BERICHTE

aus dem Fachbereich Geowissenschaften der Universität Bremen

Nr. 136

Rieß, W.

IN SITU MEASUREMENTS OF RESPIRATION AND MINERALISATION PROCESSES - INTERACTION BETWEEN FAUNA AND GEOCHEMICAL FLUXES AT ACTIVE INTERFACES

Berichte, Fachbereich Geowissenschaften, Universität Bremen, Nr. 136,
68 Seiten, Bremen 1999

ISSN 0931-0800

Die "Berichte aus dem Fachbereich Geowissenschaften" werden in unregelmäßigen Abständen vom Fachbereich 5, Universität Bremen, herausgegeben.

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angefordert werden.

Zitat:
Rieß, W.
In situ measurements of respiration and mineralisation processes – Interaction between fauna and geochemical fluxes at active interfaces.
Berichte, Fachbereich Geowissenschaften, Universität Bremen, Nr. 136, 68 Seiten, Bremen, 1999.

ISSN 0931-0800

In situ measurements of respiration and mineralisation processes - Interaction between fauna and geochemical fluxes at active interfaces

Dissertation zur Erlangung des Doktorgrades der Naturwissenschaften

im Fachbereich 5
der Universität Bremen

vorgelegt von

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Bremen, 1999

Tag des Kolloquiums: 7. April 1999

Gutachter:

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Preface

This work is submitted as a dissertation that has been supervised by Prof. Dr. Bo B. Jørgensen. Part of this study was conducted on a cruise within the frame of the European MAST III- Program CANIGO (Canary Islands Azores Gibraltar Observations). Another part was conducted in a Romanian-German cooperation (No. I/71 041) funded by the German Volkswagen foundation.

During this study five manuscripts were written in which I was directly involved. Manuscript No. I (*In situ* measurements of respiration and metabolism of the deep-sea shrimp *Heterocarpus grimaldii* (Pandalidae)- a case study) is based mainly on my own investigations. Data from F. Wenzhöfer (diffusive oxygen fluxes) and L. Dittert (pore water data) were of substantial importance for the interpretation of my own data. Manuscript No. II (Importance of mussel covered shelf sediments for remineralization processes in the Black Sea: *In situ* measurements with a free falling benthic chamber lander) is also based on my own investigations. F. Wenzhöfer added data on diffusive oxygen fluxes and U. Luth substantial data on the macrofauna. Manuscript No. III (Anoxic thermomineral cave waters and bacterial mats as habitats for freshwater nematodes) included work on the optical fibers (Dr. O. Kohls) and benefited from the discussion with Dr. S. Sarbu who also made the work in Romania possible. Prof. Dr. O. Giere was involved in the manuscript preparation and provided logistical support during the project. Manuscript No. IV (Carbon oxidation in sediments of Gotland Basin, Baltic Sea, measured *in situ* by use of benthic landers) contains significant data of total oxygen uptake, bottom water conditions and fauna that were supported by my own work. Manuscript No. V (Sulfate reduction in Black Sea sediments: *In situ* and laboratory radiotracer measurements from the shelf to 2000 m depth) contains my data on flux measurements. I was also involved in the discussion and the writing phase of the manuscript.

A detailed list of the papers is given in the introductory chapter. These five separate studies are either accepted or submitted for publication in international journals or they will be submitted simultaneously with this thesis. Manuscripts No. IV and V were part of or will be part of the thesis of Dr. O. Greef and A. Weber, respectively. Thus, they are listed with a short description of their content and their importance for this thesis but are not reprinted here.

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Introduction

Fluxes of organic matter in the ocean decrease drastically from the phototrophic zone to the sediment with the largest rate of change in the upper few hundred meters of the water column and at the benthic boundary layer (Lee et al. 1998). Processes at the sediment/water interface reflect the mutual interaction of biological and geochemical processes. The direct study of processes related to the early diagenesis of organic matter at the sediment surface, however, is hampered by the remoteness of most of the sea floor. Additionally, it has been shown that these studies need to be carried out *in situ* to get a realistic quantitative image of the processes involved in remineralization. Different technological approaches have been used to achieve this goal.

At shallower depths ROVs (remote operated vehicle) are useful tools to measure processes *in situ*. Within the range of the cable to which the ROV is connected, it is mobile and able to screen a larger area of the sediment. Unlimited energy supply and on-line data processing are also valuable characteristics of ROVs. Their use is limited to the need for a connection to a land base or a ship at the surface. Thus, they are normally used in shallow waters, although there are solutions available now for greater depths.

Manned submersibles are a preferable tool to perform *in situ* studies, since they are independent and are mobile. Thus, direct observation of the site studied is possible as well as surveys over larger areas. However, submersibles are extremely expensive to build and to operate and dive times are restricted. Submersibles also need significant support from the ship, which is not available for other purposes during the deployment.

Free-falling instrumentation with autonomous power supply and control unit, so called landers, fill the gap in this context. They are cheaper to build and operate than a submersible, and since they are not connected to a surface device, they can be used down to approx. 6000 m water depth. Although landers are limited by their power supply and are not mobile (exception: ROVER, see Smith et al. 1997) they operate independently for several days, thus saving ship time (Priede et al. in press).

In situ studies of biogeochemical processes at sediment/water interfaces with landers have been performed now for 20 years down to abyssal depths (Smith et al. 1976, Weiss et al.

1977, Hinga et al. 1979, Smith et al. 1979). Results gained by the use of lander systems revealed that differences occur between measurements performed on samples taken to the surface for shipboard analyses and measurements done *in situ* (Smith & Hinga 1983, Berelson et al. 1990, Glud et al. 1994, Aller et al. 1998). Differences are mainly due to decompression effects and warming of the samples during recovery. Free falling lander systems are a common tool now in aquatic biology and biogeochemistry. The lander systems employed for the studies described here, are derived from a microprofiling lander developed by Reimers (1987), an incubation chamber lander build after the „BECI“ lander introduced by Jahnke & Christiansen (1989) and a lander for *in situ* measurements of sulfate reduction that was developed by Greef et al. (1998). An overview of lander systems used worldwide is given in the work of Tengberg et al. (1995).

The geochemical processes connected to organic carbon degradation at the sea floor are well studied. The interaction with fauna was first described by processes like bioturbation and bioirrigation of macroinfauna at the sediment/water interface. This study shows examples where benthopelagic fauna had an effect on the transportation of organic carbon to the sediment surface and benthic fauna acted as a barrier for transportation of organic carbon over the sediment/water interface. The adaptation of organisms to their geochemical surrounding is demonstrated most vividly in the freshwater cave environment that is described as a part of this study.

For the studies discussed here, a benthic chamber lander was used for *in situ* studies. The chamber lander incubates a defined surface area of sediment together with the overlying water (Smith et al. 1976, Tengberg et al. 1995). Water samples are drawn from the incubated overlying water and the depletion of oxygen is monitored with microsensors. Thus, the oxygen consumption measured, reflects the total oxygen uptake (TOU) of the incubated water, the sediment community and epifauna giving a three-dimensional picture of the ongoing processes. This TOU is comparable to the expression „sediment community oxygen uptake“ (SCOU) or „sediment oxygen demand“ (SOD) used by various other authors (e.g. Smith 1992, Tahey et al. 1996). The measurement of overall carbon remineralization (metabolism) of the sediment/water interface is especially interesting when one can also distinguish between the oxygen consumption of the sediment and small infauna (which is supported by diffusive uptake) and the oxygen consumption connected to advective flow (which is the case with ventilating macroinfauna or with permeable sediments) and larger epifauna. This is the main reason why a combination of a chamber lander and a simultaneously deployed microprofiling lander, as used in our studies, provides the best results. The one-dimensional profile from the profiling lander is used to calculate the diffusional oxygen uptake (DOU) of the sediment (Reimers et al. 1986, Archer et al. 1989). This does not only include microbial respiration or reoxidation of reduced species, but to some extent also the respiration of fauna. This is true as long as the infauna of the sediment does not create an advective flow over the sediment/water interface.

The chamber lander is equipped with a water sampling system that takes a series of water samples for the analysis of different solutes of the overlying water (NH_4^+, NO_3^-, ΣCO_2 (DIC), Mn^{2+}, Fe^{2+}, and others) in order to monitor the changes in concentration. The increase or decrease of solutes can be evaluated by simultaneously measured pore water profiles to compare the calculated fluxes or to distinguish between flux across the interface and effects caused by incubated fauna. Increase of CO_2 or NO_3^-/ NH_4^+, as well as oxygen consumption, can be used to quantify organic matter degradation/metabolism of organisms if certain assumptions (e.g. Redfield et al. 1963, Canfield et al. 1993) are used.

Oxygen and sulfate are considered to be the most important electron acceptors in (coastal) shelf sediments (Jørgensen 1982, Henrichs & Reeburgh 1987), whereas manganese and iron reduction (Aller 1990, Canfield et al. 1993) or denitrification (Devol 1991, Reimers et al. 1992) only play a significant role under certain regional circumstances. Jørgensen (1982) quantified the processes of direct aerobic organic matter degradation and reoxidation of reduced metabolic products from sulfate reduction to be approx. 50% each. Thus, the possibility to deploy a lander for measuring sulfate reduction *in situ* together with the chamber lander and the profiling lander, added to a better understanding of the importance of different pathways of organic matter oxidation on continental shelves. The role of oxygen in the process of reoxidizing reduced sulfur instead of being used directly for remineralization, was directly measurable.

Using all three landers as well as shipboard incubations in the Black Sea allowed us to specifically determine the remineralization pathways for the organic matter as well as the impact of the fauna on these processes. The shipboard measurements could be constrained by comparison to the *in situ* measurements.

Mutual interaction between biology and geochemistry

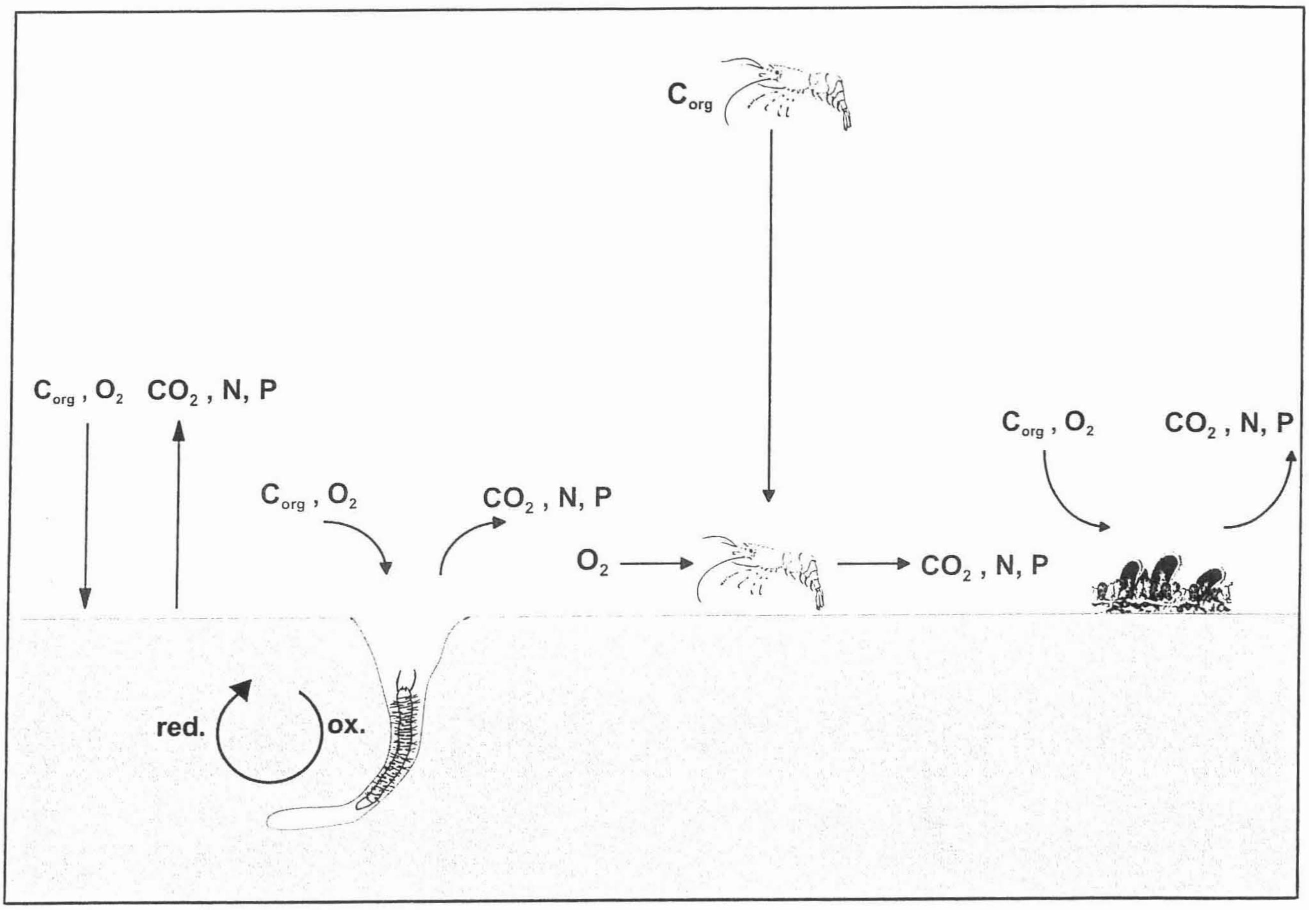

Fig. 1 Different processes at the sediment/water interface involved in organic matter oxidation. From left to right: Settling of organic matter on the sediment surface and microbial remineralization; bioturbation (shift of solid phase between different sediment horizons) and bioirrigation (advective transport over the sediment surface); biomigration as a way of enhanced flux of organic matter through the water column; mussel beds as an active biological layer limiting transport of organic carbon into the sediment.

Bioturbation and bioirrigation

In situ incubation of sediment together with fauna provides the rare opportunity to measure the effects of the fauna on the diagenetic processes at the sediment/water interface. Usually tube-dwelling macrofauna, for example larger polychaetes or crustaceans, are the object of such studies, as they significantly alter the topography of the sediment and the flow regime at the sediment/water interface (Aller 1982, Ziebis et al. 1996). The bioturbating and irrigating fauna has been shown to enhance oxygen fluxes across the sediment/water interface many-fold (Glud et al. 1994, Glud et al. 1998, see Fig. 1). On the other hand, the geochemical conditions in the habitat impact the animals and can trigger a response in their behavior. The influx of H_2S into the burrow of tube-dwelling animals for example can lead to physiological reactions (e.g. switching from aerobic to anaerobic metabolism) (Grieshaber et al. 1994, Grieshaber & Völkel 1998). Also ventilation of burrows can be triggered by the geochemical situation within burrows of *Nereis diversicolor* (Riess, unpubl.).

Biomigration

Usually organic matter reaches the sea floor, passively by sinking through the water column. During this descent the organic matter is altered (mainly microbial) in degradation processes. This leads to reduction of the share of organic matter that reaches the sea floor . The portion of organic matter from the production within the phototrophic zone that reaches the bottom depends on the time of descent through the water column, thus often on the water depth. Usually a few percent of the surface primary production reach abyssal water depths (Suess 1980, Betzer et al. 1984, Berger et al. 1987), often sinking as „marine snow“ (Alldredge & Gottschalk 1988, Alldredge & Silver 1988). Also carcasses of dead megafauna (e.g. big fishes, whales) have been shown of importance as organic carbon (C_{org}) supply especially for deep sea communities (Stockton & Delacca 1982, Smith et al. 1989). There is limited information about migrating macrofauna as vectors of organic matter to the deep sea floor (Roe 1974, Pearre jr. 1979, Hinga et al. 1979), although migrating fauna has been proposed to be an explanation for some of the discrepancies in organic carbon supply and demand in some benthic studies. We found that deep sea caridean shrimps that migrate rapidly through the water column (Domanski 1986) can contribute significantly to the oxygen consumption of the sediment/water interface. As their food (C_{org}) most likely is taken up in the surface waters, their role as a fast carrier of organic matter from productive upper zones of the water column down to the sediment surface seems likely (Fig. 1). Therefore, an enhancement of carbon flux to the sediment surface can be attributed to the presence of this macrofauna species.

Mussel beds

In contrast to the enhancement of transportation processes by fauna to the sediment, the presence of mussels beds can create the opposite effect. Large and dense mussel beds on the Romanian Shelf form a very active 2 to 3 cm thick layer of biomass that has high turnover (metabolism) rates compared to the diffusive flux rates into the sediment. These act as a barrier for organic material to reach the sediment (Fig. 1). Much of the organic material was retained in this „biozone" within a short loop and remineralized there, leaving microbial degradation within the sediment to be of minor importance. The community, mainly consisting of filtrating organisms, were able to compensate for poor environmental conditions (decreasing oxygen supply) by increasing their respiration efficiency. As the fauna decreased in density along a transect into deeper waters so did their impact on the overall carbon oxidation. Dense mussel beds frequently occur on soft bottoms. Many lamellibranch bivalves depend on hard bottom substrates but some are able to form dense mussel beds stabilizing the soft sediment underneath, where they become important for the remineralization of organic matter, limiting the processes within the sediment.

Floating microbial mats

The impact of geochemical conditions on faunal communities was shown to be crucial in a very unique system of floating microbial mats in a cave, sustained only by chemoautotrophic processes. The system developed and was stable only under conditions with reduced oxygen supply. *In situ* measurements with oxygen optodes were used to confirm anoxia in some of the floating mats. In these mats dense populations of nematodes were found. Whereas growth and survival was easy to explain by anaerobic metabolism, the reproduction that was taking place had to be addressed to another more efficient energy production process. Nitrate reduction was discussed to be an alternative, but this has never been shown to take place in metazoan animals so far. This still unsolved question awaits further investigations and might lead to the finding of a so far undescribed metabolic pathway for metazoan animals.

Overview of Research

I

Riess W, Wenzhöfer F, Dittert L

***In situ* measurements of respiration and metabolism of the deep sea shrimp *Heterocarpus grimaldii* (Pandalidae)- a case study**

Migrating macrofauna can act as fast carriers for organic material which is taken up in the water column and brought down to the sediment/water interface. At the sediment surface a large share of the organic material that was taken up in the water column is remineralized (metabolised). This behavior influences factors like oxygen consumption or nitrogen release at this sediment surface. Rates of oxygen consumption and nitrogen release were quantified and feeding habits were investigated by means of gut content analysis.

II

Riess W, Luth U, Wenzhöfer F

Importance of mussel covered shelf sediments for remineralization processes in the Black Sea: *In situ* measurements with a free falling benthic chamber lander

A benthic macrofaunal community covers large areas of the Black Sea shelf. These communities impact oxygen uptake rates, CO_2 release rates and nutrient cycling. By use of different lander systems and measurements, different pathways of organic carbon remineralization were quantified. The benthic community acts as an effective barrier for carbon flux into the sediment.

III

Riess W, Giere O, Kohls O, Sarbu SM

Anoxic thermomineral cave waters and bacterial mats as habitat for freshwater nematodes

In the cave waters of a subterranean groundwater system an exceptional „biological interface“ is formed by floating bacterial mats on top of anoxic, sulfidic freshwater. Under these extreme conditions, nematodes were shown not only to survive but also to reproduce under strict anoxia. Oxygen as an electron acceptor was ruled out, leaving nitrate as the only possible alternative for sufficient energy production.

