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Aspetsberger, F.

**BENTHIC CARBON TURNOVER IN
CONTINENTAL SLOPE AND DEEP SEA SEDIMENTS:
IMPORTANCE OF ORGANIC MATTER QUALITY AT
DIFFERENT TIME SCALES**

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**Benthic carbon turnover in continental slope and
deep sea sediments: importance of organic
matter quality at different time scales**

Dissertation
zur Erlangung des
Doktorgrades der Naturwissenschaften
- Dr. rer. nat. -

im Fachbereich Geowissenschaften
der Universität Bremen

vorgelegt von
Fanni Aspetsberger
Bremen
Juli 2005

Wenn zu perfekt, liebe Gott böse.

Nam June Paik

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Abstract

The aim of this thesis was to explore benthic carbon turnover as a function of organic matter quality at a range of different time-scales from hours to decades in sediments underlying the Benguela Upwelling System, a major high-productivity system situated off the Namibian coast. As microorganisms are the most abundant and important biological component involved in the transformation and mineralisation of organic matter, our investigation focused on the microbial compartment of the benthic community. The importance of varying qualities of organic matter on the amplitude and pathways of the benthic response on short and medium time-scales was investigated in pulse-chase labelling experiments. Organic matter of two different qualities – so-called ‘fresh’ and ‘altered’ phytodetritus – was labelled with the stable carbon isotope ^{13}C and supplied to the benthic community in *in situ*- and on board-experiments to follow its subsequent benthic processing. These experiments were used to elucidate the short- and medium-term response of the benthic community, while the long-term impact of varying organic matter quality was studied in an approach connecting sediment quality parameters to benthic flux rates.

The *in situ*-experiments, covering a time-scale of hours to days, revealed that mineralisation of fresh phytodetritus was strongly enhanced compared to altered phytodetritus over the whole depth of investigated stations (600-2000 m). Moreover, fresh phytodetritus supplied a higher uptake into macrofaunal biomass and a higher incorporation into bacterial fatty acids compared to altered phytodetritus. Obviously, on these short time-scales the fresh material was more easily available to the benthic biota. Total processing of phytodetritus was lower on northern (24.5 °S) compared to southern stations (25.5 °S). The latter stations are situated in a major centre of organic matter deposition. An increasing discrepancy between total processing of fresh and altered phytodetritus was noted at greater water depths, which was attributed to changes in the benthic community composition. Macrofaunal organisms, which are thought to be less sensitive to low organic matter quality, were more abundant at the shallower stations, where processing of fresh phytodetritus was 1.5 to 2.5 times higher than processing of altered phytodetritus. More microbially dominated communities in deep sea sediments show an increased sensitivity to changing

organic matter quality, resulting in 4.3 times increased total processing rates of fresh compared to altered phytodetritus.

On board-incubations were carried out on a medium time-scale of days to weeks at water depths of 360 to 2000 m. Again, mineralisation of fresh phytodetritus was significantly enhanced compared to that of altered phytodetritus, just as the bacterial productivity measured by ^{14}C -leucine-incorporation. Differing from that pattern, however, bacterial incorporation of ^{13}C -phytodetritus into fatty acids was higher in altered than in fresh incubations. As a result, bacterial growth efficiency as calculated from mineralisation and incorporation of labelled carbon was increased when growing on altered compared to fresh phytodetritus. The combination of mineralisation and production measurements allowed us to trace the differentiated reaction of the microbial benthic community on a medium time-scale.

On long time-scales extending from months to years and decades an experimental approach is no longer practicable. Therefore, benthic flux rates derived from pore water profiles were calculated for phosphate, nitrate and ammonium and compared to the quantity and quality of deposited organic matter at a number of stations crossing the continental slope off Namibia at water depths from 400 to 2500 m. Benthic fluxes were decoupled from organic matter concentrations and also from water depth, indicating that organic matter deposition in our study area is not dominated by vertical transport mechanisms. Organic matter quality, on the other hand, was tightly coupled to benthic flux rates. High lability of deposited organic matter coincided with high flux rates of nitrate and ammonium and to some extent also of phosphate. Phosphate profiles were partly decoupled from this connection due to the influence of ferrous iron. The cross-slope distribution of benthic flux rates measured in this study in combination with the included parameters of organic matter quality support the hypothesis of a major depocentre on the upper continental slope that is largely provided with organic matter from lateral transport processes.

The findings of this thesis reveal the critical role of the quality of organic matter that is settling or already deposited for benthic carbon turnover and burial rates in certain areas of the world's oceans. Investigations on the role of the oceans as a source or sink of atmospheric carbon dioxide have often relied on estimates of export production from surface waters or sedimentary organic carbon content. Obviously, this can not suffice unless the composition and availability of the deposited organic

matter is included in data analysis and interpretation. This work hereby contributes to the understanding of the cycling and burial of carbon in marine sediments, which is crucial to the prediction and quantification of benthic carbon exchange and the interpretation of organic carbon variations in marine sediments.

Zusammenfassung

Ziel der vorliegenden Dissertation war eine detaillierte Untersuchung des benthischen Kohlenstoffumsatzes in Abhängigkeit der Qualität organischen Materials. Auf unterschiedlichen Zeitskalen von einigen Stunden bis zu Jahrzehnten wurden dazu Studien in Sedimenten des Benguela-Auftriebsgebiets vor der Küste Namibias durchgeführt. Das Hauptaugenmerk galt der mikrobiellen Sedimentgemeinschaft, die durch ihre Abundanz und hohe Aktivität besonders bedeutsam für den Umbau und die Mineralisierung organischen Materials ist. Der Einfluss der Qualität organischen Materials auf das Ausmaß und die Wege der benthischen Reaktion wurde mit Hilfe von Tracer-Experimenten auf kurzen und mittleren Zeitskalen untersucht. Für die Experimente wurde zunächst im Labor ^{13}C -markierter Phytodetritus zweier Qualitäten (‚frisch‘ und ‚gealtert‘) hergestellt, der in weiterer Folge in *in situ*-Experimenten und Inkubationen an Bord des Forschungsschiffes auf das Sediment aufgetragen wurde. Anhand des ^{13}C -Markers wurde die benthische Reaktion verfolgt, die deutliche Unterschiede in Abhängigkeit der Qualität des zugegebenen Materials zeigte. Während diese Experimente die kurz- und mittelfristige Reaktion der benthischen Gemeinschaft aufzeigten, wurden anhand benthischer Flussraten und deren Abhängigkeit von der Sedimentzusammensetzung die langfristigen Auswirkungen einer unterschiedlichen Qualität organischen Materials untersucht.

Die *in situ*-Experimente, die Zeitskalen von Stunden bis Tagen abdecken, zeigen an allen Stationen (600 bis 2000 m Wassertiefe) eine deutlich gesteigerte Mineralisierung des frischen im Vergleich zum gealterten Phytodetritus. Auch die Aufnahme von ^{13}C -Phytodetritus durch Makrofauna und der Einbau in bakterielle Fettsäuren ist bei Zugabe von frischem relativ zu gealtertem Material erhöht. Offensichtlich ist das frische Material in diesen kurzen Zeiträumen besser für die Organismen verfügbar und nutzbar. Mit zunehmender Wassertiefe nimmt die Bedeutung der Qualität für die benthische Nutzbarkeit zu, was auf eine höhere Empfindlichkeit der mikrobiellen Gemeinschaft im Vergleich zur Makrofauna zurückgeführt wird. An den flacheren Stationen findet sich Makrofauna, welche auch qualitativ minderwertiges Material nutzen kann, in höherer Dichte. Dort wird zwischen 1,5 und 2,5 mal mehr frischer als gealterter Phytodetritus umgesetzt. An der tiefen Station, deren

Sedimentgemeinschaft deutlich mehr mikrobiell geprägt ist, steigt dieser Faktor auf 4,3. Auch die regionale Lage ist von Bedeutung für den benthischen Umsatz: An Stationen auf 25.5 °S, die in einem Zentrum hoher Ablagerung organischen Materials liegen, ist der Umsatz des zugegebenen Phytodetritus deutlich höher als weiter nördlich auf 24.5 °S.

In einem vergleichbaren experimentellen Aufbau an Bord wurde in Inkubationen die benthische Reaktion auf einer Zeitskala von wenigen Tagen bis Wochen in 360 bis 2000 m Wassertiefe untersucht. Auch hier ist die Mineralisierung bei Zugabe von frischem relativ zu gealtertem Phytodetritus deutlich erhöht, ebenso wie die bakterielle Produktivität (gemessen als ^{14}C -Leucin-Einbau). Abweichend vom in den vorherigen Experimenten vorherrschenden Muster ist jedoch der Einbau von ^{13}C -markiertem Phytodetritus in die bakteriellen Fettsäuren in den Inkubationen mit gealtertem Material höher. Daraus resultiert in weiterer Folge eine gesteigerte bakterielle Wachstumseffizienz (errechnet aus Mineralisierung und bakteriellem Einbau) auf gealtertem im Vergleich zu frischem Phytodetritus. Die Kombination von Mineralisierungs- und Produktivitätsmessungen in diesem Experiment ermöglicht uns, die komplexe mittelfristige Reaktion der mikrobiellen Sedimentgemeinschaft aufzuzeigen.

Der Einfluss der Qualität organischen Materials auf einer Zeitskala von Monaten bis zu Jahren und Jahrzehnten wurde nicht experimentell sondern mit Hilfe von benthischen Flussraten, errechnet aus Porenwasserprofilen, untersucht. An mehreren den Kontinentalhang kreuzenden Transekten wurden die Flussraten von Phosphat, Nitrat und Ammonium mit der Quantität und Qualität des vorhandenen organischen Materials verglichen. Es konnte keine Korrelation der benthischen Flussraten mit der Wassertiefe oder der Quantität des organischen Materials festgestellt werden. Das zeigt, dass vertikale Transportprozesse nur eingeschränkte Bedeutung für die Ablagerung organischen Materials im Untersuchungsgebiet haben. Die Qualität des organischen Materials ist hingegen eng an die benthischen Flussraten gekoppelt: Ein erhöhter Anteil leicht abbaubarer Komponenten am organischen Material (z.B. leicht abbaubare Aminosäuren) geht mit erhöhten Flussraten einher. Dieser Zusammenhang ist besonders deutlich für Nitrat und Ammonium, während die Phosphatprofile auch von Fe^{2+} beeinflusst werden und dadurch weniger eng an die Qualität organischen Materials gekoppelt sind. Die

regionale Verteilung der gemessenen benthischen Flussraten und der behandelten Qualitätsparameter bestätigt die Hypothese, dass am oberen Kontinentalhang vor Namibia ein zentrales Depocenter organischen Materials liegt, das zu großen Teilen aus lateral transportiertem Material gespeist wird.

Die Ergebnisse dieser Studie liefern Einblicke in die Bedeutsamkeit der Qualität sedimentierender und sedimentierter organischer Materialien für den benthischen Kohlenstoffumsatz. Um die Rolle der Ozeane als Quelle oder Senke atmosphärischen Kohlendioxids zu verstehen, reicht eine Untersuchung der Exportproduktion oder des Kohlenstoffgehalts mariner Sedimente nicht aus, solange nicht auch die Zusammensetzung und Verfügbarkeit des organischen Materials mitbetrachtet wird. Die vorliegende Arbeit trägt zum weiteren Verständnis des benthischen Kohlenstoffkreislaufs bei, was entscheidend für die Vorhersage und Quantifizierung des benthischen Kohlenstoffumsatzes und der Kohlenstoffeinbettung ebenso wie für die Interpretation von Schwankungen des Gehalts an organischem Kohlenstoff in marinen Sedimenten ist.

Chapter 1

Introduction

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1. Introduction

1.1 The Ocean's Carbon Cycle

The global carbon cycle comprises carbon fluxes - including plant photosynthesis, respiration, and decay, as well as the oceanic absorption and release of CO₂ - and carbon stocks that clearly exceed the fluxes. The largest carbon reservoir lies in the deep ocean, accounting for 38000 Gt of carbon (Fig. 1). Carbon reservoirs and fluxes differ greatly in their size and ability to respond to changes, a property often termed 'reactivity'. Large reservoirs with small in- and outfluxes are not very reactive, while small reservoirs with relatively large fluxes are very reactive. The atmosphere is a well-known example of such a reactive reservoir. However, the close coupling between different reservoirs necessitates a holistic view on processes and possible trends.

The marine environment takes a leading role in global carbon cycling (Fig. 1). Its carbon reservoir is about 60 times bigger than that of the atmosphere. A constant gas-exchange between the ocean and the atmosphere is controlled by the partial pressure of CO₂ (pCO₂), temperature and salinity. Moreover, biological processes in the photic zone of the ocean influence the equilibrium of CO₂ between ocean and atmosphere. Phytoplankton fixes CO₂ and incorporates the carbon into their biomass, thereby increasing CO₂ uptake from the atmosphere. After their death, the organisms sink down in the water column. In this biological process, there is a net movement of CO₂ from surface water into deeper parts of the ocean. The major part of the organic carbon is decomposed during sinking and can be returned to the surface by upwelling of deep water. Another portion of the organic carbon is, however, sequestered into the deep ocean, where a fraction of it becomes buried for geological times in the deep sea sediments. Little detailed information is available about the factors driving the proportions of benthic turnover and burial. The movement of CO₂ towards deep waters and back to the surface is called the 'biological pump'. Approximately 10 Gt of carbon are transported to the deep ocean that way each year (Fig. 1). About 10 % of the primary production are assumed to sink out of the photic

zone, and only 1 % arrives at the sediment surface (De Baar and Suess 1993). Following this tight coupling between ocean and atmosphere, changes in abundance and composition of primary producers are today discussed as a possible reason for fluctuations in the atmospheric CO₂ content between glacial and interglacials. Predictions of future climate developments and a possible influence of anthropogenically increased CO₂ concentrations require exact knowledge on the single processes involved in the global carbon cycle.

