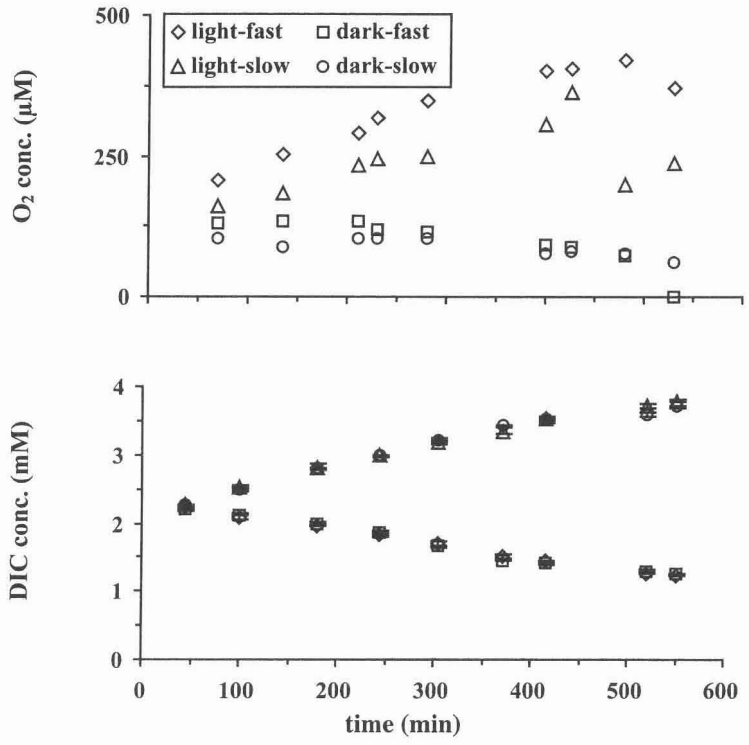


Fig. 2: Time course of oxygen (µM) and DIC (mM) during the in-situ chamber incubation with different light and stirring conditions for light-fast (diamond), dark-fast (squares),light-slow (triangles), and dark-slow (circles). Error bars of the DIC concentrations represent the standard deviation of three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

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 this incubation were similar (Table 3). Like in the first in-situ incubation, oxygen was consumed in dark and produced in light contrariwise 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 under dark as well as light conditions with

higher flux in the dark (0.384 vs 0.007 mmol m^{-2} d^{-1} for dark and light respectively. NO_2^- +NO_3^- flux calculations indicated higher uptake in the dark chambers in comparison to the light chambers (0.415 vs 0.013 mmol m^{-2} d^{-1}). PO_4^{3-} fluxes, on the other hand, indicated release in dark and uptake in the light chambers.

Experiment	*description*	O_2	*DIC*	NH_4^+	NO_2^-& NO_3^-	PO_4^{-3}	Br^-
In-situ incubation #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 incubation #2	light fast	78.6	-415.8	0.007	-0.013	-0.115	
	dark fast	-81.1	420.85	0.384	-0.041	0.062	
Lab incubation #1	dark no stirring	-6.8	30.5				
Lab incubation #2	medium sand	-5.6	96.3				
	coarse sand	-15.2	207.9				
Lab incubation #3	fast						-54.0 ± 6.8
	slow						-43.9 ± 4.6
	no stirring						-14.3 ± 4.5

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.

Lab incubations

Lab incubation #1

The time course of O_2 and DIC concentrations in the water of the dark chambers showed the same trend as in the dark in-situ incubations. However, the rates of production and consumption of DIC and O_2 in these chambers that were not stirred were lower than the rates recorded in the stirred in-situ dark incubation (e.g. the rates in the in-situ incubation 2 were 12 and 14 fold larger than those found in this incubation for O_2 and DIC

respectively, Table 3) although the same sediments were incubated. This shows the large 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 permeabilities (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). In both sediments, oxygen decreased gradually with rates of 5.6 and 15.2 mmol m^{-2} d^{-1} for medium and coarse sediment respectively. DIC, on the other hand, increased gradually with rates of 96.3 and 207.9 mmol m^{-2} d^{-1}. Oxygen consumption and CO_2 production rates were higher in the coarse than in the medium sediments (factor of 3 and 2 respectively, Table 3).