IV

Greef O, **Riess W**, Wenzhöfer F, Weber A, Holby O, Glud RN

Carbon oxidation in sediments of Gotland Basin, Baltic Sea, measured *in situ* by use of benthic landers

In the Gotland basin in the Baltic Sea, we successfully deployed three different autonomous landers simultaneously for the first time. This manuscript shows results from our first survey to measure processes at the sediment/water interface at the same set of stations simultaneously. Total oxygen uptake, diffusive oxygen uptake and sulfate reduction rates were measured *in situ* to quantify pathways of carbon remineralization. A transect from oxygenated to anoxic bottom water conditions was chosen to observe a shift in the importance of the different pathways. Sulfate reduction was shown to account for the major part of the carbon remineralization. Thus, oxygen fluxes were calculated to account mostly for the reoxidation of sulfide at 2 of the 3 stations where the bottom water was containing oxygen.

V

Weber A, **Riess W**, Wenzhöfer F, Jørgensen BB

Sulfate reduction in Black Sea sediments, *in situ* and laboratory radiotracer measurements from the shelf to 2000 m

The importance of sulfate reduction increased from well oxygenated stations on the shallow shelf to the deep anoxic basin of the Black Sea. All three different landers were used to determine the relative importance of different electron acceptors to the overall carbon degradation. While the importance of sulfate reduction in the deeper zones of the Black Sea is well established, the conditions on the shelf and especially in the vicinity of the oxic/anoxic interface at the shelf were quantified *in situ* for the first time. Values for sulfate reduction were in the range of 1-2 mmol $\cdot$ m^{-2} $\cdot$ d^{-1}. Two parameters, oxygen concentration in the bottom water and the quality of the organic matter had an effect on sulfate reduction rates.

References

Alldredge AL, Gottschalk C (1988) *In situ* settling behavior of marine snow. Limnol. Oceanogr. 33(3): 339-351

Alldredge AL, Silver M (1988) Characteristics, dynamics and significance of marine snow. Prog. Oceanogr. 20: 41-82

Aller RC (1982) The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: McCall PL, Tevesz MJS (eds.) Animal-sediment relations (2): Topics in Geobiology. Plenum Press, New York, p. 53-102

Aller RC (1990) Bioturbation and manganese cycling in hemipelagic sediments. Phil. Trans. R. Soc. Lond. A 331: 51-68

Aller RC, Hall POJ, Rude PD, Aller JY (1998) Biogeochemical heterogeneity and suboxic diagenesis in hemipelagic sediments of the Panama Basin. Deep-Sea Res. I 45: 133-165

Archer D, Emerson S, Smith CR (1989) Direct measurement of the diffusive sublayer at the deep sea floor using oxygen microelectrodes. Nature 340: 623-626

Berelson WM, Hammond DE, O´Neill D, Xu XM, Chin C, Zukin J (1990) Benthic fluxes and pore water studies from sediments of the central equatorial north Pacific: Nutrient diagenesis. Geochim. Cosmochim. Acta 54: 3001-3012

Berger WH, Fischer K, Lai C, Wu G (1987) Ocean productivity and organic carbon flux. Part I. Overview and maps of primary production and export production. Univ. of California, San Diego, SIO Reference 87-30: 1-67

Betzer PR, Showers WJ, Laws EA, Winn CD, Dituillio GR, Kroopnick PM (1984) Primary productivity and particle fluxes on a transect of the Equator at 153 ° W in the Pacific Ocean. Deep-Sea Res. 31: 1-11

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

Devol AH (1991) Direct measurement of nitrogen gas fluxes from continental shelf sediments. Nature 349: 319-321

Domanski P (1986) The near-bottom shrimp faunas (Decapoda: Natantia) at two abyssal sites in the Northeast Atlantic Ocean. Mar. Biol. 93: 171-180

Glud RN, Gundersen JK, Jørgensen BB, Revsbech NP, Schulz HD (1994) Diffusive and total oxygen uptake of deep-sea sediments in the eastern South Atlantic Ocean: *in situ* and laboratory measurements. Deep-Sea Res. 41: 1767-1788

Glud RN, Holby O, Hoffmann F, Canfield DE (1998) Benthic mineralization and exchange in Arctic sediments (Svalbard, Norway). Mar. Ecol. Prog. Ser. 173: 237-251

Greef O, Glud RN, Gundersen J, Holby O, Jørgensen BB (1998) A benthic lander for tracer studies in the sea bed: *in situ* measurements of sulfate reduction. Cont. Shelf Res. 18: 1581-1594

Grieshaber MK, Hardewig I, Kreutzer U, Poertner HO (1994) Physiological and metabolic responses to hypoxia in invertebrates. Rev. Physiol. Biochem. Pharmacol. 125: 43-147.

Grieshaber M, Völkel S (1998) Animal adaptations for tolerance and exploitation of poisonous sulfide. Annu. Rev. Physiol. 60: 33-53

Henrichs SM, Reeburgh WS (1987) Anaerobic mineralization of marine sediment organic matter: rates and role of anaerobic processes in the oceanic carbon economy. Geomicrobiol. J. 5 (3/4): 191-237

Hinga KR, Sieburth JMCN, Heath GR (1979) The supply and use of organic material at the deep-sea floor. Journal of Marine Research 37: 557-579

Jahnke RA, Christiansen MB (1989) A free-vehicle benthic chamber instrument for sea floor studies. Deep-Sea Res. 36: 625-637

Jørgensen BB (1982) Mineralization of organic matter in the sea bed - the role of sulphate reduction. Nature 296: 643-645

Lee C, Murray DW, Barber RT, Buesseler KO, Dymond J, Hedges JI, Honjo S, Manganini SJ, Marra J, Moser C, Peterson ML, Prell WL, Wakeham SG (1998) Particulate organic carbon fluxes: compilation of results from the 1995 US JGOFS Arabian Sea process study. Deep-Sea Res. 45: 2489-2501

Pearre jr. S (1979) Problems of detection and interpretation of vertical migration. J. Plankton Res. 1: 29-44

Priede G, Addison S, Bradley P, Bagley P, Gray P, Rolin J, Blandin J, LeGrand J, Witte U, Cremer A, Pfannkuche O, Tengberg A, Hulth S, Hall P, Helder W, van Weering T, Duineveld G (in press) Autonomous deep-ocean vehicles: modular approaches to design and operation. In press by Sea Technology

Redfield AC, Ketchum BH, Richard FA (1963) The influence of organisms on the composition of sea-water. In: Hill MN (ed.) The Sea. Wiley, New York, p 26-87

Reimers CE, Fischer KM, Merewether R, Smith jr. KL, Jahnke RA (1986) Oxygen microprofiles measured *in situ* in deep ocean sediments. Nature 320: 741-744

Reimers CE (1987) An *in situ* microprofiling instrument for measuring interfacial pore water gradients: methods and oxygen profiles from the North Pacific Ocean. Deep-Sea Res. 34: 2019-2035

Reimers CE, Jahnke RA, McCorkle DC (1992) Carbon fluxes and burial rates over the continental slope and rise off central California with implications for the global carbon cycle. Global Biogeochemical Cycles 6 (2): 199-224

Roe HSJ (1974) Observations on the diurnal vertical migrations of an oceanic animal community. Mar. Biol. 28: 99-113

Smith jr. KL, Clifford CH, Eliason AH, Walden B, Rowe GT, Teal JM, (1976) A free vehicle for measuring benthic community metabolism. Limnol. Oceanogr. 21: 164-170

Smith jr. KL, White GA, Laver MB (1979) Oxygen uptake and nutrient exchange of sediments measured *in situ* using a free vehicle grab respirometer. Deep-Sea Res. 26: 337-346

Smith jr. KL, Hinga KR (1983) Sediment community respiration in the deep sea. In: Rowe GT (ed.) The Sea, ideas and observations on progress in the study of the seas. Vol.8, Deep Sea Biology, Wiley Interscience, New York, p 331-370

Smith CL, Kukert H, Wheatcroft RA, Jumars PA (1989) Vent fauna on whale remains. Nature 341: 27-28

Smith jr. KL (1992) Benthic boundary layer communities and carbon cycling at abyssal depths in the central North Pacific. Limnol. Oceanogr. 37: 1034-1056

Smith jr. KL, Glatts RC, Baldwin RJ, Beaulieu SE, Uhlman AH, Horn RC, Reimers CE (1997) An autonomous, bottom-transecting vehicle for making long time-series measurements of sediment community oxygen consumption to abyssal depths. Limnol. Oceanogr. 42, 7: 1601-1612

Stockton WL, Delacca TE (1982) Food falls in the deep-sea: Occurrence, quality and significance. Deep-Sea Res. 29: 157-169

Suess E (1980) Particulate organic carbon flux in the oceans- Surface productivity and oxygen utilization. Nature 288: 260-263

Tahey TM, Duineveld GCA, de Wilde PAWJ, Berghuis EM, Kok A (1996) Sediment O_2 demand, density and biomass of the benthos and phytopigments along the northwestern Adriatic coast: The extent of Po enrichment. Oceanologica Acta 19(2): 117-130

Tengberg A, DeBovee F, Hall P, Berelson W, Chadwick D, Crassous P, Devol A, Emerson S, Gage J, Glud R, Gundersen J, Hammond D, Helder W, Hinga K, Holby O, Jahnke R, Khripounoff A, Liebermann S, Nuppenau V, Pfannkuche O, Reimers C, Rowe G, Sahami A, Sayles F, Schurter M, Smallman D, Wehrli B, De Wilde P (1995) Benthic chamber and profiling landers in oceanography-A review of design, technical solutions, and functioning. Progress in Oceanography 35: 253-294

Weiss RF, Kirsten OH, Ackerman R (1977) Free vehicle instrumentation for the *in situ* measurements of processes controlling the formation of deep-sea ferromanganese nodules. Oceans ´77 Conference Record, 44D, Marine Technology Society and Institute of Electrical and Electronics Engineers.

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

Chapter 2

In situ measurements of respiration and metabolism of the deep sea shrimp *Heterocarpus grimaldii* (Pandalidae) - a case study

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2.1. Abstract

Oxygen consumption rates of the pandalid deep-sea shrimp *Heterocarpus grimaldii* (A. Milne-Edwards & Bouvier 1900) were measured in 1360 m depth in the eastern Atlantic Ocean north west of Africa during the cruise 37/1 with R/V Meteor. A free falling flux chamber lander, designed for studies of the biogeochemisty of the sediment/water interface, inadvertantly captured four individuals of *H. grimaldii*. Due to the absence of other fauna and the opportunity to independently determine sediment microbial activity from a simultaneously deployed microprofiling lander, rates of respiration and metabolism of *H. grimaldii* could be determined *in situ*.

Oxygen uptake of the animals was measured using oxygen microelectrodes. Respiration rates of *H. grimaldii* of 0.047 μmol $O_2 \cdot$ mg wet $wt^{-1} \cdot d^{-1}$ were determined by subtracting the DOU (diffusive oxygen uptake) of the sediment from the TOU (total oxygen uptake). Water samples were also collected from the chamber for the analysis of NH_4^+ and NO_3^- during the incubation time of 12 hours. It could be shown that *H. grimaldii* released ammonia at a rate of 0.0027 μmol $NH_4^+ \cdot$ mg wet $wt^{-1} \cdot d^{-1}$. After recovery of the lander, live animals were fixed for examination of gut content. The diet of the animals appears to consist not only of benthic but also of planktonic prey (sediment samples were also taken for comparison with the gut contents).

2.2. Introduction

Measurements of oxygen uptake of the seafloor (total oxygen uptake (TOU) and diffusive oxygen uptake (DOU)), the sediment community oxygen consumption (SCOC) and animal respiration rates (individuals or populations) have been performed for some decades now (Reimers 1987, Smith & Hinga 1983, Tengberg et al. 1995, Mahaut et al. 1995). For all these measurements, the principal decision is whether these experiments should be performed on samples that were recovered from the seafloor or if it is possible to perform them *in situ*. Especially for deep-sea environments changes of pressure and temperature during the retrieval of samples can be critical because of their impact on the animals metabolism.

Multicorers, Slurp guns, net trawls or shipboard incubations under *in situ* temperature (pressure is usually not simulated) are commonly used to study deep-sea animals. There are also instruments like ROVs, submersibles and landers that are deployed to measure SCOC, TOU or DOU *in situ*.

When animals are caught and brought to the surface they are subject to changes in several parameters. Specimens that are caught in nets can be affected by temperature, salinity and pressure changes before they are incubated at *in situ* temperature again. Slurp gun respirometers like those used by Smith (1985) seem to be the best alternative since the animals are incubated at *in situ* conditions. Still some stress to the animals can occur during the capture process. After collection they remain in a container that does not supply them with their natural surrounding (e.g. without contact to the usual substrate). Nevertheless Smith (1983) stated that „during the initial 1 to 3 h of incubation, we observed no noticeable difference in behavior between the experimental echinoderms and those free on the sediment surface“. In principle it is not that easy to catch single specimens by a slurp gun. This is why many early measurements refer to ”mixed macrozooplankton” (Smith 1982, 1985). Advanced techniques including camera controlled sampling devices have improved the sampling of individual animals. Bringing animals to the surface and then later back to *in situ* conditions, can result in erroneous respiration rate measurements, even if pressure is simulated (Childress 1977, Childress et al. 1989).

Given the possible drawbacks with the methods discussed, the use of a bell jar like setup might constitute the best approach. Our lander acted as a bell jar and collected 4 *H. grimaldii*. Furthermore, the lander recovered the sediment and animals intact and returned them to the surface for further analyses. In addition a profiling lander was successfully deployed at the same site. These random events provide *in situ* measurements that can be compared to more conventional techniques.

2.3. Materials and methods

Site

The lander work was carried out on board the R/V Meteor on the cruise 37/1 from Lisboa, Portugal, to the Canary Islands in December 1996 as part of the CANIGO (Canary Islands Azores Gibraltar Observations) project. The location where *H. grimaldii* was captured was 28°53 N , 13°13 W (GeoB station 4234) at 1360 m water depth between North Africa and the Canary Islands (Fig.1). The site is located in a seasonal upwelling area with fine, silty sediments.

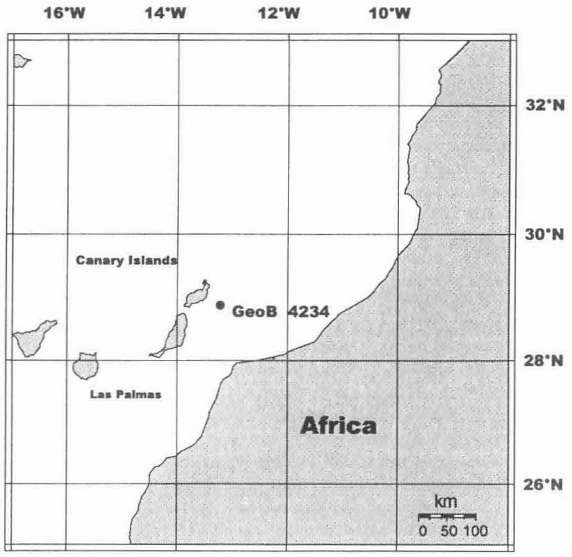

Fig. 1 Location of GeoB 4234 were animals were captured

Lander deployment

The animals were captured with a free falling autonomous flux chamber lander (Glud et al. 1994). The preprogrammed lander incubates 900 cm^2 of the sea floor with 10 to 20 cm of overlying water. Two Clark-type mini electrodes (stirring effect < 1%, 90% response time < 2 sec) recorded the depletion (<25%) of oxygen in the chamber over time. Ten water samples were taken out of the chamber during the incubation for later analysis of NO_3^- and NH_4^+. The chamber was closed by a shovel at the end of the deployment and the sediment and overlying water was brought to the surface. Subsamples of the sediment from the chamber were taken for sediment analysis. The water content was determined by drying the samples at 70°C to a constant weight. The organic content was measured by combustion of the dried samples and determining the weight loss (Giere 1993). Other subsamples were fixed with formaldehyde (5% final concentration) for the determination of meiofauna density and composition (Riemann 1988). The animals were retrieved by the flotation method (Nichols 1979) and later counted and classified at the class level under a dissection microscope.

Three of the four specimen captured were fixed in buffered formalin and later stored in 70 % ethanol. The largest specimen was deep frozen. The animals were measured and weighed, and the gut of the largest specimen was examined for gut content. The respiration rates of the animals were calculated as the total oxygen uptake in the chamber minus the diffusive oxygen uptake of the sediment divided by the total wet/fresh weight of all four specimens. Immediately after recovery of the flux chamber lander the water samples were divided and frozen in airtight containers for later analysis. The NO_3^- measurements were done with a 42C NO-NO_2-NO_x Analyzer (Thermo Environmental Instruments) (see Braman & Hendrix 1989). NH_4^+ was measured with the flow injection method (Hall & Aller 1992). Fluxes were calculated from the slope of the regression of the concentration versus time.

The simultaneously deployed microprofiling lander measured profiles of oxygen through the sediment water interface with a depth resolution of 100 µm (Glud et al. 1994). In addition, a still camera (PHOTOSEA) took pictures of the seafloor every 30 minutes showing the topography of the sediment surface around the electrodes. For this deployment the profiling lander was equipped with 6 oxygen electrodes. The oxygen micro-electrodes were also of Clark type with a guard cathode and an internal reference (Revsbech 1989). The tip diameter was 10 - 20 µm and the electrodes had a stirring sensitivity < 1% and a 90% response time < 2 sec. The oxygen electrodes were calibrated *in situ* with a two point calibration using the constant signal in the overlying water and in the anoxic zone of the sediment. The oxygen concentration in the bottom water was analyzed by Winkler titration from a water sample taken with a Niskin bottle which was fixed on the profiling lander (appr. 50 cm above the sediment surface).

The oxygen profiles were used to calculate the diffusive oxygen uptake (DOU) of the sediment using the linear oxygen gradient in the diffusive boundary layer after Fick´s first law of diffusion: $DOU = D_0\ dC/dz$

where:

DOU = diffusive oxygen uptake ($mmol \cdot m^{-2} \cdot d^{-1}$)

D_0 = molecular diffusion coeficient in sea water at *in situ* salinity and temperature (corrected from Li & Gregory 1974)

dC/dz = change in oxygen concentration at a given depth within the diffusive boundary layer

Sediment samples at the same location were taken with a „multiple corer“ (Barnett et al. 1984) and processed for the analysis of pore water solutes (NO_3^-, NH_4^+). To prevent a warming of the sediments on board, all cores were transferred into a cold room immediately after recovery and maintained at a temperature of 4°C. The multicorer cores and samples from the overlying bottom water were processed within a few hours. PH and Eh electrode measurements were performed during core processing with a minimum depth resolution of 0.5 cm (Schulz et al. 1994). The pore water was retrieved through 0.2 µm cellulose acetate membrane filters, which were treated with argon bubbled deionized water before use. Depending on the porosity and compressibility of the sediments, the amount of pore water recovered ranged between 5 and 20 ml. The porewater water was collected in pre-rinsed scintillation vials. Nitrate was measured onboard photometrically with an autoanalyser using standard methods (Grasshoff et al. 1983). Ammonium concentrations were determined onboard using the rapid flow injection technique as mentioned above. The resulting profiles were used to calculate fluxes of ammonia and nitrate at the sediment water interface. For the calculation Fick´s first law of diffusion was used taking into account the sediments´ porosity and the diffusion coefficient for ammonia and nitrate at ambient salinity and temperature. These fluxes were compared to the fluxes determined from the water samples of the flux chamber lander.

2.4. Results

Sediment and bottom water analysis

The bottom water temperature was 6.5 °C and the oxygen content was 216 μmol $\cdot$ l^{-1} which corresponds to 71% air saturation. The integrated water content of the top 10 cm of the sediment was 54% (w/w) (porosity decreasing to 66% at 10 cm depth); the organic content was 8.2% (w/w). The diffusive oxygen uptake (DOU) of the sediment measured by the profiling lander was low at 0.6 (±0.08) mmol $\cdot$ m^{-2} $\cdot$ d^{-1}, oxygen penetrating to a depth of 7.5 (±1.3) cm. Ammonia in the porewater was at the detection limit (1 μmol $\cdot$ l^{-1}) down to a depth of 8 cm and could therefore not account for a flux out of the sediment (Fig. 2). The porewater profiles of nitrate, on the other hand, resulted in a flux of 0.56 mmol $\cdot$ m^{-2} $\cdot$ d^{-1} out of the sediment, based on the amount of water in the chamber that would lead to an increase of NO_3^- in the overlying water of 1.8 μmol $\cdot$ l^{-1} during the 12 hour incubation (Fig. 2). Meiofauna density was relatively low in the sediment with 125,000 nematodes $\cdot$ m^{-2} , and a few pteropoda larvae.