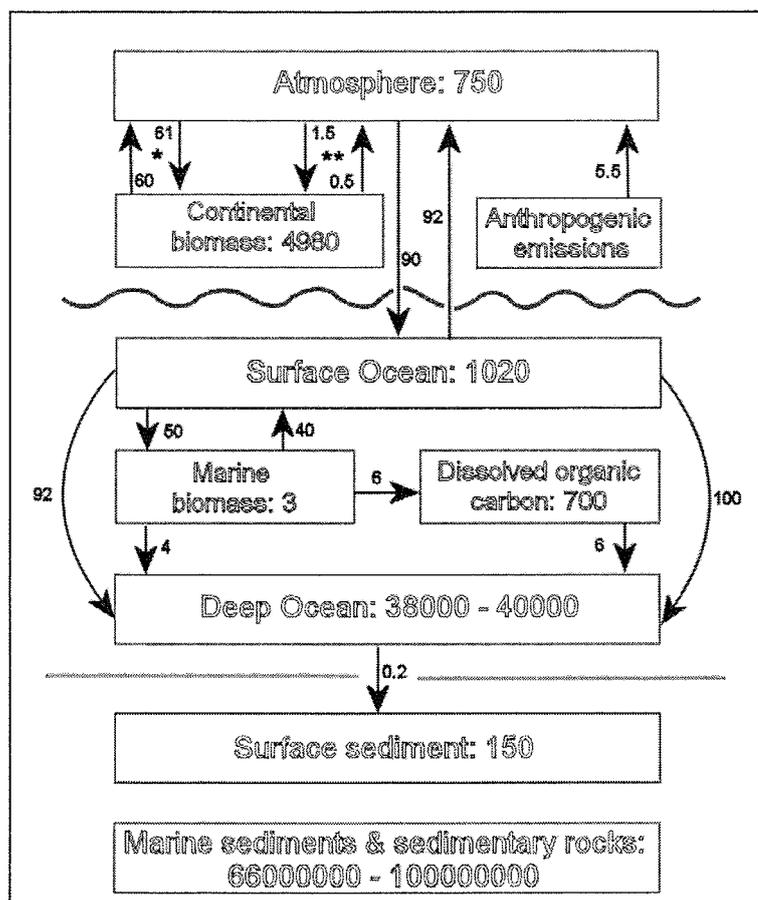


Figure 1: Major fluxes and stocks of the global carbon cycle (* Respiration; ** Land-use changes). All data on carbon stocks are given in Gt, fluxes in Gt year⁻¹. (modified after IPCC).

The bulk of carbon fixation as well as mineralisation is centered on the continental margins, where the study area of this thesis is situated. Jørgensen (1983) pointed out that even though continental margins make up for only 11 % of the surface area of the world, more than 80 % of the global benthic mineralisation takes

place there. Therefore, it is of special importance to study continental margin systems in investigations of marine carbon turnover. In such investigations, marine sediments deserve special consideration in discussions of the global carbon cycle, as they interconnect the geological and the biological cycle of organic carbon by the decay of organic matter, its deposition and burial into soils and sediments (Tissot and Welte 1984). Processes at the sediment-water interface are decisive for the fraction of biomass that is being returned to the oceanic carbon cycle and the fraction that will be stored in the sediment. Sediments thereby become the communicators between two compartments of very different dimensions in time and space, with the geological part representing the major carbon reservoir with considerably higher turnover-times (Rullkötter 2000). In the marine environment, sediments receive a continuous replenishment of organic matter from the overlaying water column and from lateral inputs. Depending on the original source of this material and its transport pathways, degradation is in many cases already advanced when it reaches the sediment surface. Nevertheless, decomposition might still be going on several hundreds of meters down into the sedimentary column, in the so-called 'deep biosphere' (Parkes et al. 1994). This clearly illustrates that there is a smooth sedimentary transition between geology and biology that needs to be considered flexibly depending on the investigated environment.

The most active layer of organic matter degradation in deep sea environments is most probably the sediment surface including the uppermost centimeters. There, freshly arrived material forms a thin layer of detritus, which becomes the base of a fast and effective organic matter breakdown even in the deep sea. Benthic activity is usually limited by the seasonally low organic influx to the sediment (Lochte and Turley 1988) and by low temperatures at great depths. However, the composition of the arriving organic matter might be another decisive factor for benthic carbon turnover, that has to date hardly been addressed in *in situ* studies and on natural mixed communities. After passage through the different compartments of the benthic community, there is seldom the chance for considerable accumulation of organic matter in the sediment and only an exiguous fraction of the settling organic matter becomes permanently buried (i.e. for geological times) in the sediment. Exceptions are areas of very low biological activity or of very high organic matter input, such as a few small ocean deeps with anoxic bottom waters, oxygen minimum zones above continental shelves, and - for the latter case - upwelling areas

such as the Benguela Upwelling system. The fraction of buried carbon depends – among others – on the rates and extent of benthic carbon turnover that are themselves in turn dependent on the input of organic carbon from the water column. The influence of organic carbon quantity versus quality on benthic processing is the major topic addressed in this thesis.

1.2 The Benguela Upwelling System

The Benguela Upwelling System is one of the four major coastal upwelling systems on earth, which are mostly situated at the eastern boundaries of the oceans. The generally high rates of benthic activity assumed to characterise this high productivity region make it a very suitable environment for studies on benthic carbon turnover processes. The coastal upwelling area of the Benguela Current ecosystem extends from southern Angola along the west coast of Namibia and South Africa. While this area shares many of the generic characteristics of other eastern boundary currents, it is unique in that it is bordered at both northern and southern ends by warm water systems (the Angola Current and Agulhas Current). Several distinct upwelling cells build up its latitudinal extension (Lutjeharms and Meeuwis, 1987), with higher seasonality in the southern cells. The principle upwelling centre is situated near Lüderitz in southern Namibia and is the most concentrated and intense found in any upwelling regime. Productivity measured along the Lüderitz and Walvis coasts is reported to reach up to $350 \text{ g C m}^{-2} \text{ a}^{-1}$ (Behrenfeld and Falkowski 1997). However, the most productive zones do not systematically occur within the main upwelling centre but on the outer fringe of the cell (Mollenhauer et al. 2002). Two major fronts correspond to bathymetric drops: an upwelling front at the inner shelf break less than 100 km offshore and an outer shelf-break front another 100 km towards the open sea. Along these fronts, organic matter is transported towards the seafloor, where it leads to the build-up of depocentres below the circulating cells (Giraudeau et al. 2000).

The spatial extension of the Benguela Upwelling System is moreover characterised by the buildup of long and rather stable filaments of high organic

matter content, which can extend several hundred kilometers westwards into the open sea (Lutjeharms and Meeuwis, 1987; Lutjeharms and Stockton, 1987). These filaments and plumes present most extensive seaward penetrations at major upwelling cells such as Cape Frio and Lüderitz/Walvis Bay (Shannon, 1985; Lutjeharms and Meeuwis, 1987). Filaments off Lüderitz have been observed to be over 1000 km long (Lutjeharms et al., 1991). They transport high loads of organic matter to waters overlaying the continental slope, and thereby constitute an important source to the underlying deep sediments (Fig. 2). However, productivity patterns from the surface waters are not necessarily mapped in the underlying sediments, as bottom currents and lateral transport processes can transport the organic matter in the water column over long distances (Brüchert et al. *subm.*; Inthorn et al. *subm.-a*). Aeolian transport of detrital material from the arid continent towards the ocean is of minor importance in the Benguela Upwelling System and terrigenous input to the sediments seems insignificant, as the prevailing wind field parallels the coastline.

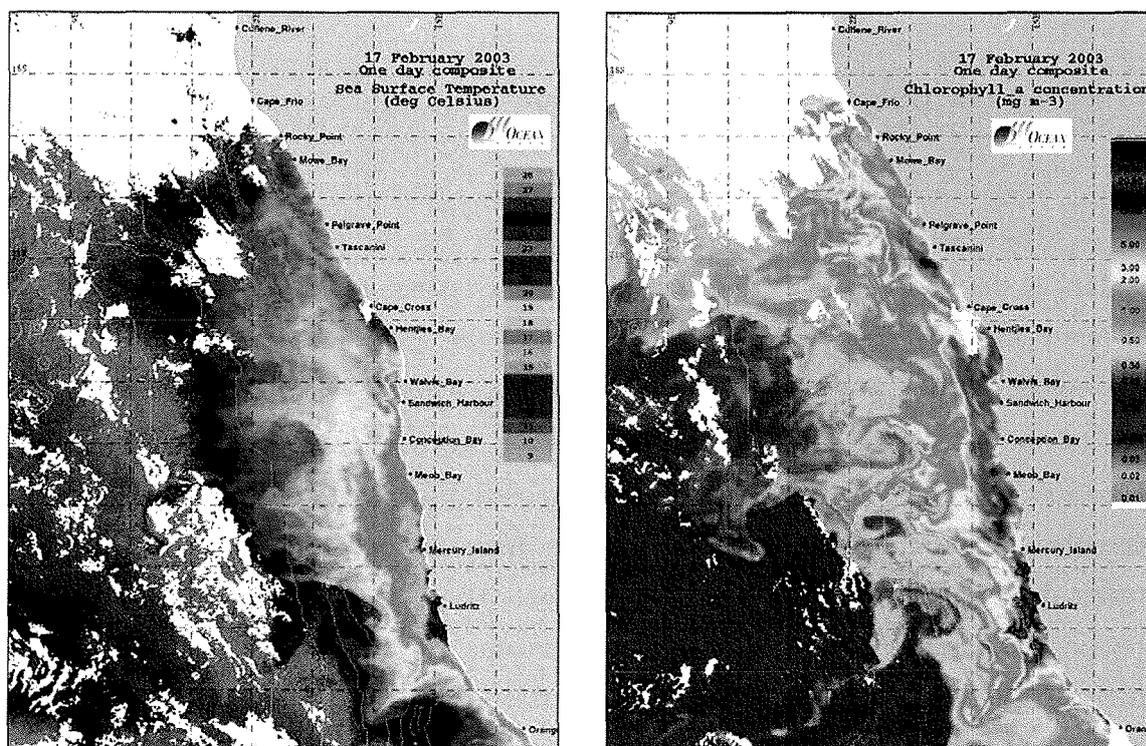


Figure 2: SeaWiFS-satellite image of sea surface temperature (left panel) and sea surface chlorophyll-*a* concentration (right panel), taken on 17. February 2003, during the time this study was carried out.

The Benguela Upwelling System is assumed to be of major importance for global climate change processes, as it lies at a major checkpoint of the 'Global Climate Conveyor Belt', a thermohaline circulation that is transporting warm ocean water from the Pacific Ocean through the Indian Ocean and into the Atlantic Ocean. However, discussion is going on whether the Benguela is a net source or sink of atmospheric carbon dioxide - with the 'physical pump' supplying CO₂ through outgassing from upwelling waters opposing the 'biological pump' removing CO₂ from the atmosphere through primary production and the marine food web. The work of Monteiro (1996) indicates that the southern Benguela may be a net sink and the northern Benguela a net source, with the Benguela as a whole being a small sink. However, that picture may change when altering its geographic range and including possible backlashes. Thus, knowledge of the processes driving carbon turnover in the Benguela and other upwelling systems, as studied in this thesis, is important for global models predicting future climate change.

1.3 The Deep Sea, and the way there

The most extensive habitat on the planet are the permanently cold, dark waters at the bottom of the deep oceans. Seventy percent of the planets surface is covered with water, of which roughly 85 % of the area and 90 % of the volume constitute the environment we call the deep sea. Although this area is the largest habitat on earth, its biology is the least known and explored. Several schemes of zonation for the deep sea have been proposed but none has been universally accepted. A popular definition describes the deep sea as the oceans below 1000 m water depth, where light is completely absent. There are exceptions, e.g. in polar regions characteristic deep sea fauna organisms can be found in only several hundred meters depth. Temperature in the deep sea is low, rarely exceeding 4 °C and falling as low as -1.8 °C in the high latitudes. Pressure ranges between 300 and 500 bar in the deep ocean abyssal plains, and exceeds 1000 bar in the deepest trenches. However, it is now becoming apparent that the diversity of the deep ocean benthos is much higher than anticipated earlier. The overriding limiting factor for life on the deep sea floor must be the availability of food, which little is known about

even today. The pattern of distribution of benthic biomass is similar to that of primary productivity in the surface waters of the world ocean, owing to the importance of vertical transport processes for organic matter supply to the sediments. This implies that high biomass contents are to be expected in sediments underlying a high productivity region such as the Benguela Upwelling System, making it a suitable environment for studies on benthic carbon turnover processes.

The vast majority of deep sea sediments are of authigenic origin, most frequently biogenic oozes consisting of shells and skeletal material from planktonic organisms or – especially in the deep ocean plains - muddy sediments of extremely fine-grained red clay with a median grain size of $< 1 \mu\text{m}$. Their global distribution varies significantly and depends upon the faunal composition of water column organisms and the position of the calcite compensation depth (CCD), below which no calcite is found.

Several processes are known to transport organic matter to the deep sea floor that are of variable importance depending on the regarded region (Fig. 3). Lateral transport was often neglected as a possible source of organic matter, but evidence is increasing that it is regionally important. Estimates from geochemical investigations in the SEEP-II (Shelf Edge Exchange Processes) program in the Middle Atlantic Bight found that material sinking from surface waters overlaying the slope can supply only a small fraction of carbon remineralised by bacteria in the intermediate water column. Up to 15 % of the particular organic carbon from coastal primary productivity is transported over the shelf break and into deep waters (Kemp 1994). A comparable importance of lateral transport is assumed for opal and terrestrially derived material. McCave et al. (2001) identified bottom nepheloid layers as transport vectors for organic matter to the deep sea floor, which has also been shown for the Benguela Upwelling system by Inthorn et al. (subm.-b).

After arrival on the deep sea sediment surface, bioturbation and bioirrigation are the most important mechanisms transporting particulate and dissolved organic matter to deeper sediment layers (Fig. 3). Bioturbation refers to the spatial rearrangement of the sediments solid phase by diverse organisms, which usually reaches down to less than 15 cm sediment depth and has great impact on geochemical processes (Sun et al. 2002). Bioirrigation describes the active transport of

bottom water through sediment organism habitats, which can locally significantly increase fluxes, e.g. of oxygen (Glud et al. 1994; Levin et al. 1997).