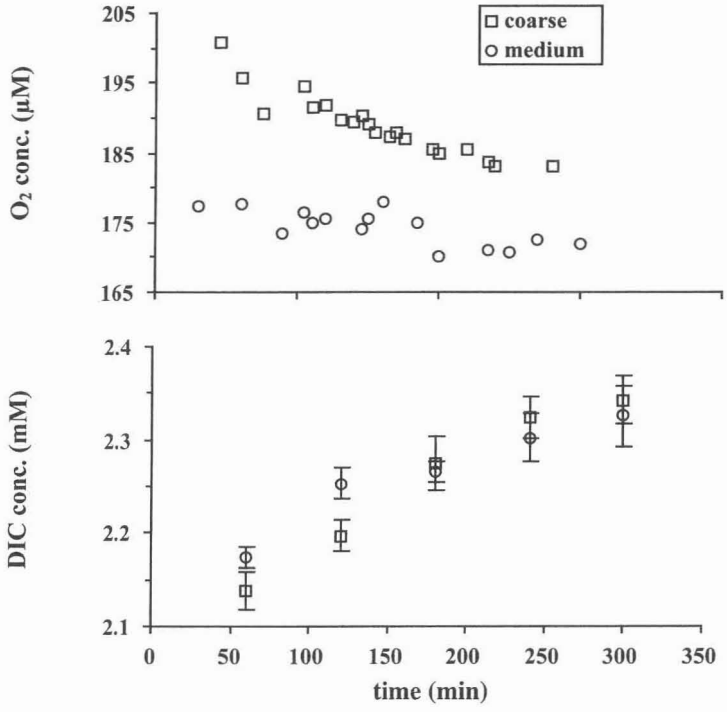


Fig. 3: Time course of oxygen (µM) and DIC (mM) during the lab incubation for coarse (squares) and medium sediments (circles). Error bars of the DIC concentrations represent the standard deviation of three samples.

Lab incubation #3

The sediment used in this experiment was highly permeable (~ 1×10^{-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. Final concentrations were 1986, 1994, and 2035 µM for 20, 10, and 0 rpm respectively (Fig. 4) corresponding to fluxes of 54.0, 43.9, and 14.3 mmol m^{-2} d^{-1} (Table 3).

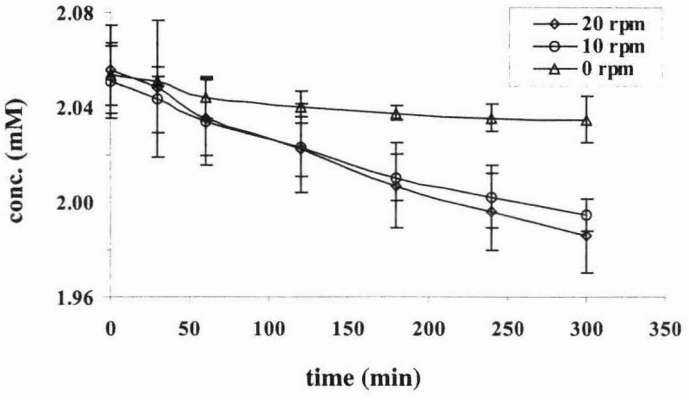


Fig. 4: Time course of Br- concentrations (mM) during lab incubation with a stirring velocity of 20 rpm (diamonds), 10 rpm (circles) and without stirring (triangles). Error bars represent the standard deviation of three incubated chambers for each stirring speed.

Oxygen consumption test

Oxygen consumption in the fine lagoon sediment was approximately 2-fold higher than in medium and coarse Shark Bay sediments (Fig. 5, Table 4). Final oxygen concentrations in the bottles were 36.8, 95.7, and 105.5 for fine, medium and coarse sediment, respectively, revealing that consumption rates in coarse and medium sands were similar (3.37 vs 2.88 mmol m^{-2} d^{-1}). In this bottle incubation, the O_2 consumption rate for the permeable SB sediments was similar to that recorded in the laboratory chamber incubation 1without stirring (5.12 vs 6.18 respectively).