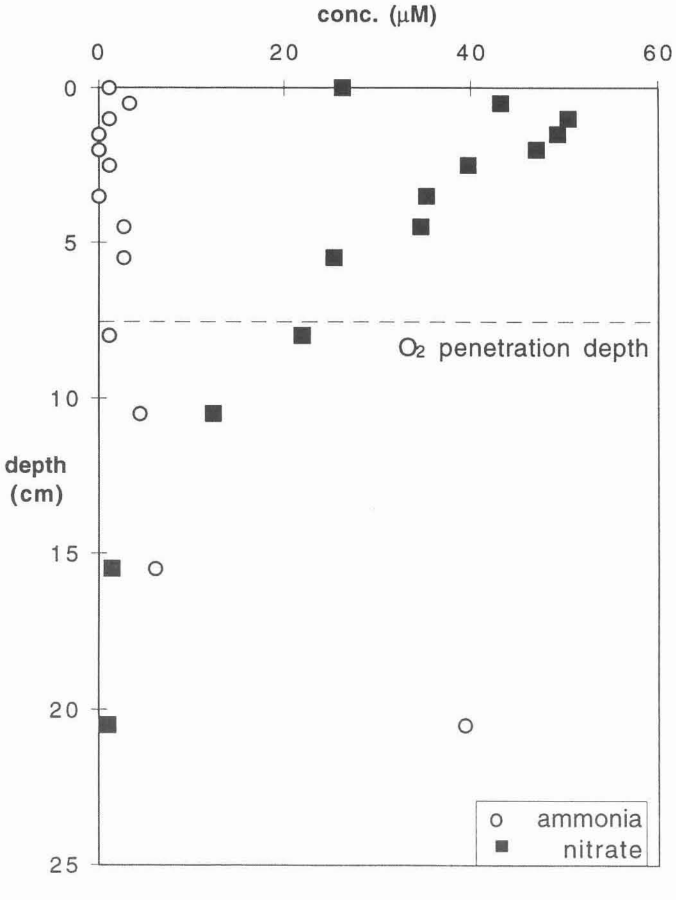

Fig. 2 Porewater profiles of ammonia and nitrate in the sediment at GeoB 4234

Respiration and metabolism of *Heterocarpus grimaldii*

Data on the four *H. grimaldii* specimens are given in Table 1. The respiration rate of *H. grimaldii* was calculated to be 0.047 µmol O_2 · mg wet wt^{-1} · d^{-1} based on the depletion of oxygen in the chamber. The animals were still alive and active after the recovery of the lander but died after appr. 30 minutes, most probably because of the high surrounding temperature.

Tab. 1 Data on the four specimens of *H. grimaldii* captured

specimen no.	wet weight (g)	total length (cm)	body length (Cephalothorax + Pleon) (cm)	telson length (cm)	rostrum length (cm)	antenna length (cm)	gut weight (g)	gut size (length x width) (cm)
1	15.84	16	12	1.5	2.5		1.39	1.9 x 1.1
2	7.13	12.5	9	1	2.5	21		
3	4.78	12	8.5	1	2.5			
4	1	7	4.5	1	1.5			

Ammonia production by the animals, calculated from the increase of ammonia in the chamber water (Fig. 3) was 0.0027 µmol · mg wet wt^{-1} · d^{-1}. There was no significant increase of nitrate in the chamber, indicating that disturbance of the sediment surface by the animals most likely did not occur.

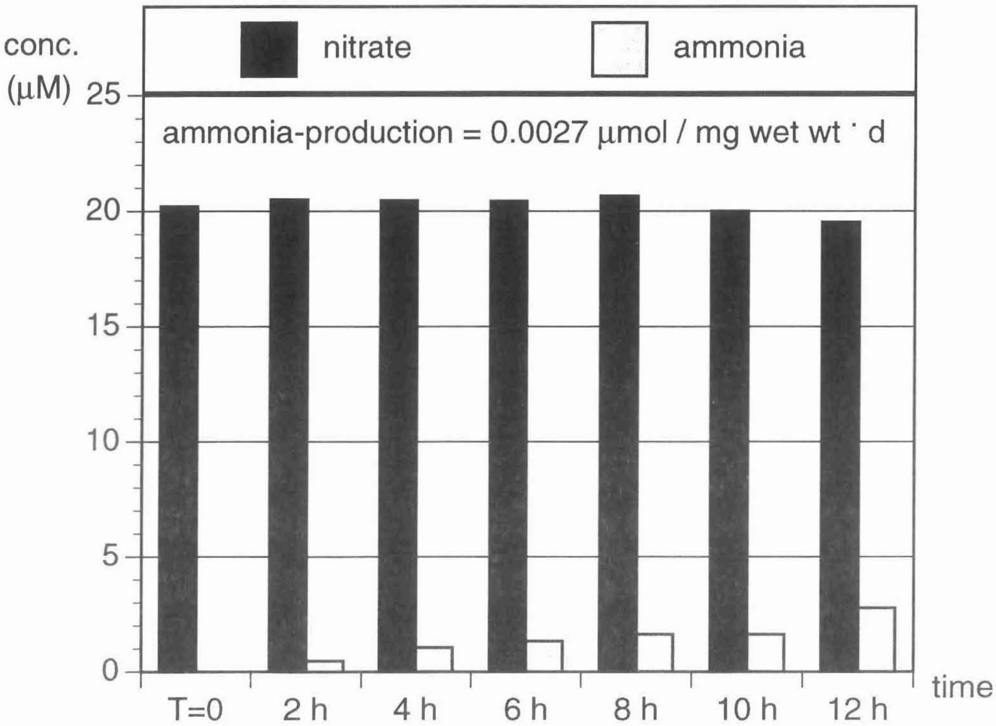

Fig. 3 Ammonia and nitrate values in the overlying water within the incubation chamber

The gut content revealed a mixture of very fine sediment particles, remains of shells and masses of nematocysts. Foraminiferan shells that were found in the gut could be attributed to different foraminiferan groups (cf. Textulariidae, cf. Nonionidae, cf. Globigerinidae). Tintinnidae shells were also found in small numbers. Diatom frustules were found in small numbers whereas nematocysts were found in extremely high numbers. Half of the nematocysts were exploded but about half of these cnidarian organelles appeared to be intact.

H. grimaldii seems to appear in high numbers based on the relatively small surface area covered by the chamber and the photos taken by the second lander. One must be aware of the problem of missing replicates, however on all of the pictures taken by the second lander one to three specimens are seen, supporting the assumption of high densities (Fig. 4).

Fig. 4 *Heterocarpus grimaldii* (A. Milne-Edwards & Bouvier 1900), picture taken *in situ*. In the background: Profiling oxygen and pH- electrodes

2.5. Discussion

The diffusive oxygen uptake of the sediment at the location was very low at 0.6 (±0.08) mmol $\cdot$ m^{-2} $\cdot$ d^{-1}. In comparison, the oxygen uptake of the shrimp calculated on an area basis was 16.4 mmol $\cdot$ m^{-2} $\cdot$ d^{-1}. It is difficult to estimate the impact of the treatment on the measured respiration rate of the animals. If the animals were stressed, one would expect the sediment surface to be disturbed by their activity, thus altering nitrate gradients and fluxes out of the sediment. The gradient of nitrate in the sediment led to a diffusive flux that raised the nitrate in the overlying water only slightly. On the other hand reworking of the uppermost centimeter of the sediment surface should lead to much higher fluxes (Fig. 2), but a significant increase of the nitrate in the chamber was not observed (Fig. 3).

Another metabolic parameter is the excretion of nitrogen. In this study a value (0.0027 µmol NH_4^+ $\cdot$ mg wet wt^{-1} $\cdot$ d^{-1}, equivalent to 2.03 µg NH_4^+ $\cdot$ g wet wt^{-1} $\cdot$ h^{-1}) was found that is in agreement with *in situ* measurements made by Smith (1982) but for mixed macrozooplankton at 1300 m water depth. Smith (1982) also noted that values in this order of magnitude are considerably lower than those measured for euphotic zone plankton. In crustaceans ammoniotelism and ureotelism occur, shifts within a specimen being possible according to the adaptation to the surrounding salinity (Chen & Chia 1996). Decapod crustaceans excrete nitrogen mainly as ammonia (Regnault 1987), especially if osmotic regulation is not critical. In the deep-sea environment stable salinity and temperature can be assumed and ammonia production is most likely the main nitrogen source.

There are no data available to date that could show how much the respiration rate is influenced by other techniques like slurp guns (Smith 1985), plexiglas incubation cylinders (Smith 1983) or net trawls (Childress 1977). Oxygen uptake values in this study were in the same order of magnitude as previous measurements using other techniques. They ranged from 0.0261 µmol O_2 $\cdot$ mg wet wt^{-1} $\cdot$ d^{-1} (Smith 1985) for mixed macrozooplankton (2600m depth, 1.7 °C), mainly consisting of the calanoid copepod *Isaacsicalanus paucisetus* to 0.0375 µmol O_2 $\cdot$ mg wet wt^{-1} $\cdot$ d^{-1} (Childress 1977) for the midwater copepod *Gaussia princeps* at 7°C and 121 atm pressure. Childress et al. (1989) measured 0.0535 µmol O_2 $\cdot$ mg wet wt^{-1} $\cdot$ d^{-1} for „combined crustaceans" that included copepods, caridian shrimp and *Gnathophausia sp.* from 1800 m water depth and 3°C although measurements were done at 1 atm pressure.

Gut content

The gut content was analyzed to identify the food source of *H. grimaldii*. Beside food of benthic origin and planktonic foraminiferan tests, masses of cnidarian nematocysts were found in the gut. Since no sessile benthic cnidarians were found in all of the sediment samples retrieved, it must be assumed that the shrimp most probably fed on pelagic cnidarians/medusae. It was also surprising to find that only half of the nematocysts were exploded whereas the rest seemed to be undamaged.

Actively swimming animals with a net vertical movement that transcends the benthic boundary layer (BBL) had been proposed as an important food source for the deep sea (Smith 1987). Therefore *H. grimaldii* could serve as a carrier of organic carbon that is produced above the benthic boundary layer and then released to the BBL in the form of excretions or feces (overview see Smith 1987). There are indications that benthic or benthopelagic shrimp do make excursions up the water column (Domanski 1986). In this context it is important to note that the meiofauna was relatively low in density and diversity in the sediment. Since the area is classified as an upwelling area and the organic content is fairly high, we have no good explanation for the low amount of nematodes in the sediment. The DOU is also very low. That leads to the suggestion that the quality of the organic material has been poor.

The results presented here have shown that *in situ* measurements with chamber landers can result in valuable *in situ* data for macrofaunal respiration and metabolism. The results were in the range of values reported from other techniques. From gut content analyses it can be concluded that at this site benthic or benthopelagic decapod shrimp seem to be able to act as an important carrier for organic material into the benthic boundary layer. Related to the low activity of the sediment the metabolic rate of the macrofauna was 25-fold higher and therefore must have played an important role in the carbon turnover at the sediment/water interface at this site.

2.6. Acknowledgements

The authors want to thank the crew of the R/V Meteor, the cruise leader Prof. Wefer for the opportunity to take part on the expedition and Dr. M. Türkay and Dr. CHJM Fransen for help in identifying the shrimp and for useful discussions. We also thank G. Eickert, A. Eggers, and V. Huebner for manufacturing the electrodes.

2.7. References

Barnett PRO, Watson J, Connelly D (1984) A multiple corer for taking virtually undisturbed samples from shelf, bathyal and abyssal sediments. Oceanol Acta 7: 399-408

Braman RS, Hendrix SA (1989) Nanogram nitrite and nitrate determination in environmental and biological materials by vanadium (III) reduction with chemoluminescence detection. Anal Chem 61: 2715-2718

Chen JC, Chia PG (1996) Hemolymph ammonia and urea and nitrogenous excretions of *Scylla serrata* at different temperature and salinity levels. Mar Ecol Prog Ser 139: 119-125

Childress JJ (1977) Effects of pressure, temperature and Oxygen on the oxygen consumption rate of the midwater copepod *Gaussia princeps*. Mar Biol 39: 19-24

Childress JJ, Gluck DL, Carney RS, Gowing MM (1989) Benthopelagic biomass distribution and oxygen consumption in a deep-sea benthic boundary layer dominated by gelatinous organisms. Limnol Oceanogr 34(5): 913-930

Domanski P (1986) The near-bottom shrimp faunas (Decapoda: Natantia) at two abyssal sites in the Northeast Atlantic Ocean. Mar Biol 93: 171-180

Giere O (1993) Meiobenthology. Springer Verlag Berlin. Berlin

Glud RN, Gundersen JK, Jorgensen BB, Revsbech NP, Schulz HD (1994) Diffusive and total oxygen uptake of deep-sea sediments in the eastern South Atlantic Ocean: *in situ* and laboratory measurements. Deep-Sea Res I 40: 1767-1788

Grasshoff K, Ehrhardt M, Kremling K (eds) (1983) Methods of seawater analysis. Verlag Chemie GmbH. Weinheim

Hall POJ, Aller RC (1992) Rapid, small volume, flow injection analysis for TCO_2 and NH_4^+ in marine and freshwaters. Limnol Oceanogr 37(5): 1113-1119

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

Mahaut ML, Sibuet M, Shirayama Y (1995) Weight-dependent respiration rates in deep-sea organisms. Deep-Sea Res I 42: 1575-1582

Nichols JA (1979) A simple flotation technique for separating meiobenthic nematodes from fine-graded sediments. Trans Am Microsc Soc 98: 127-130

Regnault M (1987) Nitrogen excretion in marine and freshwater crustacea. Biol Rev 62:1-24

Reimers CE (1987) An *in situ* microprofiling instrumentfor measuring interfacial pore water gradients: methodes and oxygen profiles from the North Pacific Ocean. Deep-Sea Res 34: 2019-2035

Revsbech NP (1989) An oxygen microsensor with a guard cathode. Limnol Oceanogr 34(2): 474-478

Riemann F (1988) Nematoda. In: Higgins RP, Thiel H (eds) Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, pp 293-301

Schulz HD, Dahmke A, Schinzel U, Wallmann K, Zabel M (1994) Early diagenetic processes, fluxes, and reaction rates in sediments of the South Atlantic. Geochim Cosmochim Acta 58(9): 2041-2060

Smith jr. KL (1982) Zooplankton of a bathyal benthic boundary layer: *In situ* rates of oxygen consumption and ammonium excretion. Limnol Oceanogr 27(3): 461-471

Smith jr. KL (1983) Metabolism of two dominant epibenthic Echinoderms measured at bathyal depths in the Santa Catalina basin. Mar Biol 72:249-256

Smith jr. KL (1985) Macrozooplankton of a deep-sea hydrothermal vent: *In situ* rates of oxygen consumption. Limnol Oceanogr 30(1): 102-110

Smith jr. KL (1987) Food energy supply and demand: A discrepancy between particulate organic carbon flux and sediment community oxygen consumption in the deep ocean. Limnol Oceanogr 32(1): 201-220

Smith jr. KL, Hinga KR (1983) Sediment community respiration in the deep-sea.In: Rowe GT (ed) The Sea.Vol.8. Wiley, New York, pp 331-370

Tengberg A, DeBovee F, Hall P, Berelson W, Chadwick D, Crassous P, Devol A, Emerson S, Gage J, Glud R, Gundersen J, Hammond D, Helder W, Hinga K, Holby O, Jahnke R, Khripounoff A, Liebermann S, Nuppenau V, Pfannkuche O, Reimers C, Rowe G, Sahami A, Sayles F, Schurter M, Smallman D, Wehrli B, De Wilde P (1995) Benthic chamber and profiling landers in oceanography-A review of design, technical solutions, and functioning. Progress in Oceanography 35: 253-294

Chapter 3

Importance of mussel covered shelf sediments for remineralization processes in the Black Sea: *In situ* measurements with a free falling benthic chamber lander

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3.1. Abstract

On a cruise off the Romanian coast in the Black Sea in September 1997 a chamber lander was deployed at 8 locations with a range of bottom water oxygen concentrations. The stations were located on a transect from the shallow shelf (62m) to the deep basin (1340m). Along the transect a significant change in the bottom water conditions indicated a shift from oxic to anoxic conditions (O_2, ΣCO_2, NO_3^-, NH_4^+, Mn^{2+} were measured). Data presented here resulted mainly from the five shallower stations where fauna were found. Macrofauna and Meiofauna were sampled for qualitative and quantitative analysis.

The coenoses at the three upper stations were dominated by bivalves (based on biomass). The well-described zonation of macrofaunal communities for the northwestern shelf of the Black Sea was also found in this study (*Mytilus galloprovinciales* coenosis at Station 1 (62 m), *Modiolus phaseolinus* coenosis at Station 2 (77 m) and 3 (100 m)). Macrofaunal biomass decreased with depth. The highest meiofauna densities (1 million ind./m^{-2}), on the other hand, were found at Station 4 (130 m, < 5 µMol O_2). Reduced predation and sufficient food supply are suggested to be of importance at that site.

The overall respiration rate of the macrofauna community did not change from the well oxygenated Station 1 (211 µMol O_2) to the oxygen depleted Station 3 (75 µMol O_2). The respiration rates at Stations 1 and 3 were almost identical with 0.014 µmol $O_2 \cdot$ mg $ww^{-1} \cdot d^{-1}$.

These results, obtained *in situ* for the first time, suggest that the overall macrofaunal community in the Black Sea does not adapt to the decreasing oxygen content in the bottom water with a lower oxygen consumption rate. The contribution of the macrofaunal assembly to the overall remineralization of organic carbon was high over the whole area where macrofauna were present, with the highest percentage (≥70%) at the shallowest station where there was the highest biomass.

3.2. Introduction

The Black Sea (Fig. 1) is a nearly enclosed basin with a varied geological and biological history over the last 5 million years. Today the Black Sea is characterized by low salinity (19 ‰) and a stable stratification of anoxic and sulfidic bottom water below approx. 130-150 m water depth down to the deep basin (2000 m). Presently there is only a small exchange of seawater with the Mediterranean Sea over the Bosporus (Izdar & Ergün 1991). The level of anoxia of the Black Sea has increased during the last 4000 years with the oxic/anoxic interface rising from 2000 m water depth to the present day level. Whether there is an anthropogenic speeding up of this trend is still an open question (Vinogradov 1991). Ecologic and economic problems arise when the surface layer of oxygenated water thins and anoxic, sulfidic water reaches shallower depths.

The upper, oxygenated water body allows for a typical zonation of certain coenoses on the shelf sediments that have been well described from the littoral down to approximately 130 m (Kiseleva 1981). During this study we measured oxygen and nutrient fluxes *in situ* and relate those to the incubated fauna directly to show the influence of the changing environmental conditions to the faunal compositions and the animal's metabolism. Friedl et al. (1998) measured oxygen and nutrient fluxes *in situ* with a chamber lander in the vicinity of the river deltas and on the shelf edge in the western Black Sea. In this study we extend these measurements across large areas of the shelf that are densely covered with mussels.

3.3. Materials and methods

Site

The lander work was carried out on board the R/V Petr Kottsov on the MPI Black Sea Cruise to the Romanian shelf in September 1997. The chamber lander was deployed along a transect at 8 Stations (Fig.1). At Stations 1 to 3 two deployments were made whereas only one deployment was made at the deeper Stations 4 to 8.