Still, in many areas the major part of organic matter for most sediment biota stems from vertical transport processes, where production from the sea surface sinks down through the water column, being partially degraded on the way. During transport through the water column, organic matter undergoes many degradational changes. The initial structures of individual compounds can be altered and the proportion of various compounds and compound classes can change as a result of varying stabilities. Residence time in the water column further influences the extent of degradation of organic matter. A compilation of these water column processes can be found in Emerson and Hedges (1988) and Wakeham and Lee (1989). The different sources and transport pathways of organic matter to the sea floor together with degradational processes on the way result in a diverse composition of the settling organic matter. The influence of this variable composition on benthic turnover, however, is still not thoroughly studied neither in deep sea nor in continental margin environments.

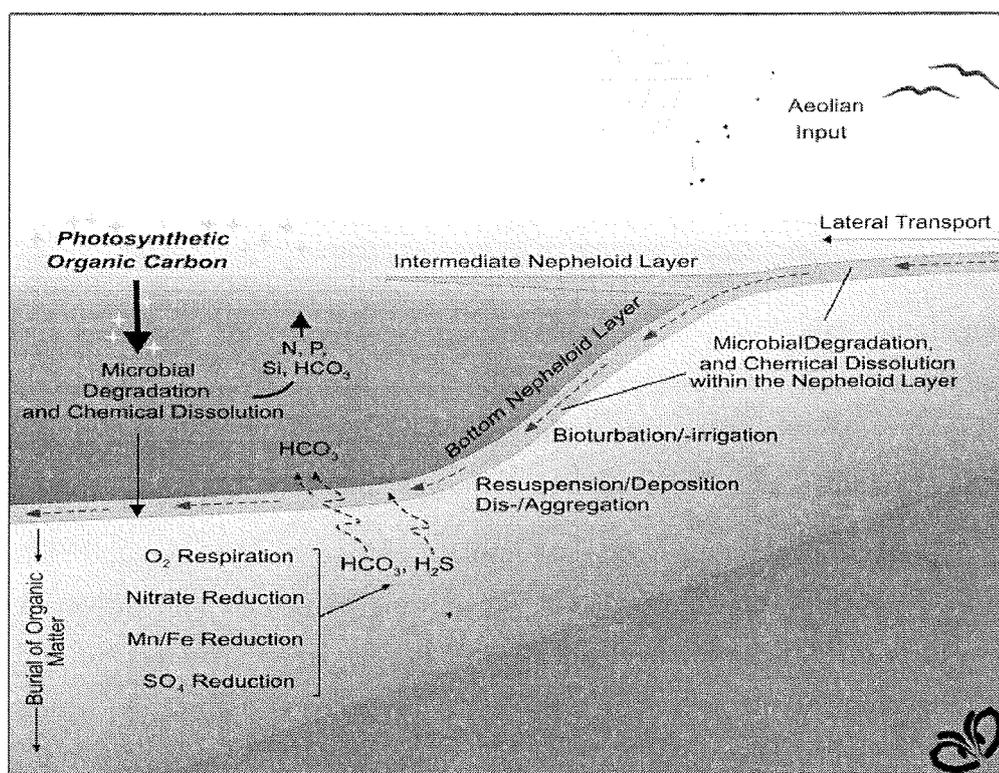


Figure 3: Sources, transport and pathways of degradation of organic matter.

Initially it was believed that the organic matter supply from the water column was delivered constantly as a fine rain of particles. Only about 20 years ago, the invention of moored time lapse cameras (Billett et al. 1983; Rice et al. 1986) revealed that the organic matter in fact often arrives highly pulsed as a seasonal accumulation of relatively fresh phytodetrital material. It derives from epipelagic phytoplankton blooms, usually as a result of increasing solar radiation and enhanced nutrient availability due to mixing processes in early spring (Purdie 1996), and can be transported towards the sea floor at rapid sinking velocities of up to 150 m per day (Lampitt 1985) due to repacking in different matrices (Alldredge and Silver 1988). The magnitude of seasonal patterns can vary widely between different geographical areas. In addition, large food falls from dead fish and whale carcasses (Goffredi et al. 2004; Rowe et al. 1986; Smith 1992) further contribute to the nutritional supply of deep sea environments during all seasons. In a much quoted passage, Moseley (1880) ventured the opinion that a “periodic variation in the supply of food falling from above [...] may give rise to a little annual excitement among the inhabitants” of the deep sea. However, studies on the fate of such pulses were often contradictory (e.g. Graf 1989; Sayles et al. 1994; Smith Jr. and Baldwin 1984; Smith and Kaufmann 1999). The benthic response obviously varies widely between different groups of organisms and different environments. Overall, however, the activity of benthic and benthopelagic organisms increases following such pulses (reviewed by Gooday 2002). No *in situ* studies on the benthic response to a pulse of organic matter have been carried out in a high productivity region as the Benguela Upwelling system to date, even though these regions might be of particular importance in global carbon budgets.

Knowing the diagenetic status of organic matter is essential for employing biomarkers in source studies and understanding carbon preservation. Organic matter reactivity, however, is a function of material matrix as well as inherent lability (Cowie and Hedges 1992, 1994; Wakeham and Lee 1989). Therefore, diverse chemical reactivities do not correlate simply to compound class or structure in consistently predictable patterns. In the equatorial Pacific, Wakeham et al. (1997) was able to identify most of the organic carbon (~ 80 %) in surface POM at the molecular level as being in amino acids, sugars or lipids. At depth (~ 4000 m), the proportion of characterisable organic matter decreased to only 24 % of total organic carbon. As Wakeham et al. (1997) point out, this inability to characterise the bulk of the

particulate organic matter at depth reinforces the general paradigm of a transition from highly labile and relatively well-characterised organic matter in organisms and surface waters to biologically and analytically recalcitrant material in the deep water column and sediments. The processes behind this compositional change are not yet fully resolved, and methodological difficulties need additional consideration when discussing organic matter composition at different depths. Applying a number of different methods for organic matter characterisation, Minor et al. (2003) found that the method of analysis strongly influenced which organic matter preservation scheme appeared to dominate. Overall, the truth seems to lie somewhere between the limits of selective preservation of certain compound classes and physical protection of normally labile compounds within a refractory matrix (Minor et al. 2003). Studies on the reactivity of complex substrates, such as phytodetritus, therefore bear the great advantage over the use specific substrates (e.g. glucose, Boetius and Lochte 1996) to allow conclusions about actual benthic rates without the necessity of being able to completely resolve settling organic matter composition.

1.4 *In situ* Measurements

The problems of investigating the deep sea benthic environment are vividly pictured in the resigned statement of Boon et al. (1975), starting their discussion on an investigation of diatomaceous oozes off Walvis Bay: "We could not sample a diatom bloom, nor the algae deeper in the water column, because no blooming occurred during the sampling program."

The pulsed arrival of organic matter at the sea floor (Billett et al. 1983; Rice et al. 1986) has severely complicated research on benthic carbon turnover for decades. Studies on benthic and especially deep sea metabolism were impossible with the traditional ways of collecting organisms – such as trawling, grabbing or coring – and the use of submersibles was too expensive, time and space consuming and dependent on weather conditions. However, in the mid-seventies the development of benthic chamber lander systems presented a way to overcome these problems in data acquisition. The first 'free vehicle respirometer' was sent down to the deep sea

in 1975 and came back with convincing results (Smith et al. 1976). Since then, numerous extensions have been developed and landers have proven to be a highly efficient way, both practically and economically, to obtain high quality results from the sea floor. *In situ* studies carried out directly in natural environments include the complexity of an ecosystem and minimise the artefacts that occur due to experimental conditions. The chamber lander used in this study presents an *in situ* experimental system to simulate the arrival of a food pulse at the deep sea floor and investigate its benthic response (Witte and Pfannkuche 2000), and has repeatedly and successfully been used in various environments (Bühring et al. in prep.; Bühring et al. in press; Moodley et al. 2002; Witte et al. 2003a; Witte et al. 2003b) (Fig. 4). The sediment retrieved with the benthic chamber lander allows detailed studies in single compartments of the benthic community, such as microorganisms, which have been a centre of this investigation.

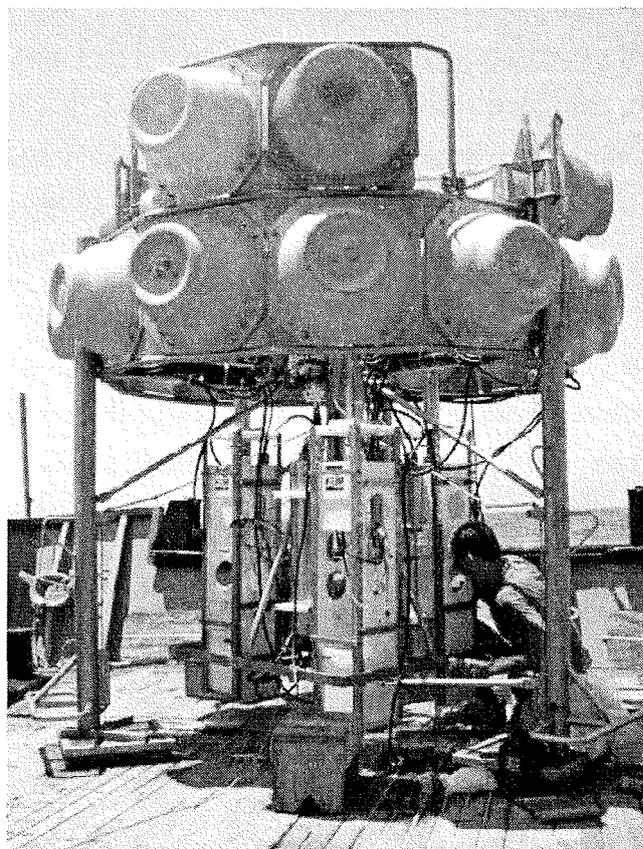


Figure 4: A benthic chamber lander, equivalent to the one used in this study.

1.5 Microbial Activity

Microorganisms mediate the close coupling between geology and biology in marine sediments to a large extent: Bacteria are the essential catalysts for many processes significant for the degradation and remineralisation of organic matter, and may accelerate these processes up to 10^{20} -fold relative to the non-biological reaction rate. According to Jørgensen (2000), three major reasons can be given for the dominance of prokaryotes in biogeochemical cycling:

- (1) their metabolic versatility with many types of anaerobic metabolisms,
- (2) their small size which allows them to inhabit nearly all environments and strongly enhances the efficiency of their catalytic activity and
- (3) the wide range of environmental conditions under which they thrive.

Especially in an extreme environment such as the deep sea, a well-adapted energy metabolism is of great importance. The best known type – also at the sea floor – is aerobic respiration, oxidising small organic molecules to CO_2 with oxygen. It is the metabolism dominating the oxic zone of the sediment, which ranges from a few millimetres in shelf sediments to maxima of several decimetres in certain deep sea sediments (e.g. Glud et al. 1994). Also in the sediments covered in this study, the major part of carbon oxidation was carried out with oxygen as the electron acceptor. Besides, many heterotrophic prokaryotes are capable of anaerobic respiration, using other terminal electron acceptors than O_2 for the oxidation of their organic substrates. Energy yields vary widely between the different terminal electron acceptors, with oxic respiration being the most efficient, followed by denitrification. Energetic benefit, however, does not finally determine the biogeochemical importance of a certain pathway, as they are primarily limited by the abundance of their electron acceptor and the supply of substrate to the sediments. For instance, even though energetically only the fifth most profitable, its high concentration in seawater makes sulphate the dominant electron acceptor in the anaerobic degradation of organic matter (Henrichs and Reeburgh 1987; Jørgensen 1983).

Before organic matter - usually arriving at the sea floor as a mixture of macromolecular compounds - becomes available to bacteria, it needs to be reduced to smaller molecular sizes. The typical size limit for bacterial uptake lies around 600

Dalton (Benz and Bauer 1988; Decad and Nikaido 1976). This depolymerisation is generally rate-limiting for all following steps in the sedimentary mineralisation process. It can either be done by the excretion of exoenzymes by the bacteria themselves, or by preceding processing of the material by higher organisms, e.g. passage through the macrofauna gut system. The role of dissolved organic matter in the benthic carbon cycle has not been resolved until today. A substantial fraction of the organic carbon synthesized by phytoplankton is released as dissolved organic carbon (DOC). Moreover, loss of dissolved organic matter as a result of cell lysis following cell death, virus attack, damage or sloppy feeding results in a DOC composition similar to intracellular fluid. Discussion is vigorous on whether it is of major importance as an easily available substrate, contributing significantly to organic carbon recycling rates, or a negligible byproduct rapidly vanishing from the system by release into the overlaying water. Methodological difficulties have further complicated the subject (Holcombe et al. 2001). However, evidence is strong today that dissolved organic matter can contribute substantially to organic matter recycling rates, with fluxes contributing > 50 % to up to 140 % of dissolved inorganic carbon fluxes (Bauer et al. 1995; Martin and McCorkle 1993). Organic matter that is not mineralised may be adsorbed to mineral surfaces and become more permanently buried with the sediment.

Thus, besides the metabolic pathway, the quality of organic matter to be oxidised is of crucial importance for benthic turnover rates. Danovaro et al. (2000) found indications that bacterial abundance was constrained rather by changes on organic matter quality than quantity in the Cretan Sea. Also bacterial activity was found to be directly regulated by the supply of appropriate food: in sediments from the deep northeast Atlantic, particulate organic matter induced higher enzyme production than equivalent amount of dissolved organic matter (Boetius and Lochte 1994). This thesis addresses the importance of organic matter quality for benthic carbon turnover with a wide variety of methods, combining an experimental tracer approach with a selection of microbiological approaches, some of which will be described in the following, to allow detailed insights into *in situ* microbial carbon turnover processes.