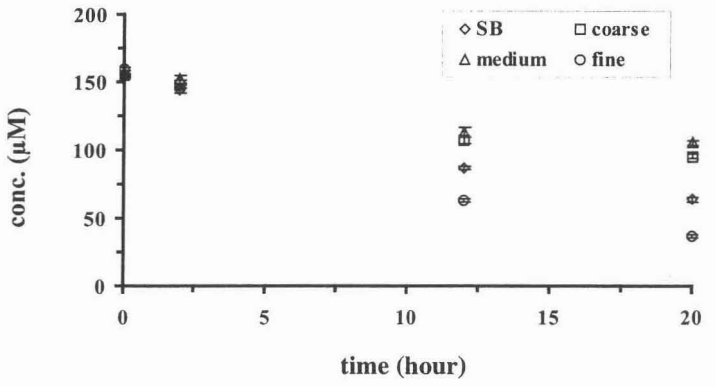


Fig. 5: Time course of oxygen concentrations (µM) during the bottles incubation experiment with Shark Bay (diamond), coarse (squares), medium (triangles) and fine (circles) sediments. Error bars represent the standard deviations of three oxygen measurements.

Sediment	*O_2 consumption*
SB	5.12
coarse	3.37
medium	2.88
fine	6.90

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

Discussion

Our study addressed the benthic respiration and nutrient fluxes in coarse permeable 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 and Rusch 2000) and may partly explain the high productivity reported for tropical and subtropical coastal carbonate sediments (e.g. Sorkin 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 that measured in other tropical and subtropical coastal sites (Table 5). Ammonium and phosphate fluxes were also higher than some of those measured elsewhere (Table. 5), and comparable with the values of Knoppers et al. (1996), Stimson and Larned (2000), and Rasheed et al. (sub.). With respect to Hines (1985) and Erftemeijer and Middelburg (1993) (Table. 5), these authors may have measured relatively low values because they calculated the diffusive fluxes from pore water concentration gradients which may. This means that fluxes resulting from bioturbation (e.g. Aller 1988, Barbanti et al. 1992) and possibly advective pore water exchange (Huettel et al. 1996, Huettel and Rusch 2000) were not considered, which, if these mechanisms are active, can increase the total flux substantially (Rasheed et al. sub.). However, our measured fluxes were relatively high. This might 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. In laboratory flume experiments, Forster et al. (1996) compared oxygen consumption in fine and coarse sediments and found higher oxygen consumption in the coarse permeable sediment. However, solute fluxes between marine sediments and the overlying water can be highly variable. This could 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), and physical and chemical properties of the sediment (e.g. Shum and Sundby 1996, Lopez et al. 1995).

Organic matter in sediments is mineralized aerobically and anaerobically. Aerobic processes take place using oxygen as electron acceptor and produce CO_2. The ratio of O_2:DIC fluxes under these conditions should be 1 (Kristensen 2000). However, DIC can also be produced by anaerobic processes using electron acceptors such as NO_3^- and SO_4^{-2}, which make the ratio between O_2 consumption and CO_2 production less than 1. In our incubation experiments, the O_2:DIC fluxes were always less than 1 (0.03-0.22) suggesting that oxygen respiration accounted only for 3 to 22% of the recorded CO_2 production. In some sediments oxygen respiration has been estimated to account for only

4-17% of total organic carbon oxidation (Canfielda et al, 1993 a, b). Charpy-Roubaud et al. (1996) found in coastal sediments from the lagoon of Tikehau Atoll that the increase in DIC was twice the oxygen depletion. However, 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 redissolution.

Location	*NH_4^+ ($\mu mol\ m^{-2}\ d^{-1}$)*	*PO_4 ($\mu mol\ m^{-2}\ d^{-1}$)*	*Oxygen ($mmol\ m^{-2}\ d^{-1}$)*	*Ref.*
Davies Reef Great Barrier Reef			-9.32 ± 0.79	Hansen et al. (1992)
Araruama Lagoon Brazil	170-1080	-30-30	-18.95 ± 4.85	Knoppers et al. (1996)
Kanoeohe Bay, reef flat, Hawaii	490	34.6		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-(-)50.8	Seiki et al. (1989)
South Atlantic Bight	5.55 ± 6.6		1.5 ± 0.15	Marinelli et al. (1998)
Bermuda	115-312	0.5-7		Hines (1985)
Gulf of Aqaba, Red sea	338 ± 30	30 ± 2	-5.92 ± 0.05	Rasheed et al. sub.
Our study, Heron Island	340	102	-54.10	This study

Table 5 : Benthic fluxes of Heron Island compared with fluxes from other coastals. Positive values are efflux and negative values are influx.