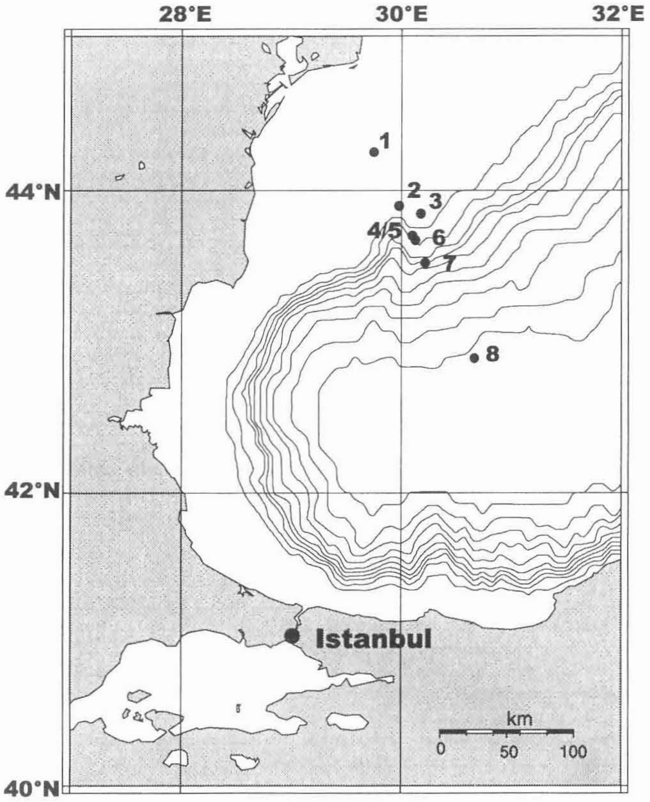

Fig. 1 Sampling stations in the western Black Sea

Lander deployments

A free-falling autonomous chamber lander (Jahnke & Christiansen 1989, Glud et al. 1994) was used to measure fluxes across the sediment water interface and, where fauna were present, the respiration rates of the dense bivalve fauna. The preprogrammed lander incubated 900 cm^2 of the sea floor with 10 to 20 cm of the overlying water. Two Clark-type minielectrodes (stirring effect < 1%, 90% response time < 2 sec) fitted in the chamber lid recorded the decrease (<25%) of oxygen in the chamber over time. The incubations ranged from 5 to 34 hours. Eight water samples were taken with syringes from the chamber with a motor driven water sampling system during incubation for later analysis of ΣCO_2, NO_3^-, NH_4^+, Mn, H_2S and other dissolved components. The chamber was closed by a shovel at the end of the deployment, and returned the incubated sediment and overlying water to the surface intact and with a virtually undisturbed sediment surface. Subsamples were taken from the chamber sediments for meiofaunal counts and identification and also for sediment analysis. The remaining sediment, down to 5 cm depth, was sieved for macrofaunal identification and quantification (500, 1000 and 2000 µm mesh size).

The water content of the integrated top 10 cm of the sediment was determined by drying the samples at 70°C to a constant weight. The organic content was measured by combustion of the dried samples and determining the weight loss (Giere 1993). Other subsamples from the chamber were fixed with formalin (5% final concentration) for the determination of meiofauna density and composition (Riemann 1988). The animals were retrieved by the flotation method (Nichols 1979) with a 45 µm mesh and counted and classified to class level under a dissection microscope. The macrofauna from each deployment were fixed with formalin and later counted and classified. Macrofauna specimen were weighed to determine biomass. Fresh weight (fw) was determined, for comparison of respiration rates, by subtracting the shells from the animal´s total wet weight (ww) according to Rumohr et al. (1987).

Immediately after the recovery of the lander the water samples were divided and frozen (NO_3^-, NH_4^+) or fixed with $HgCl_2$ (ΣCO_2) in gas tight containers (exetainer, LABCO) for later analysis. NO_3^- was determined on a 42C NO-NO2-NOx Analyzer (Thermo Environmental Instruments) (see Braman and Hendrix 1989). The NH_4^+ samples were measured by flow injection (Hall and Aller 1992). The CO_2 samples were measured on a coulometer (UIC, ASTM D-513 Method G, "Carbon Dioxide Evolution, Coulometric Titration Method"). Fluxes of the different solutes were calculated by linear regression of the time series of concentrations.

For the calculation of animal respiration, the diffusive oxygen uptake (DOU) of the sediment layers below the mussel layer (Table 2), measured by the profiling lander (see below) were subtracted from the total oxygen uptake (TOU) measured in the chamber. This value was divided by the total wet/fresh weight of individuals. This calculation was permissible due to the absence of tube-dwelling macrofauna; thus advective transport of oxygenated water over the oxic/anoxic interface into deeper sediment layers was negligible.

The simultaneously deployed microprofiling lander measured profiles of oxygen through the sediment water interface with a depth resolution of 100 µm (Reimers 1987, Glud et al. 1994). In addition, a still camera (PHOTOSEA) took pictures of the seafloor every 30 minutes showing the topography of the sediment surface around the electrodes. The oxygen micro-electrodes were also of Clark-type with a guard cathode and an internal reference (Revsbech 1989). The tip diameter was 10 - 20 µm and the electrodes had a stirring sensitivity < 1% and a 90 % response time < 2 sec. A two point calibration was performed using the constant signal in the overlying water and the zero value recorded onboard at *in situ* temperature. The oxygen concentration in the bottom water was analyzed by Winkler titration from a water sample taken with a Niskin bottle which was fixed on the profiling lander (approx. 50 cm above the sediment surface).

The diffusive oxygen uptake (DOU) of the sediment was calculated from the oxygen profiles using the linear oxygen gradient in the diffusive boundary layer after Fick´s first law of diffusion:

$$DOU = D_0 \, dC/dz$$

where:

DOU = diffusive oxygen uptake ($mmol \cdot m^{-2} \cdot d^{-1}$)

D_0 = molecular diffusion coeficient in sea water at *in situ* salinity and temperature (after Li & Gregory 1974, corrected)

dC/dz = change in oxygen concentration within the diffusive boundary layer

3.4. Results

Bottom water

Along the transect strong gradients of the chemical characteristics in the bottom water were found, shifting from typical oxic to anoxic conditions (Table 1). Oxygen in the bottom water was detectable only at Stations 1 to 4 (62 to 130 m). Electrode readings from the profiling and the chamber lander indicated that at Station 4 the oxygen content close to the sediment surface was extremely low at a few µmol · l^{-1} or zero (data not shown). Nitrate was also very low at Station 4 and not detectable at Station 5 indicating that the transition zone between oxic and anoxic conditons in the bottom water was a little below 130 m but well above 181 m water depth. This supposition is supported by ammonia and reduced manganese in the bottom water and by previous studies (e.g. Cowie & Hedges 1991). Values of both parameters were slightly higher at Station 4 compared to Station 3 but had increased significantly at Station 5 (Table 1). Dissolved inorganic carbon (DIC) increased from values around 3090 µmol · l^{-1} at Stations 1 to 3 to 3500 µmol · l^{-1} at 429 m water depth (Station 6). Values at greater depths were even higher but could not be determined accurately because of the interfering presence of high values of free hydrogen sulfide in the bottom water below 429 m (data not shown).

Tab. 1 Description of the Stations 1 to 8. BW = Bottom Water; n.d. = not determined; DIC = Dissolved Inorganic Carbon

Station	Water Depth (m)	BW Temp. (°C)	BW O_2 (µM)	BW NO_3^+ (µM)	BW NH_4^+ (µM)	BW Mn^{2+} (µM)	BW DIC (µM)
1	62	6.3	211	6.1	1.9	0.16	3089
2	77	6.9	213	3.2	1.6	0.09	3088
3	100	7.2	75	3.3	1.9	0.15	3072
4	130	7.8	20	0.34	2.4	0.41	3150
5	181	8.3	0	0	7.6	6.82	3230
6	429	8.6	0	0	40.6	6.99	3505
7	1240	8.7	0	0	100.7	4.52	n.d.
8	2134	9	0	0	99.8	4.65	n.d.

Sediment parameters

The sediment parameters on the shelf stations were influenced strongly by mussels and mussel shells. The water content increased from the mussel covered shelf stations (59%) to the slope (78%) where mussels decreased in number. The organic content in the sediment also increased with water depth which correlated negatively to the oxygen supply in the bottom water (Table 2).

Tab. 2 Sediment parameters at Stations 1 to 5. ww = wet weight; dw = dry weight; n.d. = not determined; LOI = Loss On Ignition; C_{org} values were taken from Weber et al. (in prep.)

Station	Water content (% w/ww)	Organic content, LOI (% w/dw)	C_{org} (% w/dw)	Nematodes (Ind. · m^{-2})	Diffusive oxygen uptake (mmol · m^{-2} · d^{-1})
1	59	6.7	2.7	172,000	11.9
2	62	5.9	1.5	79,550	5.8
3	62	7.7	2.0	189,900	2.3
4	62	8.0	1.9	1,040,000	n.d.
5	78	14.1	5.1	47,100	0

The sediment surface at Stations 1 to 3 was more or less completely covered by living mussels and empty mussel shells (Fig. 2). There is no distinct boundary between the sediment as such and the topmost shell layer. Nevertheless, it is referred to as the sediment surface since fluxes were measured over the interface sediment/mussels and overlying water.

Macrofauna

The coenoses at the three upper stations were dominated by bivalves based on biomass (Fig. 3). A typical depth zonation of the macrofaunal communities was found (*Mytilus galloprovinciales* coenosis at Station 1, *Modiolus phaseolinus* coenosis at Station 2 and 3, Fig. 2 and 7). Macrofaunal biomass decreased along the transect from the shallower to the deeper stations. The total biomass decreased from 1960 g ww · m^{-2} at Station 1 over 721 g ww · m^{-2} at Station 2 to only 148 g ww · m^{-2} at Station 3. Station 4 showed no significant macrofauna at all (less than 1 g ww · m^{-2}, of which larger nematodes accounted for 90% of the total individual counts). On an abundance level the dominance of the two bivalve species was less obvious (Fig. 3). At Station 1 did the crustaceans (Amphipoda, Tanaidacea) outnumber the mussels.

Station 2 showed the most diverse community on a group level with a significant share of foraminifera and small ophiuroids. At Station 3 ascidians outnumbered the bivalves and again a high number of Foraminifera were found. At Station 1 the comparatively large size of the bivalve *Mytilus galloprovinciales* lead to the dominance of the mussels in biomass, becuase specimens of all the other groups were small in size. By far the most specimens of *Mytilus* and *Modiolus* were adults. Only very few juveniles were found indicating a stable coenosis.

Most of the animals were found in the upper two centimeters of the sediment. Only at Station 1 was a significant share (25%) found in 2 to 5 cm sediment depth. At the other stations 85% to 95% of the individuals were found in the upper two centimeters (data not shown). Almost no tube-dwelling macrofauna (like larger polychaetes) were found.

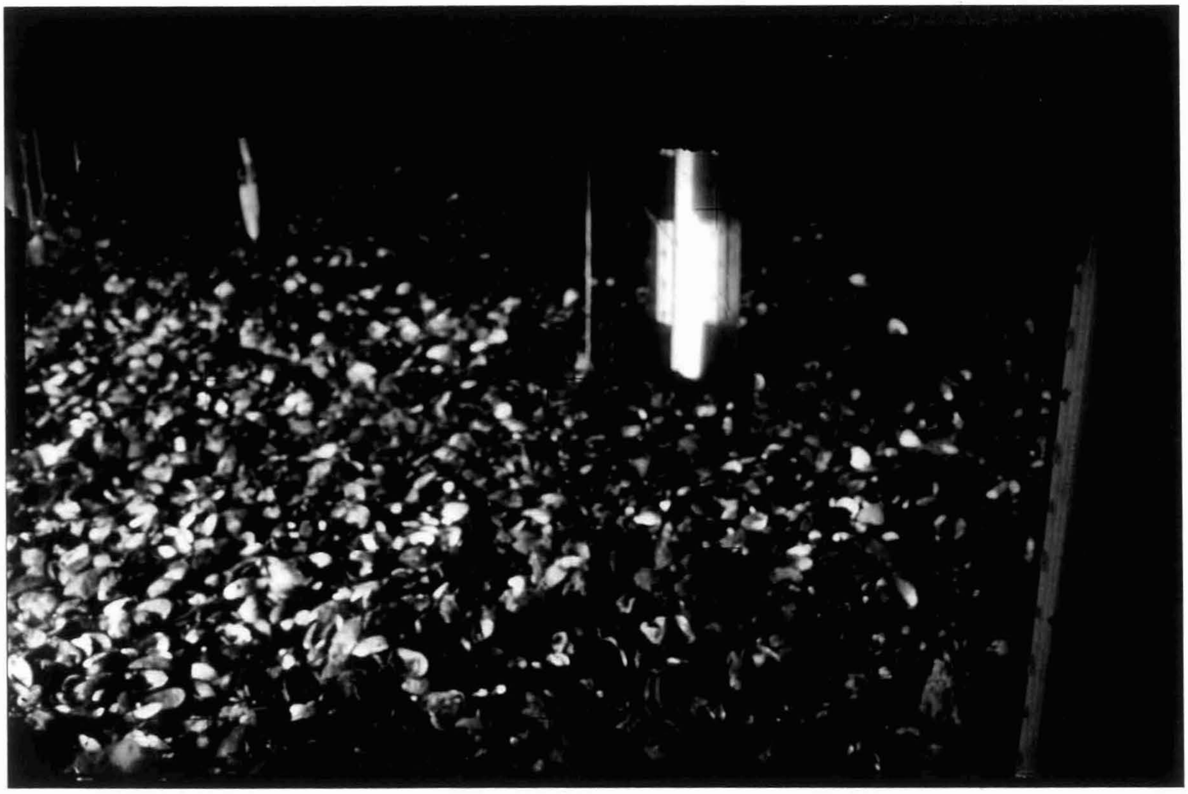

Fig. 2 Thick layers of *Modiolus phaseolinus* shells cover the sea floor

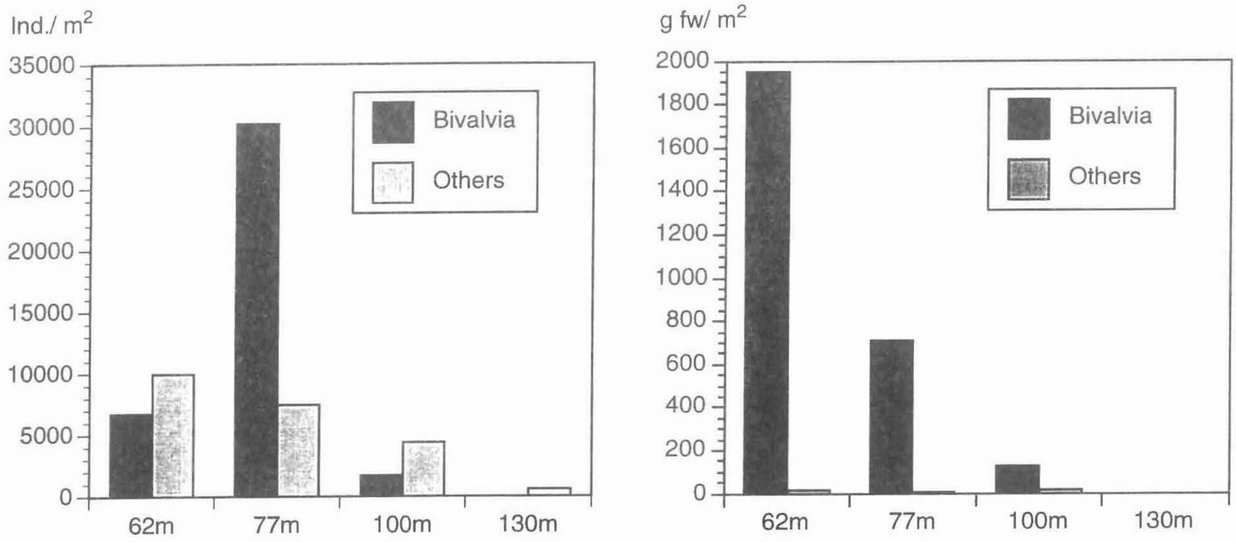

Fig. 3 Abundance and biomass of bivalves and other macrofaunal taxa

Meiofauna

The meiofauna consisted mainly of nematodes. They normally accounted for more than 90% of the total meiofauna. However, at Station 2 the share of the non-nematode interstitial fauna was 25-30%. Copepods and ostracods were found at the upper four stations in significant numbers. Small polychaetes were the third most important group. All these specimens were found to be concentrated in the upper 2 centimeters of the sediment filling the interstitial area between mussel shells. Only nematodes were sometimes found deeper in the sediment (Fig. 4); but they also showed a typical depth distribution with highest numbers at the sediment surface.

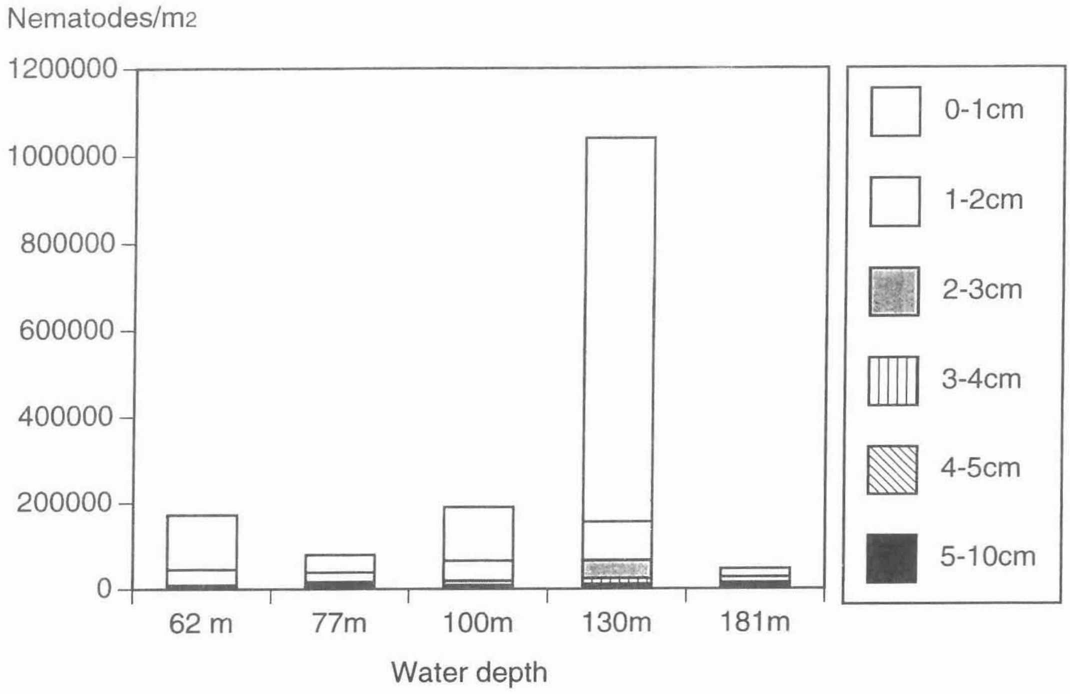

Fig. 4 Nematode abundance and depth distribution within the sediment

The highest nematode densities (1 million ind./m^2) were found at Station 4 (Table 2, Fig. 4) where the oxygen content was already very low (below 5 µM). The shallower, better oxygenated stations showed densities of 100,000 to 200,000 individuals per square meter. At the deeper Station 5 (no oxygen detectable) the density was again low with less than 50,000 individuals per square meter.