1.6 Exploring Marine Microbiology

The microbial community constitutes an essential part in the trophodynamics of the benthic ecosystem. Nevertheless, investigating this community has proven difficult without the bias of methods that require separation of the microbes from their microenvironment. Direct cell counts via epifluorescent microscopy (e.g. DAPI staining, fluorescent *in situ* hybridization - FISH) are a customary and widely used approach. However, for the microscopic evaluation of cell numbers either the microbes have to be removed from the sedimentary substrate, which is not quantitative, or assumptions have to be made on bacterial colonisation densities on hidden faces (Daley and Hobbie 1975). Also the information to be gained by direct cell counts is very limited, as bacterial density and morphology give no indication of the metabolic function or state of an organism. Chemical analysis of sediments or detritus for microbe-derived constituents and activities offers a solution to at least some of these problems. Molecular biological markers, or biomarkers, are natural products that can be traced to a particular biological origin. The most effective biomarkers are organic compounds with specific biological sources, whose structures are preserved. For example, lipid analysis allows for phylogenetic and taxonomic classifications (Ratledge 1988/1989) of microbial communities. The big advantage of phospholipids is that they are not used as reserve polymers and that they turn over rapidly after cell death, providing a sensitive measure of viable microbial biomass (White 1983, 1988). Phospholipids have been analysed for e.g. a comparison of different marine depositional environments, as a criterion for pollution, or for tracing the origin of detritus and marine organic surface deposits. Ecological studies have taken up phospholipid analysis as an indicator of biomass, to trace seasonal changes and to investigate feeding relationships (see Bobbie and White 1980; and references therein). They have been applied to very complex and dynamic ecosystems, such as biofilms inhabiting macrofaunal burrows (Marinelli et al. 2002), and have in numerous cases proven to be a sensitive and practical tool in microbial ecology. Natural abundances of stable isotopes as well as labelling approaches have been applied to elucidate the source materials and buildup of phospholipids (Boschker et al. 1998; Hayes 2001; Peterson 1999); see also chapter 1.7), with highly promising

results. Therefore, the combination of a tracer addition with phospholipid analysis has also been applied in this thesis to study bacterial carbon incorporation.

While phospholipids give evidence on the abundance and composition of viable bacterial biomass, they do not yield any information on the activity, growth rate and production of the microbial community. However, to gain an integrated picture of benthic processes an investigation of these parameters was also desired in this study. Several methods have been suggested for the measurement of bacterial production in natural aquatic systems. Estimates of bacterial production have been derived from dark uptake of $^{14}\text{CO}_2$ (e.g. Romanenko 1963). This method was later criticised because it overestimates bacterial production, and CO_2 uptake by algae can not be excluded (Overbeck 1979). Estimates of the frequency of dividing cells (Hagström et al. 1979) provide a measure for bacterial dividing rate, but this method is very time consuming and probably somewhat subjective, because division stages of small cells are hard to detect. It also seems to overestimate real production rates (Riemann and Bell 1990), possibly because only a small proportion of bacteria is active under *in situ* conditions. The measurement of phospholipid synthesis after addition of radiolabelled phosphorous (White et al. 1977) makes relatively precise production estimates possible. However, short turnover times of phosphates do not allow for long-term experiments, and a high activity is needed using this approach. Also, the addition of phosphate might enhance bacterial growth, and the handling of phosphorus isotopes may not be possible in many laboratories. Finally, very recently a new non-radioactive approach was presented by Nelson and Carlson (2005), which however has been optimised and tested only for oligotrophic open-ocean environments.

The most promising approach therefore consists in following the incorporation of radiolabelled nucleic or amino acids into bacterial DNA (via thymidine incorporation, Fuhrman and Azam 1980) or protein (via leucine incorporation, Kirchman et al. 1985). In spite of some theoretical advantages of the thymidine technique (Robarts and Zohary 1993) many researchers choose the leucine technique (e.g. Buesing and Gessner 2003; Kirchman et al. 1985; Riemann and Azam 1992). Several reasons can be given for the preference of the leucine method in this thesis: (1) More direct results are achieved by leucine compared to thymidine incorporation, as the increase of a major biomass fraction is measured. (2) the leucine

method is one order of magnitude more sensitive than the thymidine method, because the production of a bacterial cell requires about ten times the incorporation of leucine into protein than thymidine into DNA (Simon and Azam 1989). (3) leucine constitutes a rather constant fraction of the total amino acids in bacterial protein (Simon and Azam 1989), and protein itself constitutes a rather high and constant fraction of bacterial carbon (Hagström et al. 1984; Simon and Azam 1989). Thus, the conversion factors derived from leucine incorporation carbon estimates vary at maximum two-fold (Buesing and Marxsen 2005; Simon and Azam 1989), compared to a ten-fold variation in conversion factors for thymidine incorporation rates (Bell 1990). (4) Finally, the leucine method includes the potential to measure the production of anaerobic bacteria (Cole and Pace 1995; McDonough et al. 1986), although to my knowledge it has not yet been thoroughly tested in sediments. Of course, disadvantages of the leucine method also require consideration. Above all, there is a danger of leucine incorporation into other organisms than bacteria, such as algae and fungi (Horak 1986; Kamjunke and Jähnichen 2000), leading to a possible overestimation of bacterial production rates. Thymidine kinase, in contrast, controlling thymidine incorporation, is exclusive to heterotrophic bacteria and such overestimations are therefore avoidable.

In order to evaluate the role of bacteria for carbon cycling in natural systems, their dual role requires consideration: Bacteria perform two major functions: (1) respiration of organic carbon to inorganic carbon (bacterial mineralisation) and (2) production of new bacterial biomass (e.g. bacterial secondary production). The real magnitude of carbon flow requires simultaneous measurement of bacterial production (BSP) and respiration (MR). Combining those two parameters, the bacterial growth efficiency (BGE) can be calculated following the formula

$$BGE = \frac{BSP}{(BSP + MR)}$$

BGE is defined as the fraction of organic carbon consumed by bacteria that becomes incorporated into biomass (for review see Del Giorgio and Cole 1998). As simultaneous measurements of BSP and MR in natural systems are rare, surprisingly little is known about the regulation of BGE. *In situ* measurements of BGE suggest clear differences between systems, with BGE increasing from planktonic marine

environments over lakes and rivers to estuaries (Del Giorgio and Cole 1998). Moreover it appears that BGE responds quickly to subtle changes in the rate of supply and the quality of substrates (Del Giorgio and Cole 1998). The magnitude and regulation of BGE is of interest not only for investigations of the bacterial community but influences models of the whole carbon cycle in aquatic systems. The approach presented in this thesis of evaluating bacterial growth efficiency in *in situ* experiments and from labelling data presents unique data of growth efficiencies of natural assemblages and on complex substrates that have not been presented before.

1.7 Stable Isotopes and Labelling Approaches

Measurements of the ratio between the stable carbon isotopes ^{13}C and ^{12}C provide a useful tool for studying processes of carbon cycling in detail within natural systems. Carbon isotope ratios are usually reported in the conventional δ notation:

$$\delta^{13}\text{C}_{\text{PDB}}(\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] * 1000$$

where R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ isotope ratios of the sample and the international Vienna PeeDee Belemnite standard, respectively ($R_{\text{VPDB}} = 0.0112372 \pm 0.0000090$). Natural abundances of ^{13}C are often characteristic of specific sources of material (marine, terrestrial, etc.) or metabolic pathways (C_3 , C_4 -plants) (Aspetsberger et al. 2002; Hayes 2001; Peterson 1999). Phytoplankton – like most plants – use the Calvin cycle (C_3 -cycle) to incorporate carbon into their biomass, which discriminates against ^{13}C producing signatures depleted by approximately -20 ‰ relative to their carbon source. The dissolved bicarbonate serving as a source for marine algae has an initial ^{13}C -signature of about 0 ‰, consequently marine organic matter usually lies in the range of -20 ‰ to -22 ‰ (Fry and Sherr 1988; Peterson and Fry 1987). The C_4 plants use the Hatch-Slack pathway (C_4 -cycle) that leads to an isotopic shift of only -7 ‰. A popular aim of isotopic carbon source studies is methane, that has a very distinct, highly depleted ^{13}C -signature (-50 to -110 ‰, Whiticar 1999) and can therefore be easily traced in methanotrophic organisms (e.g. Hinrichs et al. 1999). Isotopic discrimination also occurs at the cell-level between different constituents of cells and organisms (Abraham et al. 1998; Hayes 2001).

Typical fractionation steps in trophic interactions can finally also be used to reconstruct food webs, which is especially true for the ^{15}N -isotope that is reported to increase by 3-5 ‰ per trophic level (Peterson and Fry 1987).

In labelling approaches as the one applied in this thesis, these internal and trophic fractionation processes do not influence data interpretation as labelling is usually high enough to overlay natural fractionation signals. Stable isotope labelling experiments have several practical advantages compared to radioisotopes, as they do not suffer from legal restrictions and health problems associated with radioisotopes and therefore can be used directly in the field (reviewed by Boschker and Middelburg 2002). A wide variety of isotopically labelled compounds is commercially available today, also allowing for cultivation of organisms on labelled substrates to create complex sources of organic matter for pulse-chase experiments. In these experiments (Fig. 5), an isotopically labelled substrate (e.g. ^{13}C -labelled phytodetritus) is added to an experimental set-up, e.g. the natural benthic community of a deep sea sediment. After a certain time-period dependent on the scientific question, the sediment organisms as well as abiotic compartments of the benthic carbon cycle are analysed for their uptake of labelled carbon. Thereby, the processing pathway of the added phytodetritus can be followed and the time-scale and amplitude of benthic turnover can be evaluated.

The first study investigating a benthic food web by the use of stable isotope labelling was carried out in 1996 by Blair et al. (1996), who used ^{13}C -labelled algae for *in situ* experiments to trace the fate of phytodetritus in ocean margin sediments off Cape Hatteras, North Carolina. Both macrofaunal carbon as well as dissolved inorganic ^{13}C exhibited a very rapid response and fast penetration into deeper sediment layers. Choosing a different approach, Middelburg et al. (2000) found similar reaction times and penetration depths when adding labelled bicarbonate to an intertidal sand. The microbial community was first explicitly targeted in a study by Boschker et al. (1998), using ^{13}C -labelled acetate to investigate the organisms involved in anaerobic carbon mineralisation at an estuarine intertidal site. Label incorporation into PLFAs proved the involvement of very distinct bacterial groups in sulphate reduction and methane oxidation, thereby allowing a direct linking of microbial activity with identity.

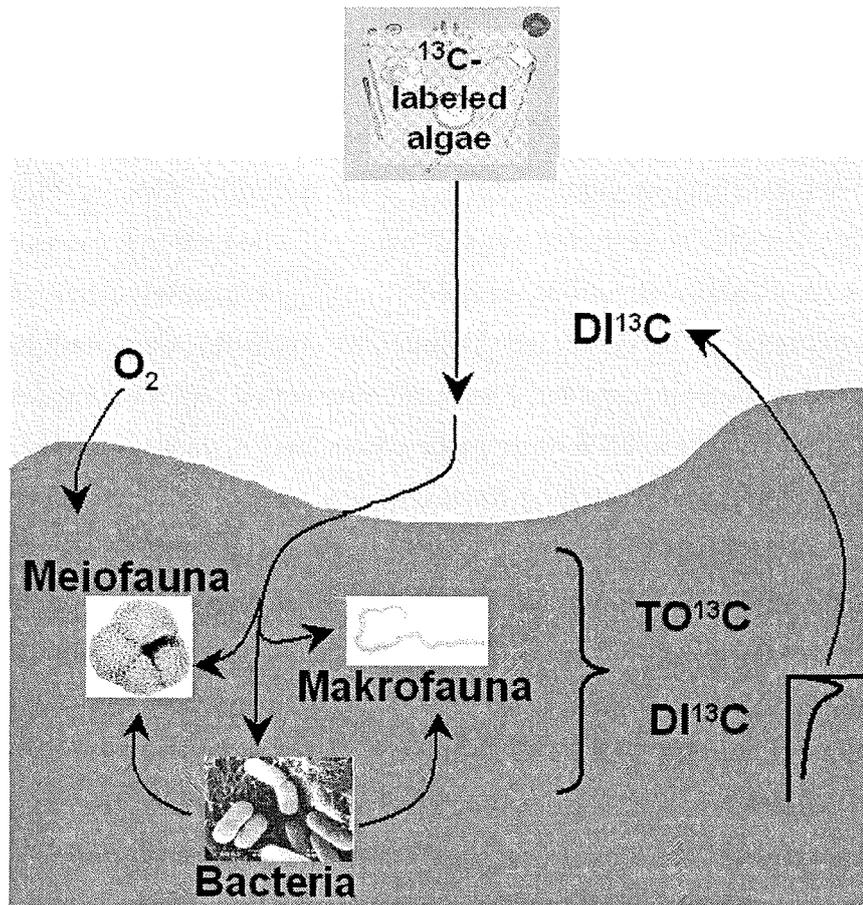


Figure 5: Schematic representation of a pulse-chase experiment as the one carried out in this study. Labelled algae are supplied to the sediment and the pathways of ^{13}C -processing through the benthic community are investigated.

Integrated approaches using enclosed systems such as benthic chamber landers and including a wider variety of benthic compartments were carried out lately e.g. by (Bühring et al. in prep.; Bühring et al. in press; Moodley et al. 2002; Witte et al. 2003a; Witte et al. 2003b). They reveal the important role of direct and indirect interactions within the benthic community for carbon turnover, such as organic matter relocation by macrofauna (Levin et al. 1997). These studies clearly demonstrate the power of this approach. However, with every answer, new questions arise, some of which we tried to answer in this thesis.

1.8 Perspectives

Pulse-chase labelling studies open a new scientific window to the vast dimensions of the world's ocean that are still barely touched when it comes to *in situ* investigations. Besides investigations on specific ecological settings, different regions and ecosystems need to be compared in order to obtain an integrated picture of global sedimentary carbon turnover. Different time scales require consideration to obtain an integrated picture of benthic carbon turnover. A variety of experimental set-ups has to be compared to account for the wide variety of sedimentation regimes and benthic communities. Recently, Bühring et al. (in press) for the first time conducted a benthic chamber lander experiment deploying different amounts of phytodetritus to an oligotrophic sediment. In this thesis, we addressed the importance of organic matter quality for benthic turnover processes in deep sea and continental slope sediments on a wide range of time scales from days to decades. *In situ*- and *ex situ*-experiments (on board) were carried out using ^{13}C -labelled phytodetritus of two different qualities ('fresh' and 'altered'). Furthermore, sediment quality parameters were compared to benthic flux rates to integrate over longer time scales and to account for the quality of naturally occurring sedimentary organic matter.