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) and a ratio of 1 for CO_2:O_2 (Berelson et al. 1998). The ratio of O:N and O:P calculated from our flux measurements were 356 and 671, i.e. much higher than the expected ratios (6.6 and 106 respectively), which implies that our measured nutrient fluxes were low. Denitrification may have reduced the DIN flux (Cowan and Boynton 1996, Berlson et al. 1998) at the end of incubations when oxygen concentrations were low. A more likely 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 can be attributed to the high removal of phosphate at the oxic sediment water interface, on the surface of the carbonate (Atkinson 1987, Ingall and Jahnke 1993, Bertuzzi et al. 1996, Spagnoli and Bergamini 1997).

Advective transport in permeable carbonate sediments

Advective transport caused by water flows into and out of the bed affects the mineralization rate of organic matter in the sediment (Shum and Sundby 1996). The magnitude of the 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 the permeability of the sediment (Huettel and Gust 1992). In this study, we investigated the effect of different pressure gradients (generated by the central stirring in the chambers) 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 # 3.

Effect of stirring velocity

The in-situ chamber incubation # 1 showed the impact of stirring velocity on oxygen and DIC consumption and production rates. Oxygen consumption and production rates in the chambers with fast stirring (20 rpm) were ca. 2-fold higher than in those chambers with slow stirring (10 rpm). 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 8 times lower than in the in-situ chambers with fast stirring where advective transport occurred in addition to diffusion. Lab incubation # 3 that compared Br^- solute tracer flux at three stirring speeds (0. 10, 20 rpm), supports the results of the 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 (1.2 and 3.8 fold respectively). From the Br^- flux and initial concentrations in each chamber, we could assess flushing rates of 311, 247, 82 ml h^{-1} for 20, 10, and 0 rpm stirring speeds, respectively. This implies stronger advective transport at higher stirring speeds, which is in agreement with some previous studies (e.g. Huettel and Rusch 2000). An increase in interfacial solute flux up to 43% has been found for stirred chambers relative to unstirred ones (Callender and Hammond 1982).

Berninger and Huettel (1997) investigated oxygen concentrations and photosynthetic oxygen production in intertidal permeable sediments under different flow velocity and concluded that advective transport in addition to diffusion became effective at high boundary layer flow velocity. 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}. In stirred flux chambers, Glud et al. (1995) found a 31% increase of total oxygen uptake when the stirring velocity was changed from 12 to 25 rpm. Water flow velocity determines the actual thickness of the diffusive boundary layer and the penetration depth of oxygen into the sediments and, thus, affects also oxygen uptake in the sediments (Kristensen 2000). With increasing flow velocity, the boundary layer is reduced in thickness, which enhances solute flux across the sediment-water interface (Jorgensen and Revsbech 1985, Glud et al. 1994).

Effect of permeability

In lab incubation # 2 we investigated sediment and DIC fluxes for medium and coarse sands. The permeability of the coarse sand was 3-fold higher than that of the medium sands (Table 1) and we found approximately 3-fold and 2-fold higher oxygen consumption and DIC production, 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. (sub.) found 1.5 fold higher organic matter mineralization rates in sediment with 2 fold higher permeability. In flume and field experiments comparing degradation of algal material in sediments with different permeabilities, Huettel and Rusch (2000) found 2.7 fold higher degradation rate in sediments with a permeability of 4.6×10^{-10} m^2 than in

sediments 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 and Sundby 1996, Huettel and Rusch 2000). However, without water flow above the sediment different sediment permeabilities would not effect the mineralization rate as shown in our bottle incubations (Table. 4). 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%). 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 the organic matter content (e.g. Kelly and Nixon 1984).

Conclusion

Carbonate sands of the Heron Island atoll have relatively high respiration and organic matter mineralization rates. This was attributed to high permeability, which results in 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 and Taylor 1992). 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 are considered strongly nutrient limited (D'Eia and Wiebe 1990). Cloren (1996) argued 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 effect mineralization of organic material in these sands. We propose that permeable carbonate sands play an

important role for the oceanic nitrogen, phosphate and carbon cycling, in tropical and subtropical regions.