Flux rates

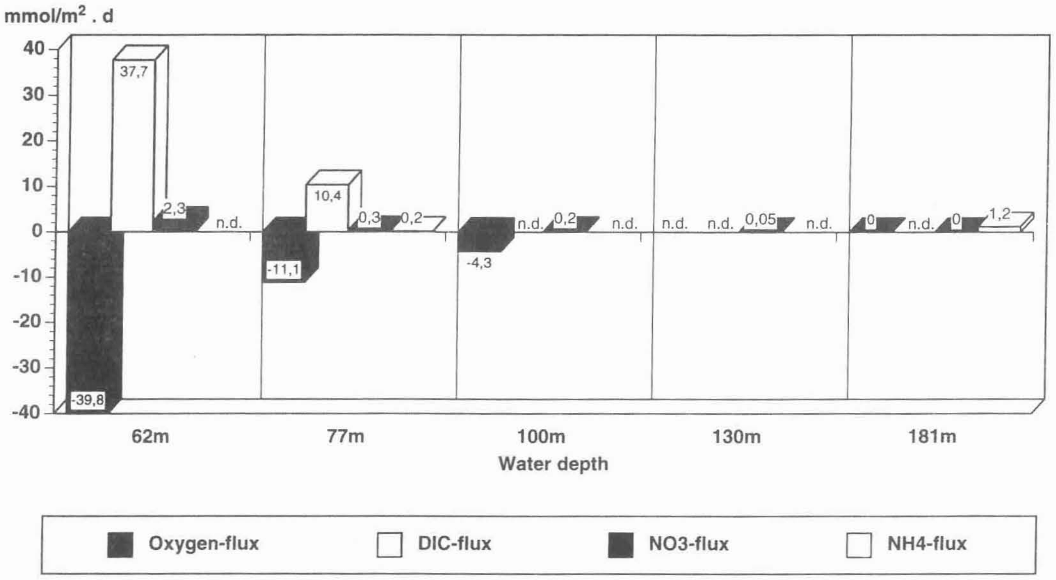

Fig. 5 Fluxes of O_2, ΣCO_2, NO_3^-, NH_4^+ at Stations 1 to 5

The fluxes of oxygen, dissolved inorganic carbon (DIC), nitrate and ammonia are shown in Fig. 5. The rates of oxygen flux (into the sediment) and DIC flux (out of the sediment) match well at Stations 1 and 2. At Stations 3 and 4 the DIC flux could not be determined from the measurements and at Station 4 the oxygen content in the bottom water was too low (< 5 µM) to detect a flux into the sediment. The flux of nitrate out of the sediment decreased with greater depth from 2.3 mmol $\cdot$ m^{-2} $\cdot$ d^{-1} at 62 m to zero at 181 m. Ammonia concentrations increased in the chamber at two stations resulting in a flux of 0.2 mmol $\cdot$ m^{-2} $\cdot$ d^{-1} at Station 2 and 1.2 mmol $\cdot$ m^{-2} $\cdot$ d^{-1} at Station 5. The diffusive oxygen uptake of the sediment decreased with increasing water depth (Table 2). This portion of the total uptake was low at Station 1 (29.9%) and increased with lower macrofaunal biomass at Stations 2 and 3 (Table 3). The diffusive uptake accounts for meiofauna respiration and aerobic microbial degradation as well as for the reoxidation of H_2S and manganese formed during sulfate and manganese reduction. No efflux of H_2S into the bottom water was measured at Stations 1 to 4. An increased concentration of manganese in the bottom water was observed at Station 4.

Tab. 3 Pathways of organic carbon remineralization at stations 1 (62 m) to 3 (100 m).
AMR = aerobic microbial respiration; MR = meiofaunal respiration

Station	TOU (mmol $\cdot$ m^{-2} $\cdot$ d^{-1})	faunal remineralisation (%)	AMR+MR (%)	sulfate reduction (%)	manganese (+iron) reduction (%)
1	39.8	70.1	23.0	5.5	1.4
2	11.1	47.7	34.3	14.4	3.6
3	4.3	46.5	≈ 3.0	46.5	≈ 4.0

Respiration rates

Respiration rates of the total faunal community were calculated. The oxygen uptake that could be contributed to the fauna (difference between TOU and DOU) was divided by the biomass to determine respiration rates. The respiration rate was 0.0142 µmol O_2 $\cdot$ mg ww^{-1} $\cdot$ d^{-1} at Station 1 and 0.0135 µmol O_2 $\cdot$ mg ww^{-1} $\cdot$ d^{-1} at Station 3. Station 2 had a slightly lower rate at 0.0082 µmol O_2 $\cdot$ mg ww^{-1} $\cdot$ d^{-1} (Fig. 6).

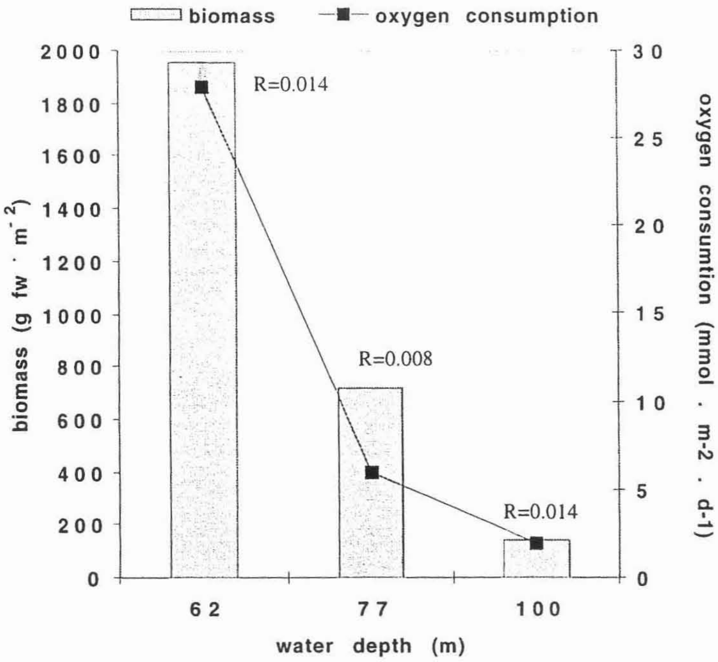

Fig. 6 Biomass of macrofauna and oxygen consumption of the fauna. Values are calculated on the basis of an area of one squaremeter. For explanation of respiration rate (R), see text.

3.5. Discussion

In the Black Sea, the transition zone between oxygenated upper water and deeper waters containing free sulfide plays a dominant role for many redox-processes and, therefore, also for the remineralization of organic compounds. This zone is therefore a very interesting place to study these processes and their impact on the biota. Other zones such as the ”cold intermediate layer” (CIL) (Filippov 1965, Ovchinnikov & Popov 1987, Murray et al. 1991) or the ”manganese particle layer” (Spencer & Brewer 1971) can be used to verify the location of the O_2/H_2S transition zone. A new biological approach was used by Luth & Luth (1997). They specified certain faunal assemblages as indicators for certain bottom water conditions.

The lower boundary of the CIL where water temperatures are below 8° C was situated around 130 m water depth in this study compared to 90 m in the study of Luth & Luth (1997). Corresponding oxygen concentrations in the bottom water were also reached slightly deeper in our study, but the beginning of the anoxic layer where no traces of oxygen were detectable was at similar depth (130 - 180 m). This suggests that in 1992 (Luth & Luth, 1997) the suboxic zone was beginning at a similar depth as in this study, both conducted at the same time of the year (September/October). The gradients of nitrate, ammonia and reduced manganese measured in the bottom water support this assumption. All three parameters revealed strong changes between Stations 4 (130 m) and 5 (181 m) indicating the transition from oxygenated to oxygen free conditions within this depth interval.

The water content was low at Stations 1 to 4 compared to the deeper stations as was the organic content in the uppermost 10 cm. The low water content resulted from the high portion of mussel shells. The organic content was comparatively low in the sediment since most of the organic material coming from the water column was retained by the large amount of filter feeders on top of the sediment and remineralized there. Evidence for higher organic supply was confirmed by high TOU rates, which are discussed later.

The overall uptake rates of oxygen were strongly influenced by the presence of the bottom fauna. The fluxes measured with the chamber lander are dominated by the metabolism rates of the animals. The microbial remineralization rates are better reflected by the uptake rates measured with the profiling lander. Nevertheless, the total uptakes can be compared to chamber measurements done by Friedl et al. (1998), although fauna was not quantified at stations along the coastline and at the shelf edge of the western Black Sea. In this study for the shallow shelf (62 m) with high macrofaunal densities, TOU was higher than the rates measured by Friedl et al. (1998) in front of the eutrophic Danube delta or the Varna Bay (26m and 24 m water depth respectively). They were also at the upper limit of the range of values measured in other estuaries or coastal seas (overview see Friedl et al. 1998). A large share of these uptake rates was based on faunal activity. The diffusive uptake rates were significantly lower and, therefore, in the ”normal” range of shelf sediments.

The typical macrofaunal coenoses of the western Black Sea shelf sediments were found in this study (Kieseleva 1981, Luth & Luth 1997). A high biomass and comparatively large number of species were found at the Station 1 (62 m) which is representative of large areas of the shelf sediments (Luth & Luth 1997, Friedl et al. 1998). Station 2 (77 m) had a much lower biomass but an even higher number of species. At Station 3 (100 m), bottom water was hypoxic resulting in a severe decrease in macrofaunal density.

Although there was a severe decrease of oxygen in the bottom water, the overall respiration rate of the macrofauna community did not change from the well oxygenated Station 1 to the oxygen depleted Station 3 (Fig. 5). The respiration rates at Stations 1 and 3 were almost identical with 0.014 and 0.015 µmol $O_2 \cdot$ mg $ww^{-1} \cdot d^{-1}$ respectively. Using conversation factors after Rumohr et al. (1987), values for the respiration of shell free fresh weight were in the range of 0.049 to 0.059 µmol $O_2 \cdot$ mg $fw^{-1} \cdot d^{-1}$. These results, calculated from data obtained *in situ* for the first time, indicate that the macrofaunal (mussel) community on the shelf of the Black Sea does not adapt to the decreasing oxygen content in the bottom water with a lower oxygen consumption rate. The members of the mussel community react as oxygen regulators in the described biocoenoses.

The respiration rates of *Mytilus* and *Modiolus* measured in situ with the chamber lander were in the same range as laboratory studies with *Mytilus edulis* (Hamburger et al. 1983). A correlation of respiration rate and size/develpoment stage of the animals was found. Adult mussels showed values of 0.060 to 0.070 µmol $O_2 \cdot$ mg $fw^{-1} \cdot d^{-1}$ (recalculated). Taylor & Brand (1975) showed that even at an oxygen concentration of 25 % air saturation which is similar to the situation at Station 3 in this study (22 % air sat.) the respiration rate of *Mytilus edulis* was 0.041 µmol $O_2 \cdot$ mg $fw^{-1} \cdot d^{-1}$ (recalculated). They confirmed the increased ability of mussels to act as oxygen regulators as the animals grow. The nutritional state of the animal also plays an important role. *Mytilus*, under conditions of nutritive stress in the laboratory, lost their ability to regulate oxygen consumption (Bayne 1971a). Taylor & Brand (1975) and Bayne (1971b) showed that *Mytilus* did not regulate oxygen consumption by a higher ventilation rate but by increasing the oxygen utilization from 5-10 % at normoxic conditions to 30-40 % at 25% air saturation. The same effect was observed by Massabuau et al. (1991). They measured constant oxygen uptake rates of 0.0029 µmol $O_2 \cdot$ mg $fw^{-1} \cdot d^{-1}$ for large freshwater mussels *Anodonta cygnea* over a large range of ambient oxygen concentrations down to approx. 5% air saturation. The oxygen partial pressure in the blood of the mussels was well regulated at a low value (1-3 kPa) independent of the ambient oxygen in the water.

The critical pO_2 were the mussel community on the Romanian shelf sediments lose the ability to regulate oxygen consumption seems to be below the 23 % air saturation that was measured at Station 3. This is consistent with Bayne (1971b) who showed similar effects down to 25% air saturation. Bayne (1971b) observed cardiac arrest (reversible) at around 12.5 % air saturation. The same effect was reported by Zaika et al. (1990) for Mytilids of the Black Sea.

Different distribution patterns than for the macrofauna were found for the meiofauna. Some meiofauna taxa, especially within the nematodes (Giere 1993) and foraminifera (Moodley et al. 1998), seem to be less sensitive to temporary anoxia and sulfide exposure than most of the macrofauna taxa (Theede 1973, Gamenick et al. 1996) and, therefore, appear regularly in hypoxic or even anoxic layers of the sediment. Macrofauna and, therefore, predation is already reduced under the hypoxic conditions at the interface zone on the shelf. Food supply in the form of relatively fresh organic material which is mixed with terrigenous input from the rivers Danube and Dniester (C:N ratio = 12,5 in the top 2 cm of the sediment, Weber et al. in prep.) is supplied frequently (and is not consumed by filter feeders). These areas at approximately 130 m depth seems to be good habitats for dense populations of (nematode-) meiofauna.

Organic matter degradation

The pathways of the remineralization of the organic carbon on the Romanian shelf were determined by the measurements of total and diffusive oxygen uptake and the simultanously measured sulfate reduction rates of the sediments (Weber et al. in prep.). Iron and manganese reduction rates were also measured and calculated to be in the same range as values for sulfate reduction (Thamdrup, pers. comm.) with the exception of Station 3 were iron and manganese reduction were assumed to contribute less based on the fraction of the DOU used for reoxidation. Denitrification was not measured directly and therefore it is not possible to estimate the significance of this process, but denitrification rates have been found to be low in comparable shallow marine sediments (Glud et al., 1998).

Bioturbation of deeper sediment layers did not play an important role in the mussel covered shelf sediment since tube-dwelling or burrowing macrofauna were not present. Mussels, on the other hand, that have an inlet and outlet both directed up to the overlying water, formed a 1 to 2 cm thick layer that separated the lower sediment layers from the active upper zone (Fig. 7). Therefore an advective water flow passing the interface between the mussel layer and the underlying sediment was not to be expected. This assumption is essential if the difference in TOU and DOU is to be addressed to faunal remineralization.

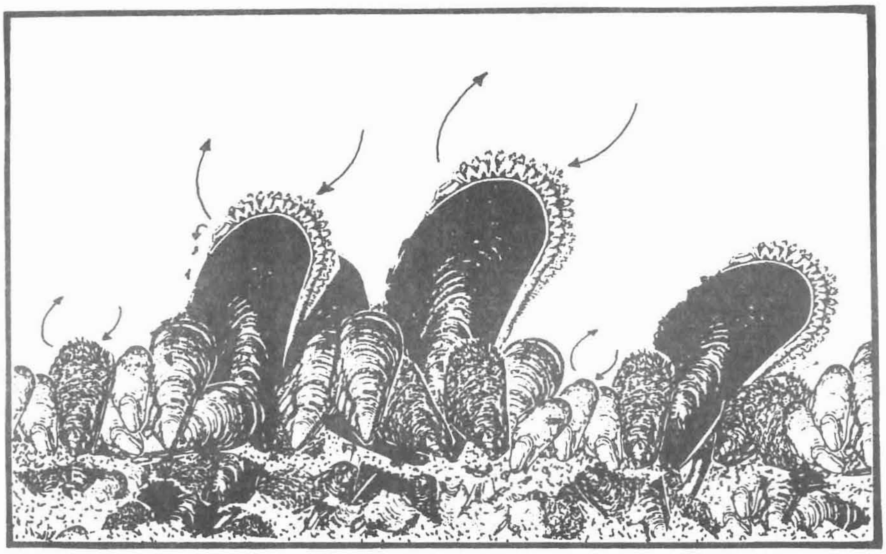

Fig. 7 Diagramm of a mussel bed. Arrows indicate water current, created by the mussels for breathing and filter feeding

For calculation of remineralization rates, TOU was assumed to represent total carbon degradation (O_2: CO_2 = 1:1) (Canfield, 1993) (the assumption actually includes reoxidation of all reduced compounds which is true for Stations 1 to 3). This was supported by matching TOU uptake and DIC release rates at Stations 1 and 2, where both parameters were measured. For sulfate reduction a production of 2 moles of CO_2 for each mole of sulfate was assumed (Westrich, 1983).

Based on these comparisons the macrofauna on the shallow stations appear to dominate remineralization. When the faunal densities were decreasing so was the percentage of direct faunal remineralization. The percentage of the different pathways of carbon remineralization is shown in Table 3. Faunal remineralization always played the major role at Stations 1 to 3. Sulfate reduction became important at Station 3 (46.5%) and was dominant or the exclusive pathway at the deeper stations (Weber et al. in prep.).

The area of the Black Sea that is occupied by benthos is restricted to the shallow shelf and covers approx. 95,000 km^2 or 23% of the total Black Sea area (Zenkevich, 1963). Thus, the shelf area also represents the only zoological active zone of the benthos of the Black Sea. The impact of the benthic faunal assemblies on the overall remineralization in the Black Sea should, therefore, not be underestimated. Taking into account the values for the populated area and medium faunal density from Zenkevich (1963) and adding our values for faunal density, composition and faunal respiration, one could calculate a carbon turnover caused by benthic macrofauna in the Black Sea between 1.17 Gt C $\cdot$ y^{-1} and 3.5 Gt C $\cdot$ y^{-1}.

3.6. Summary

- The Romanian shelf is widely covered with mussels and has very high oxygen uptake rates. These rates are higher than the sedimentary oxygen consumption rates determined at the highly eutrophic river mouths of the Danube and Dniester.

- Oxygen uptake rates measured *in situ* were correlated directly to the incubated fauna and respiration rates of the fauna were calculated. The mussel fauna act as oxygen regulators and adapt to changing oxygen conditions.

- At shelf stations the 2 to 3 cm thick layer of living bivalves appears to control remineralization, allowing for a small portion of microbial degradation in the underlying sediment.

3.7. Acknowledgements

The authors wish to thank the Crew of the RV Petr Kottsov and B.B. Jørgensen (cruise leader) and A. Weber (cruise coordinator) for providing excellent conditions for our work. Dr. S. Boehme and Dr. U. Witte are thanked for valuable discussion of the manuscript. We also thank G. Eickert, A. Eggers, and V. Huebner for manufacturing great electrodes and help with some of the sample processing as well as our technician S. Meyer for solving all the "urgent"- and "last minute"-problems. C. Luth translated many pages of Russian publications to make them available for the rest of us.