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Outline of the thesis

This thesis comprises three manuscripts, all of which have been or will be submitted to international peer-reviewed journals. Following the review-process, their final published form might slightly differ from the chapters presented herein.

This thesis was carried out within the Research Center Ocean Margins (RCOM) at the University of Bremen, funded by the Deutsche Forschungsgemeinschaft (DFG). It is part of the subproject B2, dealing with the “Origin, reactivity, and transformation of particulate organic material in the benthic boundary layer in high productivity systems” under the leadership of PD Dr. Matthias Zabel and Dr. Tim Ferdelman.

Chapter 2 (**‘Instantaneous benthic response to varying organic matter quality: *In situ* experiments in the Benguela Upwelling System’**) presents results from a series of *in situ* experiments carried out with a benthic chamber lander on sediments underlying the Benguela Upwelling System at stations between 600 m and 2000 m water depth. Isotopically (^{13}C)-labelled phytodetritus of two different degradational states (‘fresh’ and ‘altered’) was produced in the laboratory from cultures of the pelagic diatom *Skeletonema costatum*. This phytodetritus was supplied to the benthic community in the *in situ* experiments (1.5 – 3 g of algal carbon per m^2), which had a duration of 18 to 36 hours. The benthic response to this pulse of organic matter was followed via total oxygen uptake and bacterial productivity as bulk measurements of benthic activity. Moreover, phytodetritus processing in individual compartments of the benthic carbon cycle was traced by measuring ^{13}C -remineralisation, uptake of labelled phytodetritus by the benthic macrofauna and incorporation into the microbial community. The quality of phytodetritus was shown to have a major impact on the amplitude of the overall benthic response as well as on the reaction of the single investigated compartments of the benthic carbon cycle. Fresh phytodetritus was processed to a distinctly higher degree than altered phytodetritus.

As the duration of in these *in situ* experiments was restricted to less than two days by ship time and bottom water oxygen concentrations, they were not applicable to depict a possible changed benthic response on longer time scales. Therefore, additional medium-term experiments were carried out on the scale of days to weeks on board FS METEOR, allowing for incubation times of up to 15 days. These on board-experiments covered stations from 360 to 2000 m water depth and are presented in **Chapter 3 ('Microbial response to changing organic matter quality: bacterial productivity and results from medium-term labelling experiments')**. The experimental set-up was comparable to that of the *in situ*-experiments: Equivalent amounts of fresh and altered phytodetritus were deposited on the sediment surface in multicorer tubes (approximately 10 cm in diameter) that were incubated at *in situ* temperature. Total mineralisation as well as bacterial production, phytodetritus mineralisation and incorporation into bacterial fatty acids were investigated. Again, a distinct difference in the benthic response to different organic matter qualities was found. Comparable to the short-term experiments, mineralisation and bacterial production was distinctly higher in fresh compared to altered incubations. Opposite to the previous findings, however, a higher incorporation of altered phytodetritus into the microbial biomass on this medium time-scale resulted in a higher growth efficiency in altered incubations. The results from this study and the attached methodological discussion clearly emphasise the importance of timing for the benthic response to an input of available organic matter.

Stretching beyond this view at single benthic compartments and extending to long time scales of months to years and more, **Chapter 4 ('Organic matter reactivity driving diffusive benthic fluxes in the Benguela Upwelling System')** presents an investigation of the influence of the quantity and quality of deposited organic matter on diffusive benthic fluxes of nitrate, ammonium and phosphate, which were calculated from pore water profiles according to Fick's first law of diffusion. The investigated stations covered water depths from 400 to 2500 m. Besides calculations of benthic flux rates, carbon oxidation rates for the most important metabolic pathways were calculated from total oxygen uptake, sulphate reduction rates and denitrification at selected stations. Benthic fluxes were shown to be fairly decoupled from total organic matter concentrations. However, they were connected to selected

geochemical characteristics of the existing organic matter such as its concentration in total hydrolysable amino acids (THAAs), its degradation index (DI), or lability parameters derived from Rock-Eval pyrolysis of the sediments. This connection further underlines the importance of organic matter quality for benthic carbon turnover. The data presented in this manuscript support the hypothesis of a major depocentre of organic matter at the upper continental slope of the Benguela Upwelling System, which serves as a dumping site for material from a variety of sources and transport pathways.

The data presented in this thesis reveal new insights into the dynamics of benthic matter turnover and help to further understand the significance of deep sea sediments for marine carbon cycling.

Chapter 2

Instantaneous benthic response to varying organic matter quality: In situ experiments in the Benguela Upwelling System

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Abstract

The response pattern of a bathyal benthic community to organic matter (OM) input of varying quality was tested in continental slope and deep sea sediments in the Benguela Upwelling System off Namibia. A benthic chamber lander was employed to conduct experiments, in which isotopically (^{13}C -)labelled phytodetritus of two different qualities ('fresh' and 'altered') was supplied to the benthic community and its mineralisation, uptake by macrofauna and incorporation into bacteria was followed. Total oxygen uptake and bacterial secondary production were not affected beyond natural variation by our OM addition. Mineralisation dominated phytodetritus processing and bacterial incorporation of phytodetritus exceeded macrofaunal uptake at all stations. Total biological processing of phytodetritus (comprising mineralisation, bacterial incorporation and macrofaunal uptake) was higher in the southern stations situated in a major centre of OM deposition compared to stations further north. Biological processing was 1.5 to 4.3 times higher for fresh than for altered phytodetritus. This difference becomes more pronounced with increasing station depth. While total amounts of biologically processed phytodetritus significantly differ between the fresh and altered quality, relative contributions of the different benthic compartments as well as bacterial growth efficiencies remain similar. A greater response to an input of fresh compared to altered phytodetritus clearly demonstrates the importance of OM quality for benthic carbon turnover.

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Introduction

The turnover and burial rate of settling OM is largely controlled by benthic organisms that respire, assimilate and redistribute OM at the seafloor. One of the major challenges to organisms as well as scientists is that the food input to the deep sea benthos is not constant over time but strongly pulsed (Billett et al. 1983; Rice et al. 1986). Intense research has been carried out on the nature of these food pulses (Hinga et al. 1979; Honjo and Manganini 1993) and on the corresponding benthic response (Boetius and Lochte 1996; Pfannkuche 1993). However, the unpredictability of pulsed sedimentation events severely hampered an in-depth understanding of the subject. In the last years, the use of benthic chamber landers allowed *in situ* experimental simulations of food pulses. This enabled more detailed investigations of the benthic turnover processes, especially in combination with stable isotope labelling techniques (Blair et al. 1996; Witte et al. 2003b). *In situ* experiments in combination with near-natural organic substrates bear the potential to elucidate the controlling factors and dominant processes driving benthic OM turnover. These technologies have enhanced knowledge of time scales and intensities of reaction of different benthic compartments significantly. Apparently, the reaction time of a selected benthic compartment can vary substantially between different areas or oceanographic settings: e.g. in the Sognefjord on the Norwegian continental margin, Witte et al. (2003a) detected a bacterial response after only 36 h, whereas it was retarded up to 8 d in the Northeast Atlantic (Witte et al. 2003b). The intensity of the benthic reaction is also subject to differentiated changes, as was first shown in *in situ* experiments by Bühring et al. (in press) when exposing deep sea sediment to different amounts of fresh OM: a gradually enhanced response depending on the quantity of added OM revealed the high flexibility of the benthic community.

Besides its quantity, the quality of OM arriving at the deep sea floor is highly variable. Apart from its original source, the processing of OM on its way to the sediment and after arrival might significantly alter its availability to the benthic biota (Minor et al. 2003; Wakeham et al. 1997). Unfortunately, the major part of OM arriving at the sea floor has not been characterised to date and little is known about its composition and implications for benthic turnover and burial. Even though the quality of OM is widely recognised to affect the rate and extent of its mineralisation

(Westrich and Berner 1984), the specific features defining quality remain elusive. Arnosti and Holmer (2003) observed that characterisation of OM by standard bulk chemical analysis does not provide sufficient information as it can be decoupled from remineralisation. Availability of one compound might moreover not be the same for different groups of organisms, and OM reactivity could be defined individually for each group, depending on the enzymatic and/or uptake capabilities. Interactions and competition within the benthic community might be dependent on OM availability and vice versa, as has been described e.g. for macrofauna and bacteria (Boon et al. 1998). However, information is mainly available on single compartments of the benthic community and their diverse interactions are poorly studied so far. Danovaro et al. (2000) found bacterial abundance and biomass in shelf and bathyal sediments of the Cretan Sea to be strongly dependent on the input of fresh OM, as well as on its content of proteins and chloroplastic pigment equivalents (CPE). Also, enzyme production in natural mixed microbial communities – which might be considered a better measure for bacterial condition and activity than total biomass – was found to be directly regulated by the supply of appropriate food (Boetius and Lochte 1994). On the other hand, Witbaard et al. (2000) did not find an effect of seasonal changes in OM quantity or quality on bacterial dominated total oxygen uptake (TOU) in the Northeast Atlantic, which they attributed to the refractory character of the arriving OM. Still, holothurian macrofauna were able to use the supplied material, despite its rather low quantity and quality (Witbaard et al. 2001). Overall, no comprehensive picture can be derived to date on the effect of varying OM qualities on benthic biota, their interactions and their impact on benthic carbon turnover and burial.

To our knowledge, no information from *in situ* experiments is available at present on the importance of OM quality for deep sea environments. Therefore, this study investigated the short-term response of an abyssal benthic community to different qualities of settling OM using *in situ* pulse chase experiments. A high productivity region was chosen as the study area in search of a rich and active benthic community capable of a fast response to different OM qualities. In the Benguela Upwelling System at water depths between 600 and 2000 m, a benthic chamber lander was used to supply the sediment community with pulses of 'fresh' and 'altered' ^{13}C -labelled phytodetritus. The benthic response was traced via total oxygen uptake, bacterial productivity, remineralisation, uptake of added

phytodetritus by the benthic macrofauna as well as incorporation into the microbial community.

Study Area

The Benguela Upwelling System is one of the four major coastal upwelling systems in the world, with its principle upwelling centre situated near Lüderitz in Southern Namibia (Campillo-Campbell and Gordo 2004). Two major upwelling fronts correspond to bathymetric rises, along which circulating cells develop that transport OM towards the sea floor. As a result, depocentres of high OM content build up below the circulating cells (Giraudeau et al. 2000). The spatial extension of the Benguela Upwelling System is moreover characterised by long and rather stable phytoplankton-rich filaments that can extend several hundred kilometers westwards into the open sea (see Campillo-Campbell and Gordo 2004). They transport high loads of OM to waters overlaying the continental slope and deep sea, and thereby constitute an important source to the underlying sediments. The sediments on the continental slope off southwest Africa consist of an organic-rich, marine, diatomaceous ooze with only little terrigenous material and are particularly rich in OM on the Lüderitz slope (Calvert and Price 1983; Pichevin et al. 2004).

Material and Methods

Cultivation of labelled algae

Cultures of the planktonic diatom *Skeletonema costatum* (CCAP, Argyll, Scotland) were grown at 16°C on F/2 medium (Guillard and Ryther 1962) with artificial, HEPES-buffered seawater (Grasshoff et al. 1999). The algae were labelled by substituting 25 % of NaHCO₃ by NaH¹³CO₃ (99 %; Cambridge Isotope Laboratories

Inc.). Algae were harvested by centrifugation at $1500 \times g$ for 4 min and the pellet washed with sterile NaCl. Samples were stored freeze-dried.

Ahead of each deployment, a fraction of the algae was dialysed to obtain two different qualities of OM, the so-called 'fresh' and 'altered' algal material, respectively. Freeze-dried, 'fresh' *S. costatum* were soaked in sterile filtered ($0.2 \mu\text{m}$) seawater, filled into dialysis tubings (pore size 1000 MWCO), and dialysed in boiled seawater (pH 7) at 4°C at a sample:solution ratio of 1:100 for 6 h in the dark. The dialysis solution was changed every 2 h. After dialysis, samples were centrifuged at $2500 \times g$ for 7 min at room temperature and used as 'altered' algal material in our experiments. The resulting labelling was 15 % ^{13}C of the total organic carbon for both fresh and altered algae. Both fresh and altered phytodetritus had a organic carbon content of approximately 20 % and a C/N-ratio of approximately 7.1, close to the Redfield Ratio (Redfield et al. 1963). Concentrations of phospholipid fatty acids were mostly decreased in altered compared to fresh phytodetritus. Pigments as analysed by HPLC-analysis were dominated by chlorophyll (chl) *c1* and chl *a* as well as fucoxanthin in fresh, whereas chl *a* degradation products such as phaeophytine *a* and phaeophorbide *a* were major components in altered phytodetritus.

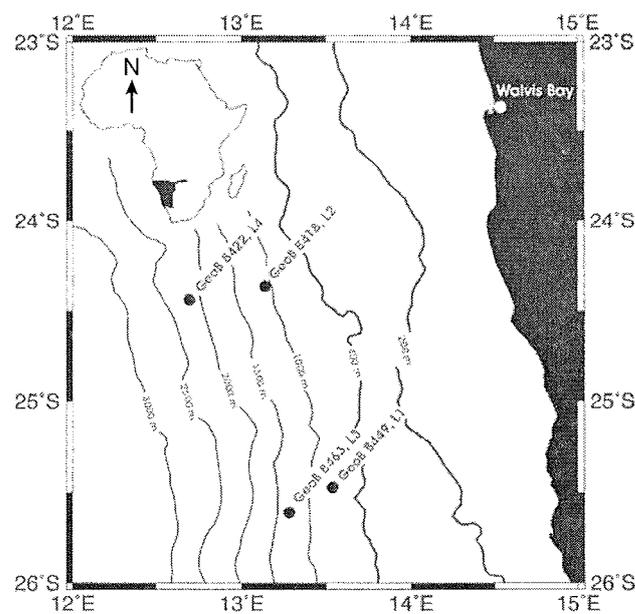


Figure 1: Study area and locations of the investigated stations. The insert shows a map of Africa, highlighted in black the area of Namibia. For further information see Table 1.