References

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

Aller AC (1983) The importance of the diffusion permeability of animal burrow linings in determining marine sediment chemistry. J Mar Res 41:299-322

Aller RC (1988) Benthic fauna and biogeochemical processes in marine sediments: the role of burrow structures. In: Blackburn TH, Sorenson J (eds) Nitrogen Cycling in Coastal Marine Environments. John Wiley & Sons, Chichester, pp 301-338

Alongi DM (1998) Coastal Ecosystem Processes. CRC Press, Boca Raton, FL

Atkinson MJ (1987) Low phosphorus sediments in a hypersaline marine bay. Est Coast Shelf Sci 24:335-347

Barbanti A, Ceccherelli VU, Frascari F, Reggiani G, Rosso G (1992) Nutrient regeneration processes in bottom sediments in a Po Delta Lagoon (Italy) and the role of bioturbation in determining the fluxes at the sediment water interface. Hydrobiologia 228:1-21

Berelson WM, Heggie D, Longmore A, Kilgore T, Nicholson G, Skyring G (1998) Benthic nutrient recycling in Port Phillip Bay, Australia. Est Coast Shelf Sci 46:917-934

Berninger UG, Huettel M (1997) Impact of flow on oxygen dynamics in photosynthetically active sediments. Aquat Microb Ecol 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 DE (1982) Nutrient exchange across the sediment-water interface in the Potomac River Estuary. Est Coast Shelf Sci 15:395-413

Canfield DE, Jorgensen BB, Fossing H, Glud R, Gundersen J, Ramsing NB, Thamdrup B, Hansen JW, Nielsen LP, Hall POJ (1993a) Pathways of organic carbon oxidation in three continental margin sediments. Mar Geol 113:27-40

Canfield DE, Thamdrup B, Hansen JW (1993b) The anaerobic degradation of organic matter in Danish coastal sediments: Iron reduction, manganese reduction, and sulfate reduction. Geochim Cosmochim Acta 57:3867-3883

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

Chanton JP, Martens CS, Goldhaber MB (1987) Biogeochemical cycling in an organic-rich coastal marine basin .7. Sulfur mass balance, oxygen-uptake and sulfide retention. Geochim Cosmochim Acta 51:1187-1199

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

Clavero V, Izquierdo JJ, Fernandez JA, Niell FX (2000) Seasonal fluxes of phosphate and ammonium across the sediment- water interface in a shallow small estuary (Palmones River, southern Spain). Mar Ecol Prog Ser 198:51-60

Cloern JE (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 JLW, Boynton WR (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 CF, Wiebe, W.J. (1990) Biogeochemical nutrient cycles in coral reef ecosystem. In: Dubinsky Z (ed) Ecosystems of the World. Coral reef, vol 25. Elsevier, Amsterdam, pp 49-74

Dauwe B, Middelburg JJ, Herman PMJ (2001) 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

DeMaster DJ, Ragueneau O, Nittrouer CA (1996) Preservation efficiencies and accumulation rates for biogenic silica and organic C, N, and P in high-latitude sediments: The Ross Sea. J Geophysl Res-Oceans 101:18501-18518

Erftemeijer PLA, Middelburg JJ (1993) Sediment-nutrient interactions in tropical seagrass beds - a comparison between a terrigenous and a carbonate sedimentary environment in South Sulawesi (Indonesia). Mar Ecol Prog Ser 102:187-198

Fenchel T, King GM, Blackburn TH (1998) Bacterial Biogeochemistry: the Ecophysiology of Mineral Cycling. Academic Press, San Diego

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

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

Glud RN, Gundersen JK, Revsbech NP, Jorgensen BB (1994) Effects on the benthic diffusive boundary layer imposed by microelectrodes. Limnol Oceanogr 39:462-467

Glud RN, Gundersen JK, Revsbech NP, Jorgensen BB, Huttel 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

Green MA, Aller RC, Aller JY (1993) Carbonate dissolution and temporal abundances of foraminifera in Long-Island Sound sediments. Limnol Oceanogr 38:331-345

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

Hansen JA, Klumpp DW, Alongi DM, Dayton PK, Riddle MJ (1992) Detrital pathways in a coral-reef lagoon .2. Detritus deposition, benthic microbial biomass and production. Mar Biol 113:363-372