3.8. References

Bayne BL (1971a) Oxygen consumption by three species of lamellibranch mollusc in declining ambient oxygen tension. Comp Biochem Physiol 40 A: 955-970

Bayne BL (1971b) Ventilation, the heart beat and oxygen uptake by *Mytilus edulis* L. in declining oxygen tension. Comp Biochem Physiol 40 A: 1065-1085

Braman RS, Hendrix SA (1989) Nanogram nitrite and nitrate determination in environmental and biological materials by vanadium (III) reduction with chemoluminescence detection. Anal Chem 61: 2715-2718

Canfield DE (1993) Organic matter oxidation in marine sediments. In Wollast R, Mackenzie FT and Chou L (eds) Interactions of C, N, P. Biochemical cycles and global change. Springer Verlag, Berlin/Heidelberg

Cowie GL, Hedges JI (1991) Organic carbon and nitrogen geochemistry of Black Sea surface sediments from stations spanning the oxic:anoxic boundary. In: Izdar E & Murray JW (eds) Black Sea Oceanography. Kluwer Academic Publishers, Netherlands, p 343-359

Filippov DM (1965) The cold intermediate layer in the Black Sea. Oceanology 5: 47-52

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

Gamenick I, Jahn A, Vopel K, Giere O (1996) Hypoxia and sulphide as structuring factors in a macrozoobenthic community on the Baltic Sea shore: colonization studies and tolerance experiments. Mar Ecol Prog Ser 144: 73-85

Giere O (1993) Meiobenthology. Springer Verlag Berlin. Berlin

Glud RN, Gundersen JK, Jorgensen BB, Revsbech NP, Schulz HD (1994) Diffusive and total oxygen uptake of deep-sea sediments in the eastern South Atlantic Ocean: *in situ* and laboratory measurements. Deep-Sea Res I 40: 1767-1788

Glud RN, Holby O, Hoffmann F, Canfield DE (1998) Benthic mineralization and exchange in arctic sediments (Svalbard, Norway). MEPS 173: 237-251

Hall POJ, Aller RC (1992) Rapid, small volume, flow injection analysis for TCO_2 and NH_4^+ in marine and freshwaters. Limnol Oceanogr 37(5): 1113-1119

Hamburger K, Møhlenberg F, Randløv A, Riisgård HU (1983) Size, oxygen consumption and growth in the mussel *Mytilus edulis*. Mar Biol 75: 303-306

Izdar E, Ergün M (1991) Recent geological evolution of the Black Sea: An overview. In: Izdar E & Murray JW (eds) Black Sea Oceanography. Kluwer Academic Publishers, Netherlands, p 379-387

Jahnke RA, Christiansen MB (1989) A free-vehicle benthic chamber instrument for sea floor studies. Deep-Sea Res 36: 625-637

Kiseleva MI (1981) Soft-bottom benthos of the Black Sea. Naukova dumka, Kiev, 168 pp. (in Russian)

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

Luth U, Luth CM (1997) A benthic approach to determine long-term changes of the oxic/anoxic interface in the water column of the Black Sea. In: Proceedings of the 30th European Marine Biological Symposium, Southampton, UK, p 231-241

Massabuau JC, Burtin B, Wheathly M (1991) How is O_2 consumption maintained independent of ambient oxygen in mussel *Anodonta cygnea*? Respiration Physiology 83: 103-114

Moodley L, Schaub BEM, van der Zwaan GJ, Herman PMJ (1998) Tolerance of benthic foraminifera (Protista: Sarcodina) to hydrogen sulphide. Mar Ecol Prog Ser 169: 77-86

Murray JW, Top Z, Özsoy E (1991) Hydrographic properties and ventilation of the Black Sea. Deep-Sea Res 38 (Suppl.2): 663-689

Nichols JA (1979) A simple flotation technique for separating meiobenthic nematodes from fine-graded sediments. Trans Am Microsc Soc 98: 127-130

Ovchinnikov IM, Popov YI (1987) Evolution of the cold intermediate layer in the Black Sea. Oceanology 27(5): 739-746

Reimers CE (1987) An *in situ* microprofiling instrument for measuring interfacial pore water gradients: methods and oxygen profiles from the North Pacific Ocean. Deep-Sea Res 34: 2019-2035

Revsbech NP (1989) An oxygen microsensor with a guard cathode. Limnol Oceanogr 34(2): 474-478

Riemann F (1988) Nematoda. In: Higgins RP, Thiel H (eds) Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, pp 293-301

Rumohr H, Brey T, Ankar S (1987) A Compilation of biometric conversation factors for benthic invertebrates of the Baltic Sea. The Baltic Marine Biologists Publication no. 9: 1-56

Spencer DW, Brewer PG (1971) Vertical advection, diffusion and redox potentials as controls on the distribution of manganese and other trace metals dissolved in the waters of the Black Sea. J Geophys Res 76: 5877-5892

Taylor AC, Brand AR (1975) A comparative study of the respiratory responses of the bivalves *Arctica islandica* (L.) and *Mytilus edulis* L. to declining oxygen tension. Proc R Soc Lon B 190: 443-456

Theede H (1973) Comparative studies of the influence of oxygen deficiency and hydrogen sulphide on marine bottom invertebrates. Neth J Sea Res 7: 244-252

Vinogradov MY (1991) The upper boundary of the hydrogen sulfide zone in the Black Sea and trends of its position. Oceanology 31(3): 299-303

Weber A, Jørgensen BB, Wenzhoefer F, Riess W (for submission in Deep-Sea Research) Sulfate reduction in Black Sea sediments; *in situ* and laboratory radiotracer measurements from the shelf to 2000 m depth

Westrich JT (1983) The consequences and controls of bacterial sulfate reduction in marine sediments. Ph.D. thesis, Yale University

Zaika VE, Valovaya NA, Povtschun AS, Revkov NK (1990) Mytilids of the Black Sea. Naukova dumka, Kiev (in Russian)

Zenkevich LA (1963) Fauna and biological productivity of the seas. In: Biology of the Seas of the USSR. Vol II. Sovetskaja Nauka, Moscow, 588 pp.

Chapter 4

Anoxic thermomineral cave waters and bacterial mats as habitat for freshwater nematodes

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4.1. Abstract

A unique chemoautotrophic system of floating microbial mats was examined in a subterranean cave in southern Romania. Oxygen measurements were made with a recently developed technique applying micro-optodes. The oxygen uptake rate of the anoxic and sulfidic cave waters over the interface was as high as 103.3 (± 9.1) mmol $O_2 \cdot m^{-2} \cdot d^{-1}$. Floating microbial mats consisting primarily of sulfide oxidizers and fungal mycelia were found to be adapted to reduced oxygen supply and thrieved even under strict anoxia. These 2 mm thick mats were inhabited by 5 different species of nematodes reaching densities of $9.8 \cdot 10^6$ individuals $\cdot m^{-2}$. Possible alternative pathways for growth of the mats and also for the persistence and reproduction of nematodes under strict anoxic conditions are discussed.

4.2. Introduction

The ability to survive in anoxic (and sulfidic) environments has been reported for many protozoa and metazoa (Bryant 1991, Giere 1992, Grieshaber et al. 1994, Grieshaber & Völkel 1998, Fenchel & Finlay 1995, Hochachka 1997). In sediments, the question whether a "thiobios" exists and how it is to be defined has been long debated after the first description of the sulfide system by Fenchel & Riedl (1970). There is a consensus that many taxa can live for extended periods of time without oxygen and, thus, are well adapted to hypoxia (i.e. exhibit physiological or behavioural adaptations). But reports regarding metazoa that live permanently under anoxic conditions remain circumstantial without detailed experimental proof whether the populations examined were able to temporarily take up traces of oxygen by moving within the vertical gradients or by extending at least a part of their body into oxic layers or microniches. Thus, the supply of some oxygen cannot be excluded (Fenchel & Finlay 1991, Fenchel & Finlay 1995). In contrast to specialized protozoa (Fenchel & Finlay 1995), all free living and parasitic metazoa seem to need oxygen at least for their reproductive stages (i.e. eggs, larvae) (Barrett 1991).

A community of five nematode species was discovered thriving within floating microbial mats under completely anoxic, experimental conditions for several months in a thermomineral sulfide-rich groundwater system in Movile Cave, Romania. A recently developed, extremely sensitive oxygen detector with very high spatial resolution and capable of detecting even traces of oxygen (detection limit 10 ppb, Klimant et al. 1997) was used to confirm complete anoxia.

The Movile Cave groundwater system was discovered in 1986 (Lascu 1989). It contains a rich and abundant community of aquatic and terrestrial invertebrates isolated from the surface for a considerable amount of time (for explanation see Sarbu & Kane 1995). The subterranean ecosystem is based entirely on food produced *in situ* by chemoautotrophic microorganisms (Sarbu et al. 1996). Sulfur-oxidizing and methane-oxidizing bacteria were identified in samples of water and microbial mats from Movile Cave (Sarbu et al. 1994, Sarbu et al. 1996, Vlasceanu et al. 1997).

4.3. Material and Methods

Site

Movile Cave is located in Southern Dobrogea, Romania, close to the coastline of the Black Sea and to the town of Mangalia (Fig. 1).

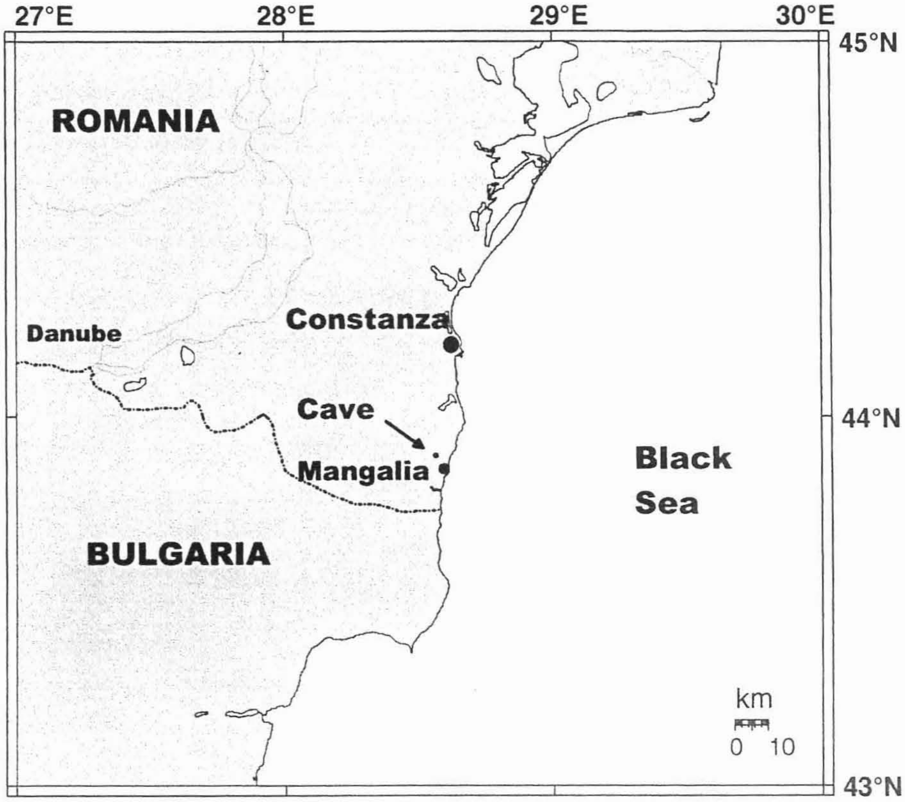

Fig. 1 Location of the cave in Southern Dobrogea in the southeast of Romania

Large subterranean voids of karst origin host a captive thermomineral sulfidic aquifer at depths of 200 m below the surface. In the Mangalia region these waters ascend to the surface along natural faults. They form natural springs and are found as sulfidic groundwaters in the superficial Sarmatian limestones (Lascu 1989).

Movile Cave, a 240 m long system of natural cave passages located 20 m under the surface, was discovered in 1986 when an artificial shaft intercepted a section of the cave. A small lake in the deep section of Movile Cave (Fig. 2) permits access to the lower level of the cave, partially flooded by thermomineral water and containing several air bells (Sarbu & Kane,1995).

The air in the lake room has an oxygen content close to normal epigean air conditions (O_2: 20%, CO_2: 1.5%) whereas in the small adjacent air bells, which can be reached by divers only, the oxygen content is lower and CO_2 and methane concentrations are higher (O_2: 7-10%, CO_2: 2-3.5%, CH_4: 1%) (Sarbu & Popa 1992, this study, Fig.2).

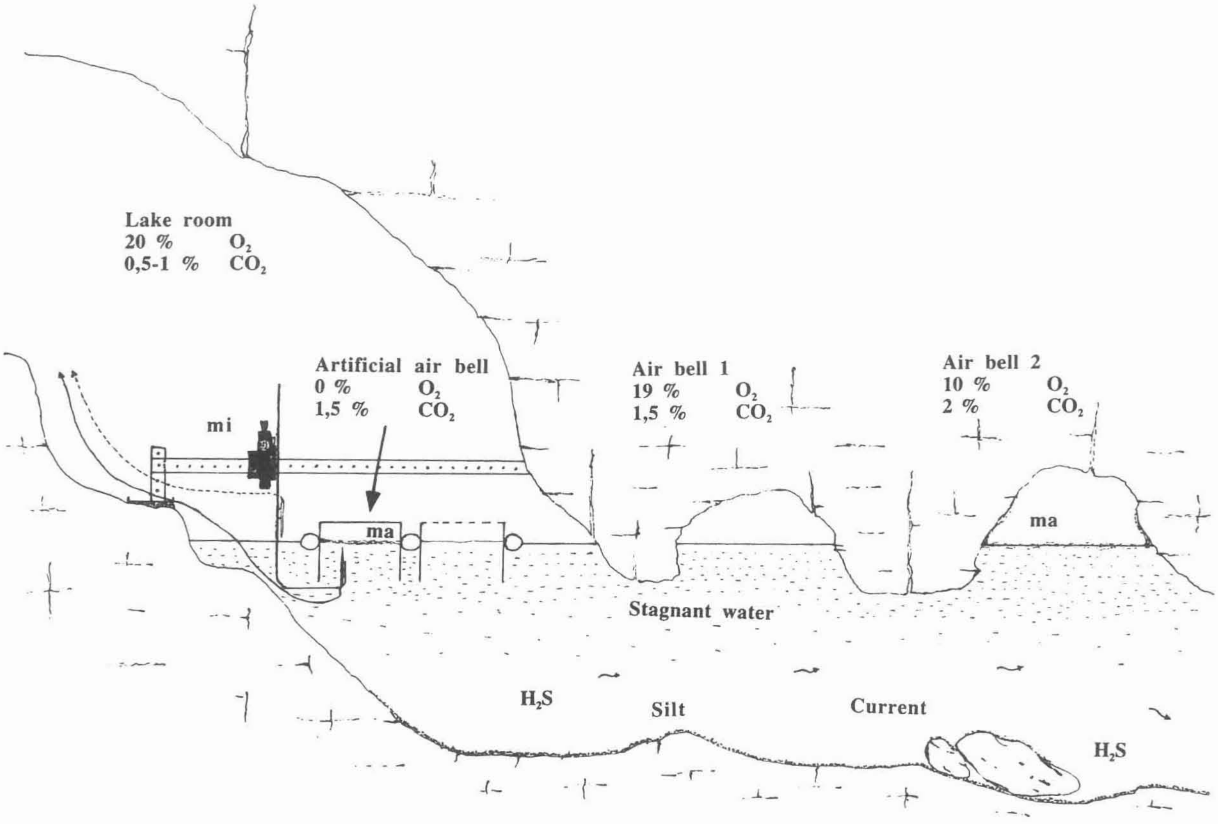

Fig. 2 Transect through the cave. Oxygen and CO_2 contents of the different compartments are given in vol.%. The oxygen measuring setup includes a micromanipulator (mi) for accurate positioning of the optodes mounted in different ways. Microbial mats (ma) only form where oxygen is significantly reduced

The specific physico-chemical conditions at the interface between the thermomineral sulfidic water and the significantly modified atmospheric conditions in the cave's air bells allow the development of floating microbial mats which can attain a thickness of 2-3 millimeters (Fig. 2). The oxygen-rich atmosphere in the lake room prevents the development of floating microbial mats on the surface of the lake. In 1992, plexiglass enclosures were set afloat on the surface of the lake to create artificial air bells (Fig. 2). Openings in their walls allowed a controlled access of oxygen. Floating microbial mats developed in those artificial air bells that resembled the atmosphere within the cave's natural air bells.

Sampling

Biological samples were collected and *in situ* measurements of the physico-chemical parameters of the subterranean environment were performed in Movile Cave and in other sulfide-rich epigean habitats in April 1994, April 1996, November 1996 and July 1998. Several different habitats were screened for the presence of meiofauna. Samples of microbial mats with their inhabitant fauna and some original water were collected in Movile Cave in April 1994 and were cultured in 50 ml centrifuge tubes (Sarstedt). The tubes, which were sealed and stored in an air-tight container in the dark at room temperature, were opened 11 months later and inspected for living animals. Additional vials containing mat material were fixed with buffered formaldehyde solution (final concentration appr. 5%) immediately after sampling. Nematodes living in the dense microbial mat substrate were sorted out and counted under a dissecting microscope immediately after return to the Center for Ecological Research, in Mangalia. Some specimens were mounted on permanent slides (Riemann, 1988) and stored for later identification.

Mat material from the anoxic artificial air bells was frozen and later processed with the French press technique (American Instruments Co.Inc., Silver Spring, USA) to measure nitrate accumulation within the cells and/or mat. The nitrate measurements were done using a 42C $NO-NO_2-NO_x$ Analyzer (Thermo Environmental Instrumens, Reference Method RFNA-1289-074) (see Braman and Hendrix 1989).

Water samples were collected in 5 cm intervals between 5 and 90 cm using 1 ml syringes to determine the concentration of hydrogen sulfide (total soluble sulfide: H_2S, HS^-, S^{2-}) in the cave water. The samples were fixed with alkaline zinc-acetate solution and were measured photometrically (Gilboa-Garber 1971, modified). The chemical composition of the atmosphere in the lake room and in the artificial air bells was determined using a DRÄGER hand pump (accuro) and DRÄGER test tubes for oxygen (No 6728081), carbon dioxide (No 8101931) and hydrogen sulfide (No 6728041).

High resolution measurements of oxygen concentrations in the water column were performed in November 1996 in the cave lake and in the artificial air bells. A fiber optical microsensor (optode) (Klimant et al 1995), was connected to an autonomous electronic system (Glud et al. in press) suitable to the specific demands of the cave environment. This battery powered system was used for one of the first *in situ* measurements within the frame of an ecological study.

Optode measurements

The principle of fiber optic oxygen measurements is luminescence quenching of a dye which is sensitive to oxygen. This type of sensor was chosen over the traditional Clark-type electrode since it does not consume oxygen and thus lacks a stirring effect. Additionally optodes have their highest sensitivity at low oxygen concentrations (because of a non-linear dependence of oxygen concentration and optical signal). A 100/140 micrometer silica/silica graded index fiber material (Radiall, Germany) was used for the preparation of fiber optical microsensors (optodes). Previous experiments have shown that it is important to create a rather short taper with the sensor chemistry and the insulation covering only the very tip of the fiber resulting in a good signal to noise ratio. Matrix material and dye solution were dissolved in chloroform with a dye concentration in the polystyrene of 5 mM.

A description of the optical measuring system is given by Klimant et al. (1995) and more recently by Glud et al. (in press). A fitted function was used for the calibration of the optode. This function was determined by adjusting the sensor signal to 9 different oxygen concentrations (0, 5, 10, 25, 40, 55, 70, 85, 100 % air saturation). Based on this function, the optode was calibrated before the measurement at 0 and 100 % air saturation. The detection limit for oxygen of 10 ppb (O_2 solved in water) can be reduced to 0.5 ppb (or 0.1 μM) by using a newly developed dye/matrix system (Klimant, pers. comm., Kühl & Revsbech, in press).

Oxygen profiles in the cave water were measured in the uppermost layers of the lake´s open water to determine the depth of oxygen penetration into the water column and to calculate oxygen fluxes under normoxic conditions. In the open water of the cave lake, oxygen profiles were taken at 100 μm intervals. Corresponding profiles were measured in the artificial anoxic air bell to prove that oxygen was absent in the enclosed floating mats and in the underlying water. Oxygen concentrations in the water column and in the floating microbial mats under the artificial air bells were first measured from under the water surface, and the optode was then lifted toward the surface in 1 mm increments. Within the floating microbial mats measurements were done at 100 μm intervals.

Fick's first law of diffusion was used for the calculation of oxygen fluxes:

$$J = - D_0 \cdot dC / dz$$

where D_0 is the diffusion coefficient in the water at the ambient temperature and salinity and where dC / dz is the change in oxygen concentration over a discrete depth interval. We assumed molecular diffusion as the mode of transport, mass conservation of oxygen and a one-dimensional flux of oxygen into the water.