Experimental Setup

FS METEOR cruise M57/2 visited the Benguela Upwelling Region off Namibia between 23°N and 27°N in February/March 2003 (Fig. 1). *In situ* experiments were conducted using a modular benthic lander system equipped with three benthic chambers of 0.04 m² each (for further details on the lander see Witte and Pfannkuche 2000). Details on the sampled stations, which cross the Namibian continental slope in a northern (L2 and L4) and a southern (L1 and L3) transect, are given in Table 1. In each deployment, two of the chambers were used for the addition of two different qualities of ¹³C-labelled phytodetritus, respectively (fresh and altered), while the third chamber served as a control. The addition of labelled phytodetritus was carried out using an injection unit integrated into the lid of each chamber. To prove that a successful injection had occurred, a small weighted rod was added to the phytodetritus to be recovered at the end of the experiment. One hour after deployment of the chambers on the sediment surface, phytodetritus was injected into each experimental chamber. The amounts of added phytodetritus were equivalent to 60 mg of algal carbon for fresh and to 120 mg of algal carbon for the altered phytodetritus, to account for losses of the low molecular weight fraction in the altered material. Experiments proceeded for 18 to 36 h. A magnetic stirrer in the lid of the chamber assured homogeneous settling of the algae onto the sediment surface. Every chamber was equipped with a syringe water sampler, retrieving seven water samples of 50 ml each at pre-programmed intervals during the incubation. At the end of the experiment, a shutter at the bottom of each chamber was closed and the chamber subsequently slowly heaved out of the sediment. On deck, a sediment subcore (diameter 78 mm) was taken from each chamber and the remaining sediment was removed and prepared for macrofaunal analysis. The subcore was sliced under *in situ* temperature in slices between 0.5 and 1 cm thickness, the slices were carefully homogenised and sampled for pore water (centrifugation at 1500 x g for 15 min) and microbiological analysis. While measurement of bacterial secondary production (BSP) was carried out immediately, samples for lipid analysis were stored frozen at -20°C. Water from the syringes was subsampled at *in situ* temperature for oxygen and DIC. Total oxygen uptake (TOU) was calculated from the results of Winkler titration

of water samples (2 replicates). All described deployments were successful except for that at L4 (1997 m), in which the closing of the shutters and therefore sediment recovery failed due to a program failure. Therefore, only bottom water response to the phytodetritus addition can be reported for that station.

Table 1: Geographical position, TOC content, bottom water temperature, O₂-concentration and TOU and bacterial secondary production in the control chambers of the stations (* data from a multicorer-deployment at the same station).

Station #	Lat. [°S]	Long. [°E]	Depl.	Water depth [m]	Temp. [°C]	TOC [%]	O ₂ [μM]	TOU [mmol m ⁻² d ⁻¹]	BSP [mg C m ⁻² d ⁻¹]
GeoB 8449	25.48	13.55	L1	605	5.5	6.46	222.3	16.41	1.61±0.32
GeoB 8418	24.36	13.14	L2	1019	3.8	3.90	199.2	8.41	2.40±0.47
GeoB 8463	25.61	13.28	L3	1335	3.3	7.40	237.6	7.44	0.56±0.37
GeoB 8422	24.46	12.72	L4	1997	3.1	4.57*	233.2	4.73	

Total organic carbon (TOC)

Sediments were freeze-dried and subsequently acidified with HCl and washed with MilliQ-water to remove all inorganic carbon. Analysis of sedimentary TOC concentration was performed aliquots on of 80-90 mg of dry sediment with a LECO CS-200 IH analysis system. For δ¹³C_{TOC} analyses, subsamples of approximately 3 mg were transferred into tin capsules. Stable isotope analysis was performed with a THERMO/Finnigan MAT Delta plus isotope ratio mass spectrometer, coupled to a THERMO NA 2500 elemental analyser via a THERMO/Finnigan Conflo II-interface. Stable isotope ratios are given in the conventional delta notation (δ¹³C) relative to PDB (PeeDee Belemnite standard). Standard deviation for repeated measurements of lab standard material (peptone) is better than 0.15 per mill (‰).

Dissolved inorganic carbon (DIC)

Pore water and bottom water samples for alkalinity and DI^{13}C analysis were filtered (0.2 μm) directly into 5 ml gas-tight vials sealed with a teflon septum, containing mercury chloride to an end concentration of 0.2 % to stop all biological activity. The samples were stored refrigerated and dark until analysis. Alkalinity was determined volumetrically by titration with HCl.

For carbon isotope measurement of DIC samples were extracted with anhydrous phosphoric acid in an automatic preparation line (Finnigan Gasbench I) coupled on-line to a Finnigan MAT 252 IRMS to determine the $^{13}\text{C}/^{12}\text{C}$ ratio in the headspace. All samples were run at least in duplicate. Reference gas was pure CO_2 calibrated against the PDB standard with an external reproducibility of 0.10 ‰ at 2σ .

Bacterial Secondary Production (BSP)

Substrate saturation and linearity of leucine incorporation was tested prior to the experiments, as described in Chapter 3 of this thesis. For measurement of BSP, sediment subsamples were transferred into glass tubes under argon saturated atmosphere and sealed with rubber stoppers under exclusion of any gas. In the isotope lab, [^{14}C]leucine (SA 1500 Bq nmol^{-1} , 20 μM , CFB183, Amersham, U.K.) was added, the tubes were sealed again and incubated in the dark at *in situ* temperatures for 8 h.

Incubations were stopped with trichloroacetic acid (TCA) at a final concentration of 5 %. Subsequently samples were sonified for 1 min and centrifuged for 2 min at 11,500 $\times g$. Supernatant and sample were cleaned by multiple centrifugation and washing steps according to Buesing and Gessner (2003). The filter and pellet were combined in a centrifuge tube and protein was dissolved in an alkaline solution (0.5 N NaOH, 25 mM EDTA, 0.1 % SDS) for 60 min at 95°C. After centrifugation (4 min at 16,000 $\times g$) an aliquot of 100 μl was added to 15 ml Ultima Gold™ XR (Packard BioScience) and radioassayed in a liquid scintillation counter (Packard Tri-Carb 2500TR).

Bacterial protein production (BPP) was calculated following Simon and Azam (1989). A conversion factor of 0.86, based on investigations on pelagic bacteria, was used to transfer bacterial protein production into bacterial carbon production (BSP). This conversion factor allows us to directly calculate bacterial carbon production without knowledge of bacterial cell volumes or abundances (Simon and Azam 1989).

Analysis of Phospholipid fatty acids (PLFAs)

Lipids were extracted ultrasonically from wet sediment using dichloromethane-methanol and esterified according to Elvert et al. (2003). Concentrations were determined by gas chromatography-flame ionisation detection (Hewlett Packard 5890, Series II). Stable isotope composition was determined by GC-c-IRMS (Finnigan Delta plus MS connected via a Finnigan Combustion Interface III to a HP 6890 Series GC) and unknown compounds were investigated using GC-MS (Thermoquest Trace GC interfaced to a Finnigan Trace MS). For detailed description see (Bühning et al. 2005). The carbon isotopic ratios were corrected for the one methyl group inserted during derivatisation.

Results

Total oxygen uptake (TOU)

Initial bottom water oxygen concentration ranged from 199.2 to 237.6 $\mu\text{mol L}^{-1}$ and was slightly higher at greater water depths (Fig. 2). TOU showed no obvious differences between treatments and varied between 4.73 and 16.41 $\text{mmol m}^{-2} \text{d}^{-1}$ for the control, 4.84 and 13.69 $\text{mmol m}^{-2} \text{d}^{-1}$ for the fresh and 7.16 and 13.86 $\text{mmol m}^{-2} \text{d}^{-1}$ for the altered incubations. Natural variation of TOU within a single station was high, e.g. in the controls of two lander deployments at one station (1335 m), TOU

varied by a factor of 2. In the controls, TOU clearly decreased with increasing water depth (Fig. 2).

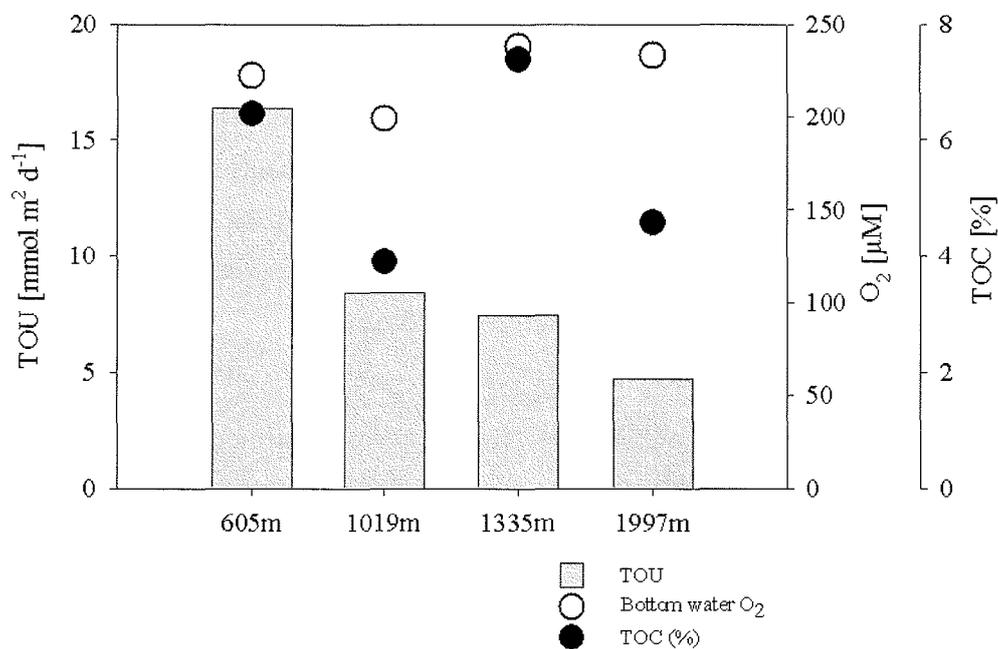


Figure 2: Depth distribution of TOC content in the surface sediment (closed circles), bottom water O_2 - concentration (open circles) and total oxygen uptake (bars).

Bacterial Secondary Production

BSP at the sediment surface (0-1 cm) ranged from 0.56 to 2.40 $\text{mg C m}^{-2} \text{d}^{-1}$ in the controls (Tab. 1), from 0.60 to 1.94 $\text{mg C m}^{-2} \text{d}^{-1}$ in the fresh incubations and from 1.12 to 1.33 $\text{mg C m}^{-2} \text{d}^{-1}$ in the altered incubations. No consistent changes in BSP following our phytodetritus addition could be detected (data not shown).

Total Organic Carbon

TOC concentration at the sediment surface (0-1 cm) varied between 3.9 % and 7.4 % (dry weight, d.w.) (Tab. 1; Fig. 2). They showed little variation throughout the sampled sediment depth.

While our addition of phytodetritus did not significantly increase the total amount of TOC in the sediment and did therefore not influence TOC profiles, TO¹³C clearly showed the presence of our added carbon. Concentrations of TO¹³C ranged from 12.9 mg ¹³C m⁻² to 57.8 mg ¹³C m⁻² in the fresh and from 13.2 mg ¹³C m⁻² to 78.0 mg ¹³C m⁻² in the altered incubations (Tab. 2). Concentrations of TO¹³C were usually highest at the sediment surface, only at L2 a subsurface maximum was detected at 2 cm sediment depth in the fresh incubation (Fig. 3a).

Table 2: Recovery of labelled carbon in the investigated compartments of the benthic carbon cycle. All values are given in mg ¹³C m⁻².

	L1 – 605 m		L2 – 1019 m		L3 – 1335 m	
	fresh	altered	fresh	altered	fresh	altered
TO ¹³ C	57.8	78.0	14.6	13.2	12.9	23.8
DI ¹³ C	4.71	2.85	1.94	0.95	5.08	1.20
Bacteria	0.224	0.282	0.565	0.098	0.519	0.106
Macrofauna	0.036	0.081	0.222	0.053	0.005	0.006
Total	62.77	81.21	17.33	14.30	18.50	25.11

Mineralisation

Alkalinity in the bottom water varied between 2.42 and 2.47 mmol L⁻¹ and did not change during the incubation. Bottom water concentrations of DI¹³C immediately increased after the algal addition and continued to do so with proceeding incubation time (Fig. 4). This increase was distinctly greater in incubations with fresh compared to altered phytodetritus. In the fresh incubations of L1 and L3 (southern transect), a very steep initial increase in bottom water DI¹³C concentrations could be observed