Heip CHR, Goosen NK, Herman PMJ, Kromkamp J, Middelburg JJ, Soetaert K (1995) Production and consumption of biological particles in temperate tidal estuaries. Oceanogr and Mar Biol - an Annual Review, Vol 33, vol 33, pp 1-149

Hines ME (1985) Microbial biogeochemistry in shallow water sediments of Bermuda 5th international Coral Reefs Congr, vol 3, pp 427-432

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

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

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

Ingall E, Jahnke R (1993) Evidence for enhanced phosphorus regeneration from marine-sediments overlain by oxygen depleted waters. Geochim Cosmochim Acta 58:2571-2575

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. Continent Shelf Res 20:109-127

Jorgensen BB (1996) Material flux in the sediment. In: Jorgensen BB, Richardson K (eds) Eutrophication in Coastal Marine Ecosystems, vol 52. American Geophysical Union, pp 115-135

Jorgensen BB, Revsbech NP (1985) Diffusive boundary layers and the oxygen uptake of sediments and detritus. Limnol Oceanogr 30:111-122

Kelly JR, Nixon SW (1984) Experimental studies of the effect of organic deposition on the metabolism of a coastal marine bottom community. Mar Ecol Prog Ser 17:157-169

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. American Society of Agronomy

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. Est Coast Shelf Sci 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 JA (1995) Sediment metabolism in a transitional continental marine area - the Albufera-Fo-Majorca (Balearic-Islands, Spain). Mar and Freshwater Res 46:45-53

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

Menard HW, Smith SM (1966) Hypsometry of ocean basin provinces. J Geophys Res 71:4305-4325

Miyajima T, Suzumura M, Umezawa Y, Koike I (2001) Microbiological nitrogen transformation in carbonate sediments of a coral-reef lagoon and associated seagrass beds. Mar Ecol Prog Ser 217:273-286

Muller PJ, Schneider RR, Ruhland G (1994) Late quaternary pCO2 variations in the Angola current: evidence from organic carbon d13C and alkenon temperatures. In: Zahn R, Kaminski M, Pedersen TF (eds) Carbon Cycling in the Glacial Ocean: Constraints on the Ocean's Role in Global Climate Change, vol 17. Springer, Berlin, pp 343-366

Nicholson GJ, Longmore AR, Berelson WM (1999) Nutrient fluxes measured by two types of benthic chamber. Mar and Freshwater Res 50:567-572

Ott J (1988) Meereskunde. Verlag Eugen Ulmer, Stuttgart

Pedersen AGU, Berntsen J, Lomstein BA (1999) The effect of eelgrass decomposition on sediment carbon and nitrogen cycling: A controlled laboratory experiment. Limnol Oceanogr 44:1978-1992

Rasheed M, Badran MI, Richter C, Huettel M (in press.) 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

Reay WG, Gallagher DL, Simmons GM (1995) Sediment-water column oxygen and nutrient fluxes in nearshore environments of the lower Delmarva Peninsula, USA. Mar Ecol Progr Ser 118:215-227

Revsbech NP (1989) An oxygen microsensor with a guard cathode. Limnol Oceanogr 34:474-478

Rhoads DC, Hecker B (1994) Processes on the continental slope off North Carolina with special reference to the Cape Hatteras region. Deep-Sea Res Pt II-Top St Oce 41:965-980

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

Rutgers van der Loeff MM (1981) Wave effects on sediment water exchange in a submerged sand bed. Netherlands J Sea Res15:100-112

Sansone FJ (1985) Methane in the reef flat porewaters of Davies Reef, Great Barrier Reef, Australia. Proc. Fifth Int. Coral Reef Congress. 3:415-419

Sansone FJ, Chanton JP, Haberstroh PR, Bozeat. R (1993) Methane cycling in coral reef frameworks. In: R Guerrero and C Pedros-Alio (eds.) Trends in Microbial Ecology. Spanish Soc. Microbiol. pp. 157-162

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

Seiki T, Izawa H, Date E (1989) Benthic nutrient remineralization and oxygen consumption in the coastal area of Hiroshima Bay Japan. Water Res 23:219-228

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

Sloth NP, Blackburn H, Hansen LS, Risgaardpetersen N, Lomstein BA (1995) Nitrogen cycling in sediments with different organic loading. Mar Ecol Prog Ser 116:163-170