4.4. Results

The atmosphere in the cave appeared to be free of H_2S since it was not detected by its characteristic smell (detection limit at concentrations of 0.03 to 1 ppm; see Marquardt & Schäfer 1994). A slight stirring of the water surface of the lake caused a very strong smell of hydrogen sulfide, which indicated that only a very thin superficial layer of the water was devoid of free sulfide. The water temperature was stable at 20.5 °C (±0.1), as was the pH at 7.4. The total mineral content was 1 $g \cdot l^{-1}$, of which 0.5g represented bicarbonates and 0.4g NaCl. Sulfate reached values of up to 64 $\mu mol \cdot l^{-1}$, nitrate was as low as 8 $\mu mol \cdot l^{-1}$.

Oxygen / sulfide conditions and fluxes at the water surface

Lake water: A steep oxygen gradient was measured in the lake water with an oxygen penetration depth of 0.8 mm (Fig. 3). This gradient served as a basis for calculating the fluxes of oxygen from the atmosphere into the water and yielded oxygen uptake rates of 103.3 (± 9.1) mmol $O_2 \cdot m^{-2} \cdot d^{-1}$.

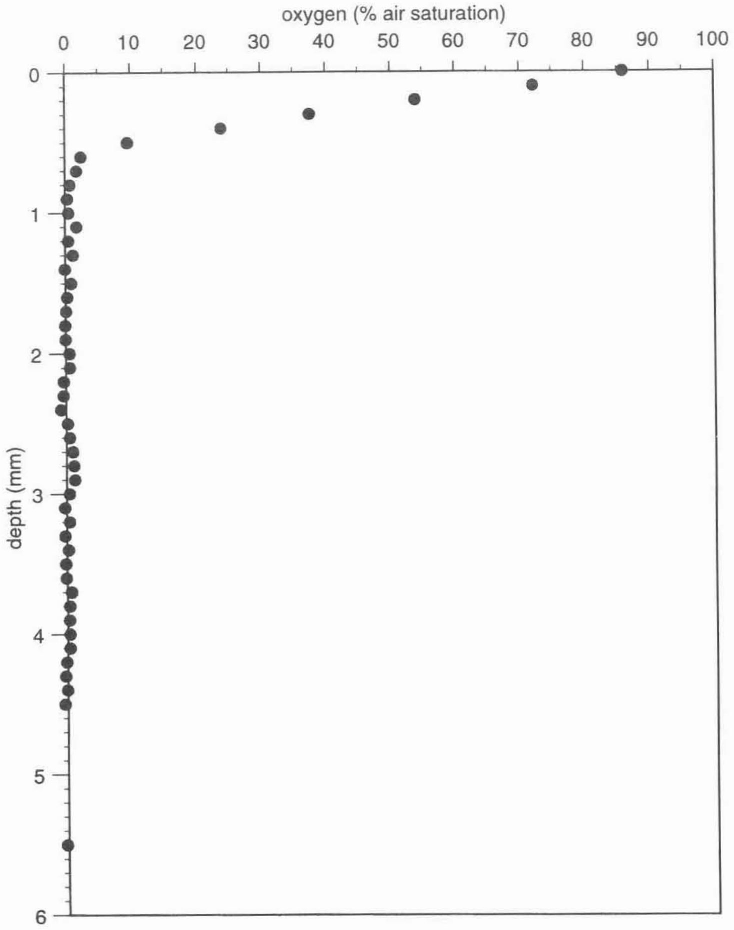

Fig. 3 Oxygen profile at the lake's water surface without a floating mat. Depth resolution 100 µm. Oxygen penetration depth 0.8 mm

The sulfide content in the water column was 300 (± 34) µmol · l^{-1} This value remained fairly constant throughout the water column from 5 to 90 cm depth. A steep gradient in sulfide concentrations appeared to exist between the water surface and the depth of 5 cm, but no measurements were performed above 5 cm. Assuming a sulfide gradient ranging from 0 µmol · l^{-1} at the water surface to 325 µmol · l^{-1} at a depth of about 0.8 to 0.9 mm, where no traces of oxygen could be detected, the upward flux of sulfide was calculated to be 64.2 mmol · m^{-2} · d^{-1}.

Artificial air bell: Within the artificial air bell, there was complete anoxia both in the water column and in the microbial mat (Fig. 4). As soon as the optode's sensor tip was out of the mat and into the air, a significant offset was seen due to different refractory indices of the aqueous and gas phase. In addition, no oxygen was found in the atmosphere entrapped in the experimental air bell that was isolated from the cave atmosphere. Free hydrogen sulfide was measured in the atmosphere under the anoxic tank but the values exceeded 15 ppm which was the upper limit of the Dräger test tubes used.

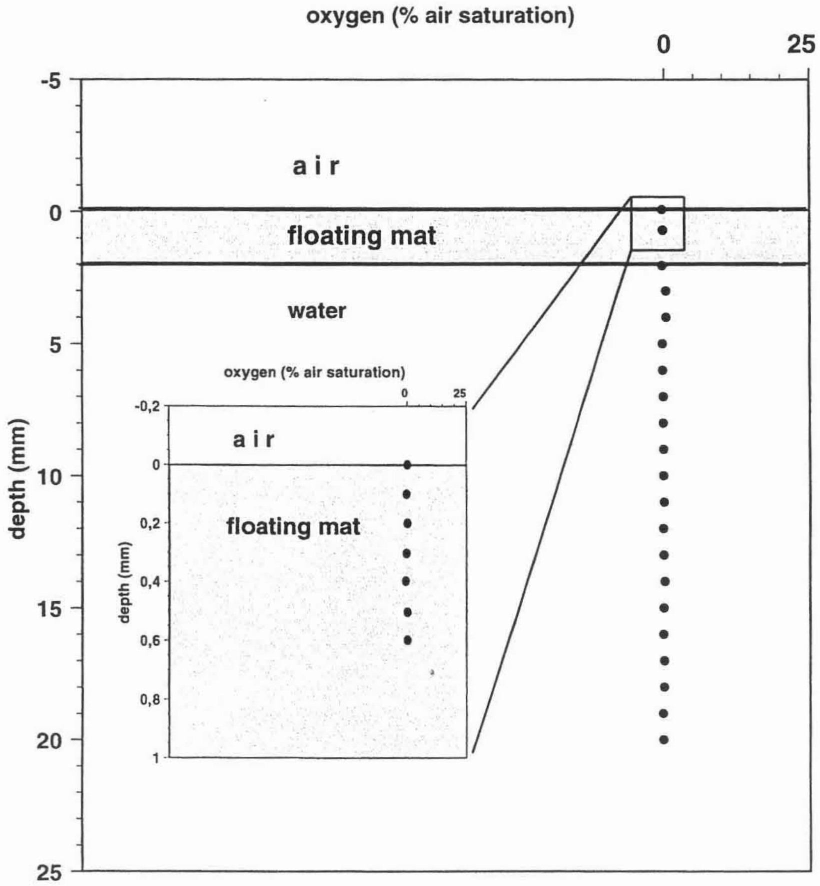

Fig. 4 Oxygen measurement in the artificial air bell. Depth resolution 1 mm. Inset: Uppermost millimeter of the mat, depth resolution 100 μm

Microbial mats

As predicted from the observations in the natural air bells, where mats occurred naturally, microbial mats developed only under those experimental tanks with hypoxic conditions above the water surface. However, a thick microbial mat also developed in the anoxic tank completely isolated from the cave air. Mats consisted of a variety of sulfide oxidizing bacteria such as *Thiotrix* spp., large gliding *Beggiatoa* spp, *Beggiatoa*-like immobile bacteria and *Thiospira* spp. (Küver, pers. comm.). *Thiobacillus thioparus* was identified with molecular techniques by Vlasceanu et al. (1997). S(0) aggregates within the mats indicated sulfide oxidizing activity by bacteria. In addition to sulfur bacteria spirochaetes were also found in the mats (Küver, pers. comm.). The texture of the mats is stabilized by a significant share of fungal mycelia. Within the processed samples of the anoxic mat material we measured nitrate values (serving as a potential electron acceptor for the sulfide oxydizing bacteria) of 156 $\mu mol \cdot l^{-1}$.

Fauna inhabiting the mats

The fauna of the mats is dominated by nematodes and flagellates. The highest populations of nematodes were found in the mats under the experimental tank experiencing complete anoxia for at least several months. The density of the animals within the 2 mm thick mat was calculated to be $9.8 \cdot 10^6$ individuals $\cdot$ m^{-2} which is in the order of magnitude of the highest reported densities in organic rich Wadden Sea areas (Giere 1993). Cultivation experiments with some mat material and original water showed that the nematodes could be kept alive and active for more than one year without any supply of oxygen in a clearly sulfidic environment (smell!).

To date, five nematode species have been found in the mats. These include *Chronogaster troglodytes* sp.n., an endemic species described from Movile Cave (Poinar & Sarbu 1994), *Panagrolaimus* sp., *Protorhabditis* sp., *Udonchus tenuicaudatus* and one species probably belonging to the genus *Monhystrella.* Ultrastructural studies on the nematode species are currently being performed.

4.5. Discussion

Growth of microbial mats and presence of nematodes

Normoxic conditions

Floating microbial mats do not occur under the normoxic surface conditions in the open lake. Only a very thin film is clearly detectable on the water surface. According to the stoichiometry of the oxidation of reduced sulfur, the gradients we found - $J(O_2)$:$J(S^{2-})$ ratio of

1.6 - suggest an oxidation of H_2S to elementary sulfur or even to sulfate with a $J(O_2):J(S^{2-})$ ratio of 1 or 2 respectively. Therefore, growth of sulfide oxidizers is not limited since there is also substantial amounts of dissolved inorganic carbon (DIC) as a potential carbon source. On the other hand, we found a high number of heterotrophs mainly in the upper thin water layer (0.8 mm) that contains oxygen, especially flagellates and crustaceans reach high numbers. It seems very likely that these heterotrophs cause a significant grazing effect on the microorganisms as long as they have enough oxygen.

Since the habitat for substrate-depending forms like nematodes is limited, nematodes occur in small numbers only. Nematodes tend to stay in contact to a certain substrate, but they are able to swim and were present in small numbers in the uppermost layer of the water column.

Hypoxic conditions

The situation changes when conditions become hypoxic in the air bells. Reduced grazing permits the development of thick floating microbial mats consisting not only of sulfide oxidizers but also of significant amounts of fungal mycelia. Large numbers of nematodes live within these mats.

Despite the hypoxic conditions there is enough oxygen in the water and in the mats for the sulfide oxidizers and for the nematodes to perform aerobic respiration. Gnaiger (1991) found that even under 0.5 % air saturation animals were able to fulfill one third of their metabolism aerobically. An oxygen content of 10 % in the air bell´s atmosphere is thus not a major problem for the nematodes´ metabolism and obviously also not for reproduction.

Anoxic conditions

Under the artificial enclosures floating on the water surface in the lake room, conditions are completely anoxic (Fig.4). Nevertheless floating mats started to form only 15 days after the enclosures were installed and the mats reached the final 2 mm thickness about five months later. Diffusion of oxygen through plexiglass was calculated to account for a daily oxygen flux that corresponds to only 0.23 % of the total volume of air under the experimental tank (for calculation see Smith et al. 1997). Free hydrogen sulfide was measured in the entrapped atmosphere also indicating the absence of oxygen and reducing conditions. Since the oxygen that existed at the start of the experiment is depleted within approximately 9 days, the sulfide oxidizers have to switch to a different electron acceptor. Nitrate is sparse in the water column, but Fossing et al. (1995) and McHatton et al. (1996) showed that *Thioploca* and *Beggiatoa* are able to accumulate nitrate in their vacuoles up to 4000 fold compared to the ambient water. The nitrate measurements of the anoxic mat material showed the increase of nitrate to be approximately 20 fold compared to the ambient water (156 μM and 8 μM respectively). The low nitrate content in the water and the possible need to accumulate an electron acceptor could be an explanation for the relatively slow growth of the microbial mats under anoxic conditions.

Surprisingly, the highest numbers of nematodes were found in these anoxic mats. As noted above, only a very small number of nematodes was present in the enclosures at the start of the experiment. As conditions became anoxic very soon after the installation of the enclosures, it is hard to assume that nematodes would be attracted from the surrounding body of water. In addition, millions of animals would have to swim distances of several meters out of their original habitat, the floating mats in the cave's natural air bells. The chamber walls descended 15 cm into the cave water, representing a barrier to nematode migration into the chamber. Thus, the high population density in these mats is assumed to result from *in situ* reproduction.

Growth and reproduction under anoxic conditions

The term anoxia, its definition, and the ability of guaranteeing anoxia under experimental conditions has been widely discussed in the literature (overview see Gnaiger 1991). It is significant whether animals have to face anoxia or just hypoxia. Measuring very low levels of oxygen is difficult and highly dependent on the method used. So far this has limited the interpretation of true anoxic conditions. The oxygen optode is very sensitive to small quantities of O_2. In addition we found a habitat with extraordinarily high chemical and biological oxygen uptake rates, thus limiting the access of O_2 to the nematodes even if a few molecules of oxygen might still get into the system.

Nitrate respiration has never been reported from nematodes although experiments have been performed to determine its existence (Riemann, pers. comm.). Previous reports of metazoans living and reproducing under anoxia (Famme & Knudsen 1984, 1985) have been disputed in the literature (Gnaiger & Staudigl 1987, Schöttler & Bennet 1991).

Adult animals in the floating mats are not food limited. Thus, the survival under anoxia would be possible even taking into account the low efficiency of anaerobic pathways. Energy production would therefore not be critical. For reproduction on the other hand, especially for the development of eggs, there should be another more efficient pathway of energy production with an inorganic electron acceptor, since the energy demand for the early reproductive stages is very high (especially for cell divisions). Jensen (1995) found only reproductive adults of the nematode *Theristus anoxybioticus* at the oxygenated sediment surface of muddy sediments (at methane seepages/ northern Kattegat, Denmark) for a short period of time whereas juveniles were typically restricted to the deeper anoxic layers suggesting that even this facultative anaerobe nematode needed to reach oxygen for its reproduction. Other oxygen sensitive processes, for example the collagen synthese (Barrett 1991), have also to be taken into account.

If we assume the nitrate accumulation in the microbial mat to be significant and look for a way for the nematodes to benefit from this source of electron acceptor, the next step would be to search for

- modifications in mitochondria. Several authors found that the ultrastructure of mitochondria/hydrogenosomes changed with the occurrence of nitrate reduction in organisms like the ciliate *Loxodes* (Finlay et al. 1983, Finlay 1985) or in other animals from anoxic or sulfidic environments (overview see Dubilier 1992).
- the presence of symbiotic bacteria
- the presence of nitrate reductase in the animals or in symbionts

Other questions arise regarding the detoxification of sulfide in the absence of oxygen. In the presence of oxygen, detoxification could take place to a certain level (Dubilier 1992, Völkel & Grieshaber 1991). Vismann (1991) grouped the physiological mechanisms of sulfide defenses into a hierarchy and suggested a distinction between sulfide tolerant and non-tolerant species. Somero et al. (1989) described that in far the most cases the resistance of animals against the poisoning effects of sulfide is achieved by preventing sulfide from reaching sensitive areas in the body. Powell (1989) stated that thiobiotic meiofauna must be sulfide insensitive which is relevant especially under anoxic conditions when animals switch to an anaerobic metabolism. Detoxification of sulfide might therefore not be critical. Still other possible metabolic consequences such as disruptive effects on proteins caused by H_2S (Vetter et al. 1991), have to be taken into account.

4.6. Acknowledgements

The project was supported by the Volkswagen-foundation/Germany (No.I/71 041). V. Meyer (MPI) built much of the electronics and adapted it for the use in the cave for which we are very grateful. We thank F. Riemann for his advice in identifying the nematodes and for helpful suggestions. We also thank the members of the GESS team for support during field work. The manuscript benefitted from the comments of three reviewers for which we are also very grateful.

4.7 References

Barrett J (1991) Parasitic helminths. In: Bryant C (ed) Metazoan life without oxygen. Chapman and Hall, London, p 146-164

Braman RS, Hendrix SA (1989) Nanogram nitrite and nitrate determination in environmental and biological materials by vanadium (III) reduction with chemoluminescence detection. Analytical Chemistry 61: 2715-2718

Bryant C (1991) Metazoan life without oxygen. Chapman and Hall, London

Dubilier N (1992) Ökophysiologische und morphologische Anpassungen des marinen Oligochaeten *Tubificoides benedii* (d'Udekem) an Sauerstoffmangel und Sulfid. Dissertation, Univ. Hamburg

Famme P, Knudsen J (1984) Total heat balance study of anaerobiosis in *Tubifex tubifex* (Müller). J. Comp. Physiol. 154: 587-591

Famme P, Knudsen J (1985) Anoxic survival growth and reproduction by the freshwater annelid *Tubifex* sp. demonstrated using a new simple anoxic chemostat. Comp. Biochem. Physiol. 81 A: 251-253

Fenchel TM, Riedl RJ (1970) The sulfide system: A new biotic community underneath the oxidized layer of marine sand bottoms. Mar. Biol. 7: 255-268

Fenchel T, Finlay BJ (1991) The biology of free-living anaerobic ciliates. Eur. j. protistol. 26: 201-215

Fenchel T, Finlay BJ (1995) The evolution of life without oxygen. In: Slatkin M (ed) Exploring evolutionary biology. Sinauer Associates Inc., Sunderland, p 123-130

Finlay BJ (1985) Nitrate respiration by Protozoa (*Loxodes* spp.) in the hypolimnetic nitrite maximum of a productive freshwater pond. Freshw. biol. 15: 333-346

Finlay BJ, Span ASW, Harman JMP (1983) Nitrate respiration in primitive eukaryotes. Nature 303: 333-336

Fossing H, Gallardo VA, Jørgensen BB, Hüttel M, Nielsen LP, Schulz H, Canfield DE, Forster S, Glud RN, Gundersen JK, Küver J, Ramsing NB, Teske A, Thamdrup B, Ulloa O (1995) Concentration and transport of nitrate by the mat-forming sulphur bacterium *Thioploca*. Nature 374: 713-715

Giere O (1992) Benthic life in sulfidic zones of the sea- ecological and structural adaptations to a toxic environment. Verh. Dtsch. Zool. Ges. 85: 77-93

Giere O (1993) Meiobenthology. Springer-Verlag, Berlin

Gilboa-Garber N (1971) Direct spectrophotometric determination of inorganic sulfide in biological materials and in other complex mixtures. Anal. Biochem. 43: 129-133

Glud RN, Klimant I, Holst G, Kohls O, Meyer V, Kühl M, Gundersen JK (in press) Adaptation, test and *in situ* measurements with O_2 microoptodes on benthic landers.Deep-Sea res. (Instruments and Methods)

Gnaiger E (1991) Animal energetics at very low oxygen: Information from calorimetry and respirometry. In: Woakes AJ, Grieshaber MK, Bridges CR (eds) Physiological Strategies for Gas Exchange and Metabolism. Cambridge University Press, Cambridge, p 149-171

Gnaiger E, Staudigl I (1987) Aerobic metabolism and physiological responses of aquatic oligochaetes to environmental anoxia: Heat dissipation, oxygen consumption, feeding and defecation. Physiol. Zool. 60, 6: 659-677

Grieshaber M, Völkel S (1998) Animal adaptations for tolerance and exploitation of poisonous sulfide. Annu. Rev. Physiol. 60: 33-53

Grieshaber MK, Hardewig I, Kreutzer U, Poertner HO (1994) Physiological and metabolic responses to hypoxia in invertebrates. Rev. Physiol. Biochem. Pharmacol. 125: 43-147.

Hochachka PW (1997) Oxygen - a key regulatory metabolite in metabolic defense against hypoxia. Amer. Zool. 37: 595-603.