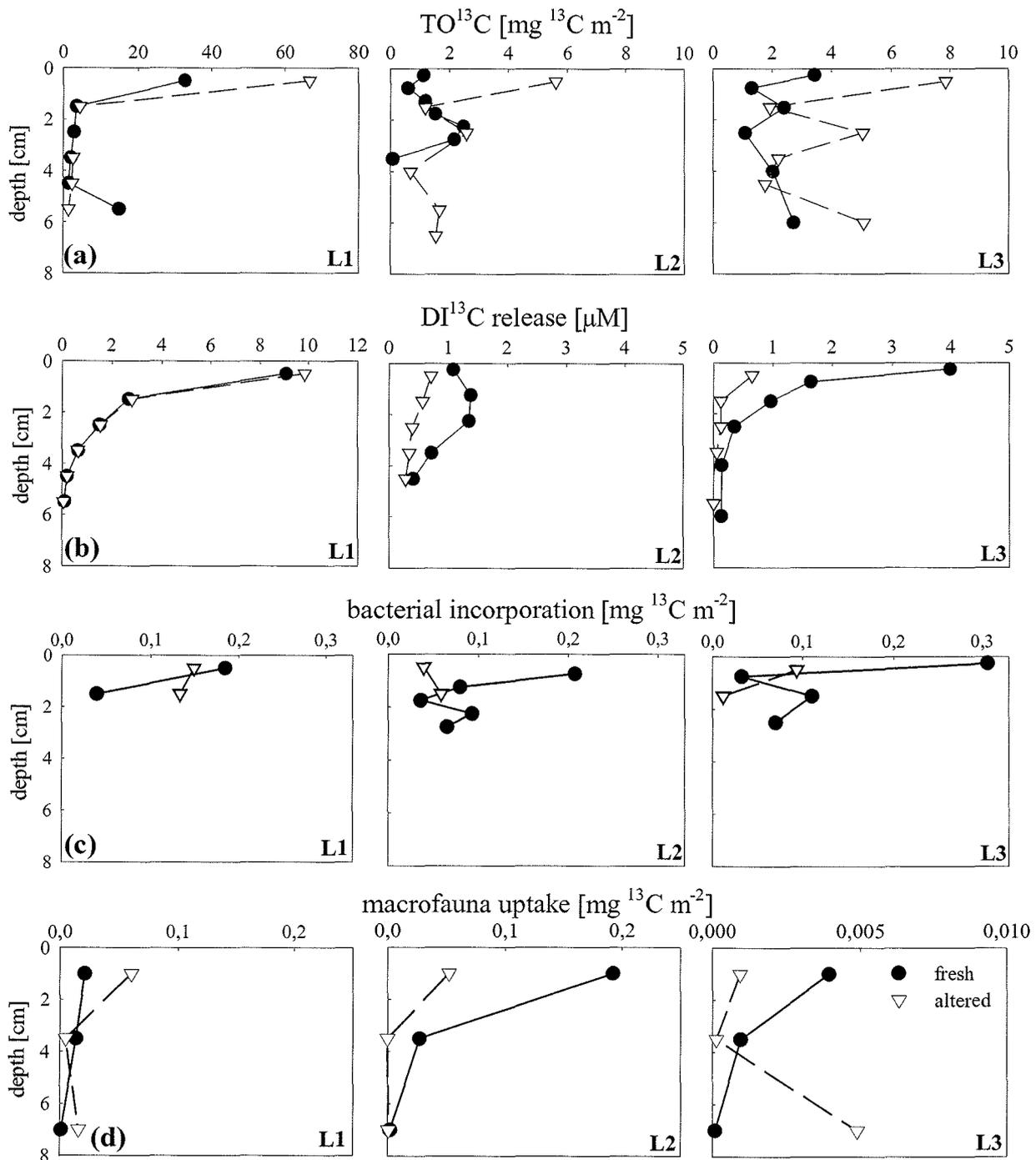


Figure 3: Concentration of added algal carbon at the end of the incubation in the investigated compartments of the benthic carbon cycle: total organic carbon (a), release to pore water DIC (b), incorporation into bacterial fatty acids (c) and uptake by macrofauna organisms (d). Fresh incubations are marked by closed symbols, altered incubations by open symbols. Note the different scales.

within less than 10 h after addition of the labelled phytodetritus (Fig. 4). Afterwards, rates of mineralisation remained more or less constant during the rest of the incubation. The pore water profiles of DI^{13}C showed generally the same pattern of higher DI^{13}C release in fresh compared to altered incubations (Fig. 3b). DI^{13}C release was usually highest at the sediment surface, however with one exception at L2 ('fresh' incubation) where a subsurface maximum was detected at approximately 2 cm sediment depth (Fig. 3b) corresponding to the TO^{13}C maximum. Highest DI^{13}C concentrations at the sediment surface were measured at L1, lowest ones at L2 (Fig. 3b). The total release of added label into the DIC pool for the fresh and altered incubations is given in Table 2. The corresponding total carbon mineralisation rates are given in Table 3.

Bacterial Fatty Acids

A typical distribution of bacterial fatty acids ($i\text{C}_{15:0}$, $ai\text{C}_{15:0}$, $i\text{C}_{16:0}$, $10\text{Me-C}_{16:0}$, $i\text{C}_{17:0}$, $ai\text{C}_{17:0}$, and $\text{C}_{17:1\omega6}$, see e.g. Boschker and Middelburg 2002; Rütters et al. 2002), taken from the sediment surface in the fresh incubation at L3, is shown in Figure 5. The most abundant bacterial fatty acid was $ai\text{C}_{15:0}$. Absolute as well as relative abundances of the individual fatty acids showed little variation between stations or with sediment depth.

Incorporation of added ^{13}C was detectable for all bacterial fatty acids, although in different amounts. Figure 5 shows an example of the total incorporation of label into selected bacterial fatty acids in the surface sediment of the fresh incubation at L3. Incorporation did not correlate with fatty acid abundances, and was usually highest for $i\text{C}_{16:0}$, followed by $i\text{C}_{15:0}$ and $ai\text{C}_{15:0}$ or $\text{C}_{17:1\omega6}$. No clear differences in incorporation into specific fatty acids between the different experimental treatments were detected. Incorporation of added carbon into bacterial fatty acids generally decreased with increasing sediment depth. However, fresh incubations showed a tendency towards the formation of subsurface peaks (Fig. 3c) that corresponds to the DI^{13}C profile at L2. Incorporation at the sediment surface was highest at L1 and minimal at L2 (Fig. 3c). Bacterial incorporation of the added phytodetritus was clearly different for the fresh and altered incubations (Tab. 2). The

corresponding bacterial carbon processing rates are given in Table 3 and depicted in Figure 6.

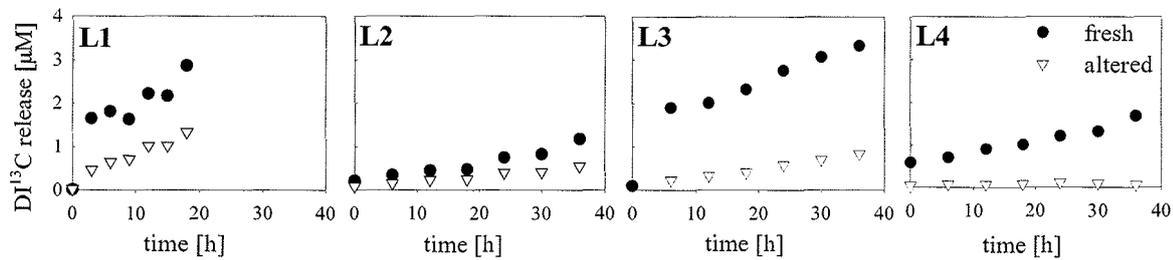


Figure 4: DI¹³C release to the bottom water during the experiment. Closed symbols indicate incubations with fresh phytodetritus, open symbols indicate incubations with altered phytodetritus.

Macrofauna

Macrofauna biomass at the sediment surface (0-2 cm) in the fresh and altered incubations amounted to approximately 2430 and 490 mg d.w. m⁻² in L1, to 3390 and 900 mg d.w. m⁻² in L2, and to 85 and 78 mg d.w. m⁻² in L3, respectively. No consistent pattern of macrofauna biomass with sediment depth could be detected. Except where cnidarians were present, macrofauna biomass was dominated by polychaetes that consistently displayed their maximum biomass at lower sediment layers (5-10 cm). The sum of other taxa (e.g. Bivalvia, Gastropoda, Scaphopoda, Crustacea) had highest biomasses at the sediment surface.

Macrofaunal incorporation of added carbon is shown in Table 2. Total carbon processing by the macrofaunal community is given in Table 3 and depicted in Figure 6. Highest total faunal uptake of added algal carbon was measured in the fresh incubation at L2. Uptake was maximal at the sediment surface, only the altered incubation at L3 showed a maximum at 5-10 cm sediment depth (Fig. 3d). Polychaetes took up the largest fraction of labelled carbon, followed by the other taxa (see above).

Total carbon processing

We define all the ^{13}C that was recovered in DIC, bacterial fatty acids or macrofauna at the end of the incubation as biologically processed. The sum of processed carbon was distinctly higher in fresh compared to altered incubations (Fig. 6). The difference in total processed carbon between fresh and altered incubations is smallest at the shallowest station (1.5 times higher in the fresh than in the altered incubation), and continuously increases with increasing water depth (2.5 x at L2 and 4.3 x at L3) (Fig. 6). Conversely, in the TOC pool consistently more label was recovered in the altered than in the fresh incubations.

The major fraction of the added phytodetritus was recovered in the TOC pool, which is assumed to be unprocessed. It is therefore not included in our further analysis of benthic carbon turnover. However, it is also possible that foraminifera, that were not separately treated in our survey, have taken up a fraction of the phytodetritus, as they can ingest it directly and have been shown to be capable of a fast reaction to an OM pulse (Altenbach 1992; Moodley et al. 2002), although Witte et al. (2003b) report a retarded response of foraminifera of 8 to 23 days in the abyssal Northeast Atlantic. Besides foraminiferal incorporation, the phytodetritus recovered in the TOC pool might have been taken up by benthic organisms and then excreted again by the end of our incubation. However, by our definition it would still remain unprocessed and not bias the interpretation of our results.

The majority of processed carbon was mineralised during the whole course of the incubation (Tab. 2, Fig. 4). Following mineralisation, bacterial incorporation of added phytodetritus constitutes the second largest fraction of processed phytodetritus (Tab. 2, Fig. 6). Macrofaunal uptake of labelled phytodetritus contributes least to total processing (Tab. 2, Fig. 6). Macrofaunal uptake was not directly related to macrofaunal biomass, even though at L3 both parameters were significantly lower than at the shallower stations.

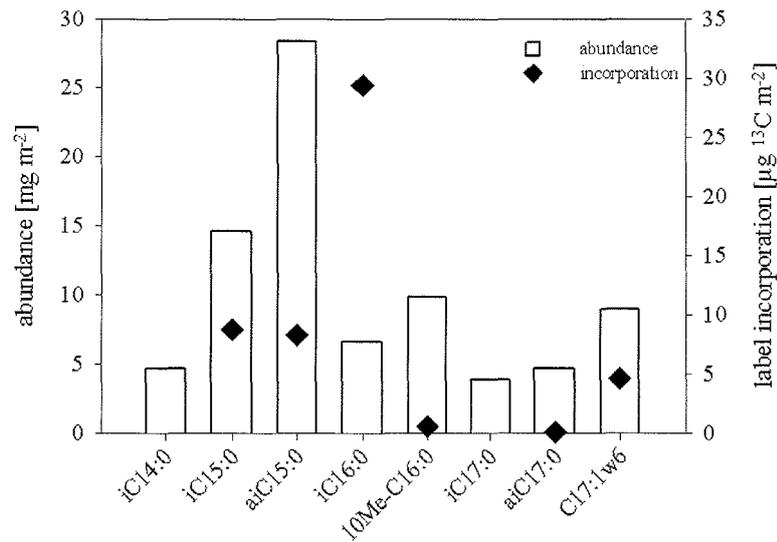


Figure 5: Concentration of bacterial fatty acids (bars) and incorporation of added algal carbon (diamonds) in an exemplary sample (L3, fresh, 0-0.5 cm).

Discussion

There are three major possibilities for the short-term fate of OM after arrival at the sea floor: It can (1) be respired, (2) become incorporated into benthic biomass or (3) become buried as part of the existing OM. Oxidic respiration, being the dominant respiratory process in slope and deep sea sediments, follows a simple stoichiometry:



Accordingly, total oxygen uptake (TOU) constitutes a well-established measure of total benthic carbon remineralisation in areas with well-oxygenated bottom waters. Moreover, TOU not only represents aerobic degradation, as indicated in equation (1), but also the ultimate oxidation of reduced species, such as H₂S, arising from anaerobic respiratory processes. However, TOU remains unable to track the pathways and specific rates within the benthic carbon cycle and the alternative fates of OM incorporation and burial. Therefore, this study used ¹³C-labelled phytodetritus as a tracer of organic carbon that allowed us to investigate these

alternative fates and follow the reactions of single benthic compartments all contributing to TOU.

Total benthic activity

Our oxygen consumption rates (Fig. 2) correspond well to those reported by Glud et al. (1994) and match the compiled data for the whole central and South Atlantic by Wenzhöfer and Glud (2002), who found *in situ* rates of TOU to decrease with increasing water depth. The addition of phytodetritus in our experiments caused no significant changes in TOU. Rather, any changes in TOU lay within its high natural variability caused by local variation in macrofaunal densities (Glud et al. 1994).

The experimental input did not substantially enrich the existing TOC pool, because it represented at most 0.3 % of the natural TOC at the sediment surface. Our results agree with those of Blair et al. (1996), who also found no measurable increase in TOU due to tracer addition in a comparably low concentration (0.4 % of the natural TOC pool). Rather than the fraction of the existing natural TOC pool, the proportion of the annual export production that is added in a pulse chase experiment provides an indication of the impact this addition will have on sediment TOU. Using trap data from the vicinity of the sampled stations (G. Fischer, unpublished data) for calculation, we obtain a proportion of 15.6 - 80.9 %. For comparison, Bühring et al. (in press) added up to half of the yearly export production in similar experiments in the oligotrophic Cretan Sea, resulting in significant increases of TOU. However, discrepancies between sediment trap fluxes and the sum of organic carbon burial rates and organic carbon degradation have been reported for the study area (e.g. Ferdelman et al. 1999). Moreover, Inthorn et al. (in prep.) suggest that lateral transport is an important mechanism of OM transport to the sediment in the Benguela Upwelling System. Based on oxygen fluxes in Glud et al. (1994) and this study, we estimate that we added between 5.5 ± 3.3 % (fresh incubations) and 11.0 ± 6.7 % (altered incubations) of the annually arriving OM in our experiments. The lack of change in TOU following tracer addition indicates that no sufficient amount of OM was added to produce a significant short-term impact on *in situ* sediment TOU.

The absence of a consistent reaction of BSP following our phytodetritus addition can most probably be attributed to similar reasons that have been named for TOU: High natural small-scale variability in combination with a minor addition of OM did not significantly change *in situ* microbial productivity. Moreover, in Chapter 3 of this thesis it is shown that the investigated time scale is of major importance to detect changes in BSP: in shipboard experiments with addition of phytodetritus in amounts equivalent to this study, significant changes in BSP were detected only after a week of incubation.

The addition of small amounts of labelled OM to the sediment allowed us to follow the pathways of benthic carbon processing under pristine conditions. Consequently, this tracer experiment presents a well suited and valid approach to investigate the short-term *in situ* benthic carbon turnover.

Table 3: Total carbon processing rates for the investigated compartments of the benthic carbon cycle and corresponding TOU. All values except TOU are given in $\text{mg C m}^{-2} \text{d}^{-1}$. Values in parenthesis are converted to $\text{mmol C m}^{-2} \text{d}^{-1}$. Bacterial growth efficiency (BGE) has been calculated from bacterial incorporation and mineralisation according to the formula $\text{BGE} = \text{BSP}/(\text{BSP} + \text{Mineralisation})$ (see Del Giorgio and Cole 1998).