Smith KL, Hinga KR (1983) Sediment community respiration in the deep sea. In: Rowe GT (ed) The Sea. Wiley, New York, pp 331-370

Sorkin YI (1995) Coral Reef Ecology. Ecological Studies, vol 192. Springer-Verlag, Berlin

Spagnoli F, Bergamini MC (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 ST (2000) Nitrogen efflux from the sediments of a subtropical bay and the potential contribution to macroalgal nutrient requirements. J Exp Mar Biol Ecol 252:159-180

Tengberg A, Hall P, Hulth S (1996) Free vehicle modular bottom-lander technology for biogeochemical in situ studies. Gff (Sweden)118:125-126

Tribble GW (1993) Organic matter oxidation and aragonite diagenesis in a coral reef. J Sediment Petrol 63:523-527

Tribble GW Sansone FJ, Smith SV (1990) Stoichiometric modeling of carbon diagenesis within a coral- reef framework. Geochim Cosmochim Acta 54:2439-2449

Vanderborght JP, Wollast R, Billen G (1977) Kinetic-models of diagenesis in disturbed sediments 1. Mass- transfer properties and silica diagenesis. Limnol Oceanogr 22:787-793

Walsh JJ (1988) On the Nature of Continental Shelves. Academic Press, New York

Webster IT, Taylor JH (1992) Rotational dispersion in porous media due to fluctuating flow. Water Resources Research 28:109-119

Chapter 7

General Conclusion

Conclusion

Our study presents two main interesting findings. The first is a view of some nutrient sources in the reef, which will increase our understanding regarding the nutrient cycling in the oligotrophic coral reef waters. The second will improve our understanding of the role of the sediments in organic matter decomposition. Our results also show for the first time a direct comparison of the mineralization rates of organic matter between silicate and carbonate sediments in coral reef regions, and thus will allow a better evaluation of nutrient cycling in the reef environment.

The main conclusions that can be inferred from this study are

1- During summer months, when nutrient concentrations in the offshore water were almost depleted, nutrient and chlorophyll a concentrations were significantly higher in the coastal reef waters than in the offshore waters. This emphasizes the role of internal recycling of nutrients in the reefs and may explain the high productivity in these systems despite the relative low nutrient concentrations in the reef waters. In winter, however, the concentrations were higher in both reef and offshore waters than in summer, due to the intrusion of nutrients originating from deep waters.

2- The elevated nutrient and chlorophyll a concentrations in summer were attributed to different factors. The reef framework as a source of this elevation has been discussed. In this framework, there is an excess of organic matter resulting from coral growth. The mineralization of the substances and the filtration and subsequent decomposition of particulate matter flushed through the framework may account for the elevated nutrient concentrations. Mineralization of the organic matter in the reef framework occur mainly by the activity of the abundant encrusting organisms, predominantly filter-feeders living within the reef framework such as sponges which form up to 60% of these organisms. On the other hand, reef sediments may also act as biocatalytic filters. The pore space of these permeable sands may be a suitable and active site for organic matter decomposition and thus, a source for nutrients, which are needed for sustaining primary production during summer.

3- The comparison between carbonate and silicate sands originating from the same site in the Gulf of Aqaba revealed higher organic matter accumulation and filtration rates and subsequent higher mineralization rates in the carbonate sand. The porous carbonate grains increase the permeability of the sediment and provide a larger surface area for sorption processes and bacterial colonization. These characteristics increase the filtration capacity and mineralization rates of organic materials in the carbonate sands.

4- Inorganic nutrient fluxes and oxygen consumption rates in the shallow permeable carbonate and silicate sands were higher than those in the silt-muddy deep site sediments. The permeable shallow sands have higher transport rates than the impermeable silt-clay. This can be a reasonable cause for the high nutrient fluxes and oxygen consumption that resulted as a consequence of high organic materials degradation rates. The high transport velocity in the permeable sediment result in high advective metabolic transport that accelerates the mineralization rates.

5- Carbonate sands are found mainly in coral reefs that have relatively low water nutrient concentrations. Due to their mineral structures, high permeabilities, high surface area, and high porous grains, these sands have high filtration and mineralization rates and thus, can sustain the high primary productivity in the reef waters. This may be one explanation for the "coral reef paradox" that addresses the high productivity of coral reefs growing in nutrient-poor environments.