Jensen P (1995) *Theristus (Penzancia) anoxybioticus* n. sp. (Nematoda: Xyalidae) from sublittoral methane seepages in the northern Kattegat, Denmark. J. nematol. 27, 2: 231-236

Klimant I, Meyer V, Kühl M (1995) Fiber optic oxygen microsensor, a new tool in aquatic biology. Limnol. Oceanogr. 40, 6: 1159-1165

Klimant I, Kühl M, Glud RN, Holst G (1997) Optical measurement of oxygen and temperature in microscale: strategies and biological applications. Sens. actuators B Chem. 38-39: 29-37

Kühl M, Revsbech NP (in press) Microsensors for the study of interfacial biochemical processes. In: B.P. Boudreau & B.B. Jørgensen (eds) The Benthic Boundary Layer. Oxford University Press, Oxford

Lascu C (1989) Paleogeographical and hydrogeological hypothesis regarding the origin of a peculiar cave fauna. Misc. speol. 1: 13-18

Marquardt H, Schäfer SG (1994) Lehrbuch der Toxikologie. Bibliographisches Institut & F.A. Brockhaus AG, Mannheim

McHatton SC, Barry JP, Jannasch HW, Nelson DC (1996) High nitrate concentrations in vacuolate, autotrophic marine *Beggiatoa* spp. Appl. environ. microbiol. 62, 3: 954-958

Poinar jr. GO, Sarbu SM (1994) *Chronogaster troglodytes* sp.n. (Nematoda: Chronogasteridae) from Movile Cave, with a rewiev of cavernicolous nematodes. Fundam. appl. Nematol. 17: 231-237

Powell E (1989) Oxygen, sulfide and diffusion: Why thiobiotic meiofauna must be sulfide-insensitive first-order respirers. J. mar. res. 47: 887-932

Riemann F (1988) Nematoda. In: Higgins RP, Thiel H (eds) Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, p 293-301

Sarbu SM, Popa R (1992) A unique chemoautotrophically based cave ecosystem. In: Camacho AI (ed)The natural history of biospeleology. Monografias Museo Nacional de Ciencias Naturales, Madrid, p 638-666

Sarbu SM, Kinkle BK, Vlasceanu L, Kane TC, Popa R (1994) Microbiological characterisation of a sulfurous thermal groundwater ecosystem. Geomicrobiol. J. 12: 175-182

Sarbu SM, Kane TC (1995) A subterranean chemoautotrophically based ecosystem. NSS Bulletin 57: 91-98.

Sarbu SM, Kane TC, Kinkle BK (1996) A chemoautotrophically based cave ecosystem. Science 272:1953-1955

Schöttler U, Bennet EM (1991) Annelids. In: Bryant C (ed) Metazoan life without oxygen. Chapman and Hall, London, p 165-185

Smith jr. KL, Glatts RC, Baldwin RJ, Beaulieu SE, Uhlman AH, Horn RC, Reimers CE (1997) An autonomous, bottom-transecting vehicle for making long time-series measurements of sediment community oxygen consumption to abyssal depths. Limnol. Oceanogr. 42, 7: 1601-1612

Somero GN, Childress JJ, Anderson AE (1989) Transport, metabolism and detoxification of hydrogen sulfide in animals from sulfide-rich marine environments. Rev. Aquat. Sci. 1: 591-614

Vetter RD, Powell MA, Somero GN (1991) Metazoan adaptations to hydrogen sulphide. In: Bryant C (ed) Metazoan life without oxygen. Chapman and Hall, London, p 109-128

Vismann B (1991) Sulfide tolerance: Physiological mechanisms and ecological implications. Ophelia 34 (1): 1-27

Vlasceanu L, Popa R, Kinkle BK (1997) Characterization of *Thiobacillus thioparus* LV43 and its disribution in a chemoautotrophically based groundwater ecosystem. Appl. Env. Microbiol. 63: 3123-3127

Völkel S, Grieshaber MK (1991) Schwefelwasserstofftoleranz und -entgiftung beim Wattwurm *Arenicola marina*. Verh. Dtsch. Zool. Ges. 84: 433

Chapter 5

Summary of results

The main aim of this thesis was to show the importance of *in situ* data for achieving a reliable record for the estimation of the interaction between geochemical processes and fauna in the processes of organic carbon degradation and energy utilization. It could be shown that multidisciplinary approaches made the quantitative determination of many single processes within carbon cycling and energy transfer possible. The effect of daily migrating macrofauna for the organic carbon transport and oxygen consumption in the benthic boundary layer could be shown by the use of a profiling lander, a chamber lander and pore water profiles. Calculated on an area basis the oxygen consumption and therefore the carbon oxidation of the animals was 25-fold higher than the turnover rates of the sediment.

To quantify the different processes involved in the remineralization of organic carbon at the sediment/water interface on the shelf, the simultaneous use of three different lander types has proved to be very appropriate. This was shown in studies performed in the Baltic Sea and in the Black Sea. Shipboard laboratory incubations are still used to verify the results measured *in situ*, but possible artifacts caused by the recovering of sediment can now be excluded by the *in situ* measurement of the most important metabolic pathways. It could be shown that the importance of oxic remineralization by dense benthic fauna is correlated to their abundance and sulfate reduction becomes more important as the fauna diminishes. At highest fauna densities 70 % of the carbon turnover was mediated by the macrofauna, leaving less than 10 % of the total carbon input for anaerobic degradation pathways in the underlying sediment. This is an unusual finding in an eutrophic shelf system like the northwestern Black Sea and due to the activity of the fauna that overcomes limitations in oxygen supply by creating their own advective flow.

This study showed three examples of the effects that fauna has on transportation processes at the sediment/water interface and effects that geochemical conditions have on the development of biological systems and adaptations of animals. The latter was especially important for the development of a unique system of floating bacterial mats, harboring fauna even under anoxic conditions in an extreme environment. Since fermentation processes do not supply enough energy for the reproduction of metazoan fauna, the possibility for another pathway had to be taken into account and the preconditions for such a process were confirmed.

Since copying of *in situ* conditions for biological systems in the laboratory is often difficult or not even possible yet, further *in situ* measurements will be needed, although the technical and financial effort is usually much higher than for laboratory studies. Models using data for predictions of future situations depend on a lot of data as an input. The quality of the data, that means their proximity to the real *in situ* conditions, directly influences the quality of the results of the predictions by modeling.

A new technique for oxygen measurements, the so called optode, was used as an alternative to the Clark-type electrodes, although the use on a chamber lander needs still to be improved. The need of an *in situ* two point calibration is up to now contrasting their advantages in faster and cheaper production and a better detection limit. The implementation of syntactic foam as buoyancy for two of our lander systems was a success leading to a much higher reliability in recovering the instruments avoiding the loss of landers caused by the implosion of glass spheres.

Further developing of lander systems will lead to systems that will be able to deliver more data with each deployment. For several reasons the possibility of profiling within the chamber of an incubation lander will be one of the next technical aims. To combine the data achievement for DOU and TOU will lead to less interpretative problems caused by spatial heterogeneity of the sediment, that arise with the use of two separate landers. The improvements on the optode measurements include the use of a simpler technique, leading to simpler and cheaper construction of measuring devices and to less problems with pressure and temperature effects on the measuring device. The combined use of lander systems for measuring different processes simultaneously should further on lead to best *in situ* results.

Danksagung

Bei Herrn Prof. Dr. Bo B. Jørgensen möchte ich mich für die Vergabe der vorliegenden Dissertation und die Begutachtung bedanken. Herrn Prof. Dr. Horst D. Schulz danke ich für die Erstellung des Zweit-Gutachtens.

Eine finanzielle Unterstützung erfolgte durch die Max-Planck Gesellschaft. Während der Anfertigung dieser Arbeit wurden zwei Kammerlander aus Mitteln des Sonderforschungsbereiches 261 „ Der Südatlantik im Spätquartär: Rekonstruktion von Stoffhaushalt und Stromsystemen" gebaut. Für die Bereitstellung dieser nicht geringen Beträge sowie der Möglichkeit der Teilnahme an den Meteor-Ausfahrten danke ich der DFG.

Diese Arbeit wäre, wie die meisten technisch aufwendigen Forschungsprojekte, nicht ohne die Hilfe vieler technischer Mitarbeiter entstanden. Bedanken möchte ich mich daher bei Gaby, Anja, Vera, Swantje, Kirsten, Volker, Axel, Stephan, Georg, Christine, Axel, sowie Corinna, Jens, Hartmut, Jörg, Anja und den anderen fleißigen Helfern am MPI. Bernd hat bei der Literaturbeschaffung wahre Wunder vollbracht, wofür ich ihm herzlich danke.

Für wissenschaftliche Diskussionen standen eigentlich alle wissenschaftlichen Mitarbeiter, sowohl am MPI, als auch im Fachbereich Geologie der Universität Bremen, ständig zur Verfügung, was eine große Hilfe war. Neben, Ola, Susan, Ursula, Eric, Oliver, Gerhard, Nicole, BoT, Stefan, Wiebke, Matthias, Sabine und Lars, sei auch Karsten und Ramon besonders gedankt. Herrn Prof. Dr. Olav Giere sei gedankt für sein stetes Interesse an meiner wissenschaftlichen Arbeit.

Mein ganz großer Dank gilt natürlich Andreas und Frank, die als direkte Lander-Mitstreiter eine große Hilfe in allen Lebenslagen waren. Vor allem als ständige Motivationsstütze halfen sie, den Doktoranden-GAU zu verhindern.

Fisch-Kopp sei gedankt für erstklassige Fischgerichte, die nicht nur den Magen füllten, sondern auch die Stimmung hoben.

Das in den letzten drei Jahren eingeschränkte Privatleben wurde erheblich bereichert durch Peter, Andre, Ralf, Joe, Dirk, Ralph, Svenja, Tamara und viele andere geduldige Freunde, wofür ich sehr dankbar bin.

Meiner Mutter und meinem Bruder gilt der größte Dank. Dafür, daß sie mich schon immer, noch immer und wohl auch für immer für fähig hielten, halten und halten werden, das, was ich mir vorgenommen habe, auch zu tun.

In dieser Reihe bereits erschienen:

Nr. 1 **Wefer, G., E. Suess und Fahrtteilnehmer**
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Mechanismen der Sedimentbildung in der Fram-Straße, im Arktischen Ozean und in der Norwegischen See. 167 Seiten, Bremen, 1991.

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Spätquartäre Produktivitätsänderungen im östlichen Angola-Becken: Reaktion auf Variationen im Passat-Monsun-Windsystem und in der Advektion des Benguela-Küstenstroms.
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Spätquartäre Stratigraphie und Paläozeanographie in der Fram-Straße. 174 Seiten, Bremen, 1991.

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Zur klimaabhängigen Bildung biogener und terrigener Sedimente und ihrer Veränderung durch die Frühdiagenese im zentralen und östlichen Südatlantik. 202 Seiten, Bremen, 1992.

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Rekonstruktion der spätquartären Bodenwasserzirkulation im östlichen Südatlantik über stabile Isotope benthischer Foraminiferen. 205 Seiten, Bremen, 1992. (vergriffen)

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Bericht des Graduierten Kollegs. Stoff-Flüsse in marinen Geosystemen.
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Frühdiagenetische Verteilung von Schwermetallen in Schlicksedimenten der westlichen Ostsee.
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Sedimentology, Morphodynamics and Facies Association of a mesotidal Barrier Island Shoreface (Spiekeroog, Southern North Sea). 370 Seiten, Bremen, 1993.

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Magnetische Eigenschaften von Sedimenten des östlichen Südatlantiks und ihre paläozeanographische Relevanz. 170 Seiten, Bremen, 1993.

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Zyklische Sedimentation von organischem Kohlenstoff in der Japan See: Anzeiger für Änderungen von Paläoozeanographie und Paläoklima im Spätkänozoikum.
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Frühdiagenetische Stoff-Flüsse gelöster Schwermetalle an der Oberfläche von Sedimenten des Weser Ästuares. 107 Seiten, Bremen, 1994.

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Frühdiagenetische Stoff-Flüsse in Oberflächen-Sedimenten des äquatorialen und östlichen Südatlantik. 129 Seiten, Bremen, 1994.

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Magnetotaktische Bakterien und ihre Magnetosome in Oberflächensedimenten des Südatlantiks.
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Saisonale Variationen von Porenwasserprofilen, Nährstoff-Flüssen und Reaktionen
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Bericht über den 3. JGOFS-Workshop. 5./6. Dezember 1994 in Bremen. 84 Seiten, Bremen, 1995.

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southern Tibet, China. – Excursion Guide to IGCP 362 Working-Group Meeting
"Integrated Stratigraphy". 113 Seiten, Bremen, 1995. (vergriffen)

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Liefergebiets - Charakterisierung proterozoischer Goldseifen in Ghana anhand von
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The Nature of the Sediment Distribution Patterns in ther Spiekeroog Backbarrier Area,
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Transportverhalten von Schwermetallkationen und Oxoanionen in wassergesättigten Sanden.
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182 Seiten, Bremen, 1995.

Nr. 68 **Hebbeln, D. und Fahrtteilnehmer**
Report and preliminary results of SONNE-Cruise SO 102, Valparaiso - Valparaiso, 95
134 Seiten, Bremen, 1995.

Nr. 69 **Willems, H. (Sprecher), U. Bathmann, U. Bleil, T. v. Dobeneck, K. Herterich, B.B. Jorgensen, E.-M. Nöthig, M. Olesch, J. Pätzold, H.D. Schulz, V. Smetacek, V. Spieß. G. Wefer**
Bericht des Graduierten-Kollegs Stoff-Flüsse in marine Geosystemen.
Berichtszeitraum Januar 1993 - Dezember 1995. 45 & 468 Seiten, Bremen, 1995.

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Bericht über den 4. JGOFS-Workshop. 20./21. November 1995 in Bremen.
60 Seiten, Bremen, 1996. (vergriffen)

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Pliozän-quartäre Karbonatsedimentation und Paläozeanographie des Nordatlantiks und
des Europäischen Nordmeeres - Hinweise aus planktischen Foraminiferengemeinschaften.
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Phylogenetische und ökologische Untersuchungen an Bakterien des oxidativen und reduktiven
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Biogeochemische Charakterisierung von Sinkstoffen und Sedimenten aus ostatlantischen
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Saisonalität im Diatomeen- und Silikoflagellatenfluß im östlichen tropischen und subtropischen
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Report and preliminary results of METEOR-Cruise M 38/1, Las Palmas - Recife, 25.1.-1.3.1997, with Appendix: Core Descriptions from METEOR Cruise M 37/1. Bremen, 1997.

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Report and preliminary results of METEOR-Cruise M 38/2, Recife - Las Palmas, 4.3.-14.4.1997.
126 Seiten, Bremen, 1998.

Nr. 96 **Neuer, S. und Fahrtteilnehmer**
Report and preliminary results of VICTOR HENSEN-Cruise 96/1, Las Palmas - Las Palmas, 10.1. - 4-3.1996. 76 Seiten, Bremen, 1997.

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Fahrtbericht SO 111, 20.8. - 16.9.1996. 115 Seiten, Bremen, 1997.

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Late Cretaceous - Early Tertiary sequence stratigraphy, paleoecology and geodynamics of Eastern Sinai, Egypt. 218 Seiten, Bremen, 1997.

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Verwertung von Bremer Baggergut als Material zur Oberflächenabdichtung von Deponien - Geochemisches Langzeitverhalten und Schwermetall-Mobilität (Cd, Cu, Ni, Pb, Zn).
Bremen, 1997.

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Der Einfluß des Redoxmilieus auf die Mobilität von Chrom im durchströmten Aquifer.
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Einfluß von Viskosität und Dichte des Seewassers auf Transport und Ablagerung von Wattsedimenten (Langeooger Rückseitenwatt, südliche Nordsee).
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Elastische Wellenausbreitung in marinen Sedimenten - Neue Entwicklungen der Ultraschall Sedimentphysik und Sedimentechographie. 298 Seiten, Bremen, 1997.

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Rezente und spätquartäre Sedimentation planktischer Foraminiferen im Peru-Chile Strom.
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Sulfur isotope fractionation in marine sediments and bacterial cultures.
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Endbericht zum Forschungsvorhaben 060 des Landes Bremen: Baggergut der Hafengruppe Bremen-Stadt: Modelluntersuchungen zur Schwermetallmobilität und Möglichkeiten der Verwertung von Hafenschlick aus Bremischen Häfen. 98 Seiten, Bremen, 1997.

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Entwicklung und Erprobung eines benthischen Landersystemes zur *in situ*-Bestimmung von Sulfatreduktionsraten mariner Sedimente. 121 Seiten, Bremen, 1997.

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Bericht über den 6. JGOFS-Workshop am 4./5.12.1997 in Bremen. Im Anhang: Publikationen zum deutschen Beitrag zur Joint Global Ocean Flux Study (JGOFS), Stand 1/1998.
122 Seiten, Bremen, 1998.

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CoTReM, ein Multi-Komponenten Transport- und Reaktions-Modell.
142 Seiten, Bremen, 1998.

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Fahrtbericht SO 124, 4.10. - 16.10.1997. 90 Seiten, Bremen, 1997.

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Biostratigraphie und Sedimentationsmuster einer nordostägyptischen Karbonatrampe unter Berücksichtigung der Alveolinen-Faunen. 142 Seiten, Bremen, 1998.

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Report and preliminary results of METEOR-Cruise M 41/1, Málaga - Libreville, 13.2.-15.3.1998.
Bremen, 1998.

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Untersuchungen an strömungsbeeinflußten Sedimentationsmustern im Südozean. Interpretation sedimentechographischer Daten und numerische Modellierung.
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Spätquartäre Variationen des terrigenen Sedimenteintrags entlang des chilenischen Kontinentalhangs als Abbild von Klimavariabilität im Milanković- und Sub-Milanković-Zeitbereich. 141 Seiten, Bremen, 1998.

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Dokumentation von kurzfristigen Klimaschwankungen des Spätquartärs in Sedimenten des westlichen äquatorialen Atlantiks. 96 Seiten, Bremen, 1998.

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Mixed layer characteristics in the equatorial Atlantic during the late Quaternary as deduced from planktonic foraminifera. 132 Seiten, Bremen, 1998.

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Late Quaternary Planktic Foraminifera Assemblages in the South Atlantic Ocean: Quantitative Determination and Preservational Aspects. 165 Seiten, Bremen, 1998.

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Kalkige und organisch-wandige Dinoflagellaten-Zysten in Spätquartären Sedimenten des tropischen Atlantiks und ihre palökologische Auswertbarkeit. 121 Seiten, Bremen, 1998.

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Redoxreaktionen im Grundwasser: Etablierung und Verlagerung von Reaktionsfronten und ihre Bedeutung für die Spurenelement-Mobilität. 122 Seiten, Bremen 1998.

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Report and preliminary results of METEOR-Cruise M 41/3, Vítoria, Brasilien – Salvador de Bahia, Brasilien, 18.4. - 15.5.1998. Bremen, 1999.

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Report and preliminary results of METEOR-Cruise M 41/4, Salvador de Bahia, Brasilien – Las Palmas, Spanien, 18.5. – 13.6.1998. Bremen, 1999.

Nr. 131 **Schlünz, B. und G. Wefer**
Bericht über den 7. JGOFS-Workshop am 3. und 4.12.1998 in Bremen. Im Anhang: Publikationen zum deutschen Beitrag zur Joint Global Ocean Flux Study (JGOFS), Stand 1/ 1999. 100 Seiten, Bremen, 1999.

Nr. 132 **Wefer, G. und Fahrtteilnehmer**
Report and preliminary results of METEOR-Cruise M 42/4, Las Palmas - Las Palmas - Viena do Castelo; 26.09.1998 - 26.10.1998. 104 Seiten, Bremen, 1999.

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Climate and ocean variability reconstructed from stable isotope records of modern subtropical Corals (Northern Red Sea). 111 Seiten, Bremen, 1999.

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Magnetic Cyclostratigraphy of South Atlantic Sediments. 82 Seiten, Bremen, 1999.