	L1 – 605 m		L2 – 1019 m		L3 – 1335 m	
	fresh	altered	fresh	altered	fresh	altered
Mineralisation	20.95 (1745.8)	12.65 (1054.2)	8.63 (719.2)	4.23 (352.5)	22.59 (1882.5)	5.35 (445.8)
Bacteria	1.00 (83.3)	1.25 (104.2)	2.51 (209.2)	0.43 (35.8)	2.31 (192.5)	0.47 (39.2)
Macrofauna	0.16 (13.3)	0.36 (30.0)	0.99 (82.5)	0.24 (20.0)	0.02 (1.7)	0.03 (2.5)
Total	22.10 (1841.7)	14.27 (1189.2)	12.13 (1010.8)	4.90 (408.3)	24.92 (2076.7)	5.85 (487.5)
TOU [$\text{mmol m}^{-2} \text{d}^{-1}$]	13.69	11.07	7.65	13.86	4.84	7.16
BGE	0.05	0.09	0.23	0.09	0.09	0.08

Effect of organic matter quality

In the ^{13}C -tracer experiments, an instantaneous response of the benthic community to a pulse of OM was detected that is obviously not driven by the amount but rather by the quality of added algal carbon. The molecular weight fraction smaller than 1000 Dalton comprised in the fresh phytodetritus increases mineralisation rates of the added OM dramatically (Fig. 4). Within a few hours after addition of the OM, the easily available low molecular weight components appear to be mostly respired and mineralisation rates level off, however still remaining higher than on altered phytodetritus (Fig. 4). Bacterial incorporation of fresh OM correspondingly exceeds that of altered material at all stations except L1 (Fig. 6), most probably similarly resulting from the fast assimilation of the low molecular weight compounds. Even though standard chemical characterisation of the bulk phytodetritus (e.g. C/N-ratio, carbon content) is similar for both qualities, they result in very different total processing rates (Fig. 6). Apparently, this bulk characterisation does not reflect the reactivity and bioavailability of the substrate to the benthic microbial and macrofaunal community. Carbon mineralisation and incorporation are obviously fuelled by a small fraction of the total OM, not distinguishable by measurement of bulk parameters. The typical size limit for bacterial uptake lies around 600 Dalton (Decad and Nikaido 1976). Therefore, OM arriving at the sea floor usually needs to be reduced to smaller molecular sizes prior to bacterial uptake. This depolymerisation can be rate-limiting for all following steps in the sedimentary mineralisation process. As low molecular weight compounds smaller than 1000 Dalton were removed in our altered phytodetritus, bacterial assimilation of added altered phytodetritus was restricted on the covered short time scale while fresh material could be assimilated immediately. Macrofauna, not requiring initial depolymerisation before assimilating phytodetritus, proved less sensitive to OM quality.

Relative contributions of the single compartments of the benthic carbon cycle are similar in both fresh and altered incubations. The major fraction of processed phytodetritus becomes mineralised, averaging 88 % in fresh and 89 % in altered incubations. As a consequence, total benthic processing rates are mainly driven by mineralisation (Fig. 6). A dominance of mineralisation in phytodetritus processing

has previously been reported in different slope (Witte et al. 2003a) and deep sea environments (Bühring et al. in press; Witte et al. 2003b). However, a comparatively low contribution of mineralisation to total carbon processing has been found in coastal sediment at very short incubation times (Bühring et al. in prep.), or in the deep sea with different experimentally added carbon loads (Bühring et al. in press). Then, bacterial incorporation obtains a leading role.

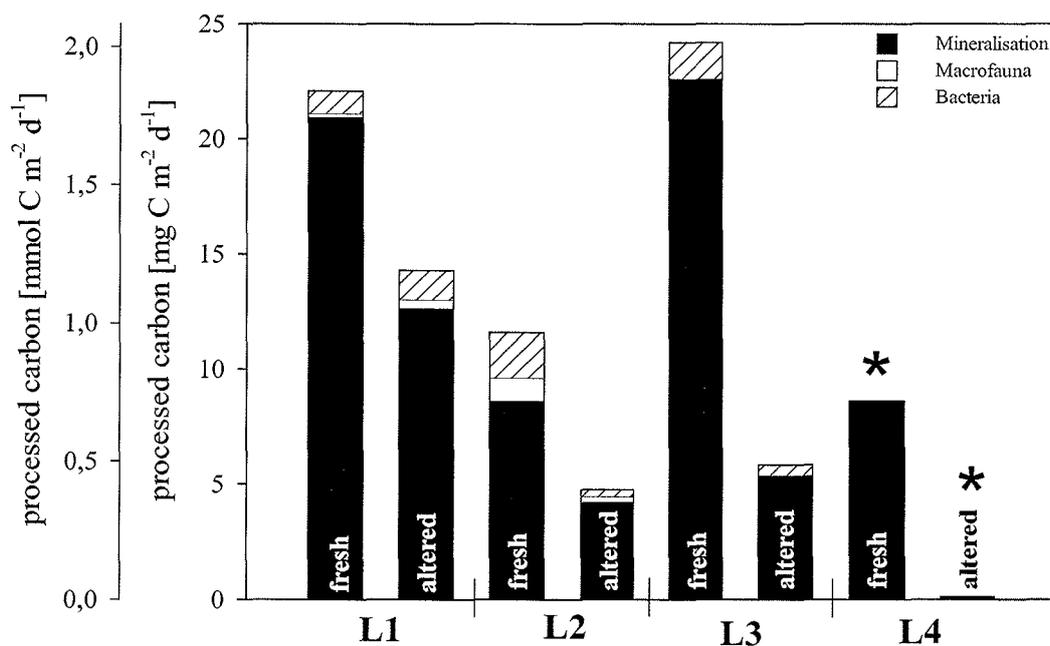


Figure 6: Total biological processing rates of added algal carbon for mineralisation (black bars), macrofaunal organisms (white bars), and bacterial fatty acids (hatched bars) in $\text{mg C m}^{-2} \text{d}^{-1}$ and $\text{mmol C m}^{-2} \text{d}^{-1}$, respectively. Diamonds indicate the corresponding TOU. * Data from station L4 are only available for bottom water DI^{13}C concentrations, as no sediment was retrieved from that station.

Following the predominant role of mineralisation in carbon processing, bacterial growth efficiencies on the added material, as calculated from bacterial incorporation and mineralisation of ^{13}C -labelled compounds, are low and similar in both fresh and altered incubations at two of the stations (Tab. 3). The incorporation of labelled carbon by bacteria in all experiments clearly documents the capacity of

the bacterial community to rapidly assimilate OM. After only 36 h, a distinct isotopic signal is detectable for a number of fatty acids down to at least 2 cm sediment depth. However, that uptake differs between individual bacterial fatty acids (Fig. 5), probably owing to diverse metabolic preferences of the bacteria and different pathways of fatty acid synthesis. The branched-chained fatty acids *iC*_{16:0}, *iC*_{15:0} and *aiC*_{15:0} show a particularly fast and high label incorporation (Fig. 5), suggesting a quick biosynthesis of these fatty acids. This corresponds well with data available for a variety of marine sediments (Bühning et al. in press; Middelburg et al. 2000), e.g. in the deep Cretan Sea, where *aiC*_{15:0} and *iC*_{16:0} showed the highest incorporation rates, but on average contributed only 2-6 % to the total fatty acid concentration (Bühning et al. in press). These fatty acids are described as typical for a variety of bacteria, and they are particularly abundant in gram-positive prokaryotes (Boschker and Middelburg 2002; White et al. 1996). The fast incorporation of label indicates that these bacteria have direct access to the phytodetritus by either taking up DOC released from the algae or by instant production of exoenzymes. On the other hand, label incorporation is comparatively low in the C₁₇ fatty acids (Fig. 5) that are characteristic of sulphate reducing bacteria (SRB) (Boschker et al. 1998; Rütters et al. 2002). SRB mainly rely on the uptake of secondary carbon products (e.g. acetate and other short chain carbon sources, Widdel and Bak 1992) that need to be supplied by other organisms feeding directly on the phytodetritus. The short incubation time of 36 h may not suffice for fermentation and for most SRB to obtain these secondary substrates, leading to low label incorporation in that group. Longer incubation times would probably result in higher incorporation of label into SRB biomarkers, as has been shown on North Sea shelf sediments using a comparable experimental design but incubation times of up to 132 h (Bühning et al. in prep.).

Regional patterns

Compared to studies using similar experimental set-ups, the amount of total biologically processed carbon (comprising mineralisation, bacterial incorporation and macrofaunal uptake) in our experiments is relatively high (Tab. 3). In the abyssal Northeast Atlantic, naturally poor in OM input, Witte et al. (2003b) reported total carbon processing rates of 4 mg C m⁻² d⁻¹. Similarly, Moodley et al. (2002) found rates

of $4.3 \text{ mg C m}^{-2} \text{ d}^{-1}$ in the deep Northeast Atlantic. In the Cretan Sea, which is highly oligotrophic, Bühring et al. (in press) measured carbon processing rates of $8 \text{ mg C m}^{-2} \text{ d}^{-1}$ after moderate addition of phytodetritus. However, after adding as much as half of the yearly export production in carbon, processing rates increased to $53 \text{ mg C m}^{-2} \text{ d}^{-1}$. Outside the deep seas, rates of $19 \text{ mg C m}^{-2} \text{ d}^{-1}$ measured on the continental slope off western Norway (Witte et al. 2003a) and of $19.1 - 21.7 \text{ mg C m}^{-2} \text{ d}^{-1}$ on the North Sea shelf (Bühring et al. in prep.) resemble those found in the fresh incubations of this study (Tab. 3). There appears to be a clear separation in overall benthic processing rates between abyssal plains and continental slopes, with higher rates in the latter. Moreover, a time-lag in the benthic response as reported for deep sea environments (e.g. Witte et al. 2003b) can not be detected on the continental slope. Moodley et al. (2002) suggested that low temperature in combination with low biomass concentrations and composition slows down the recycling of OM at their deep sea study site. Following this hypothesis, Bühring et al. (in press) attributed their high processing rates in the deep Cretan Sea to the higher bottom water temperature of up to 16°C . However, in the Benguela Upwelling System, exhibiting the same low bottom water temperatures as the deep Northeast Atlantic, this hypothesis does not appear to be applicable. Temperature is low at all investigated stations, ranging between approximately 3 and 6°C (Tab. 1) and does not show any measurable effect on benthic processing rates. Our comparably high processing rates can be best explained by the high overall productivity and mineralisation in our study area, resulting in high biomasses, and by a benthic community well-adapted to a constant and high OM input.

Distinct differences apparent in absolute processing rates of the single compartments of the benthic carbon cycle are visible not only when comparing the two qualities of phytodetritus, but also the different investigated stations in terms of depth and latitude. From the shallow to the deep station, the discrepancy in total OM processing between the corresponding fresh and altered incubations gradually increases (Fig. 6, Tab. 3). The great difference in processing between different incubations principally results from a changed degree of mineralisation (Fig 4). At L3, macrofauna abundance was decreased by more than an order of magnitude compared to the shallower stations, matching results from other deep sea environments (Heip et al. 2001; Martin and Sayles 2004). Macrofauna therefore probably hardly contributed to total mineralisation that was mainly driven by

microbial activities at the deeper sites. Macrofaunal contribution to total metabolism is reported to be high in shelf and upper slope sediments (Heip et al. 2001), which is supported by a comparatively high macrofauna abundance at the shallowest station in our own results as well as in Glud et al. (1994). At that station (L1), total processing of altered phytodetritus is highest compared to the deeper stations, resulting in a comparatively reduced difference in total processing of different OM qualities. A generally greater importance of macrofauna compared to microorganisms at upper slope sediments, as proposed by Heip et al. (2001), together with a generally greater ability of macrofaunal organisms to utilise low-quality OM (Witbaard et al. 2001), probably explains the lesser difference in biological processing between the different phytodetritus qualities at the shallowest station.

Regional differences are also visible between the two transects. Stations situated on the northern transect (L2, L4) reveal lower processing rates than stations on the southern transect (L1, L3) (Fig. 6). Both southern stations lie within an area reported to serve as a main depocentre of organic carbon in the Benguela Upwelling system. While Ferdelman et al. (1999) suggest a main centre of benthic activity on the north Cape Basin continental slope between 1100 and 1800 m water depth, Seiter (2004) confines this maximum to a patch at approximately 1300 m water depth. Inthorn et al. (in prep.) compiled a large set of data on surface sediment TOC contents in the Benguela Upwelling region and found a prominent centre of OM deposition on the upper continental slope. Accordingly, the most extensive processing of added material in the fresh incubation was measured at L3 at approximately 1300 m depth (Fig. 6), well within this centre of deposition. These high rates correspond to maximum rates of diffusive O₂ uptake (Glud et al. 1994) and sulphate reduction (Ferdelman et al. 1999) at midslope depth, and clearly support the hypothesis of a main depocentre on the Namibian continental slope around that depth. The northern stations are placed outside the centre of high benthic activity and correspondingly show lower total processing rates (Fig. 6). Apparently, the benthic community on the southern transect is accustomed to a high input of TOC, supplying high rates of benthic activity. It can therefore process an input of highly reactive OM (i.e. phytodetritus) faster than the benthic community on the northern transect, which is less accustomed to such rich conditions. The fact that bacterial growth efficiencies are similar if not higher on the northern transect (Tab. 3) supports the hypothesis that it is rather a timing effect (as the altered material still requires

break-up to smaller molecular sizes) than a reduced ability of the benthic microbial community to utilise the phytodetritus that causes the reduced total processing rates on the northern transect.

Conclusions

Our experiments – tracer experiments that did not significantly change total benthic activity - reveal an instantaneous response of the benthic community to an input of fresh phytodetritus, while the benthic reaction is much less pronounced after addition of altered OM. Low molecular weight appears to be a driving factor for a fast bacterial incorporation and mineralisation, while macrofaunal uptake is less dependent on the quality of OM. Within 36 hours, the processed material hardly becomes passed on between benthic compartments, and effects e.g. on sulphate reducing bacteria do not yet become apparent. The major part of added phytodetritus becomes mineralised in the instantaneous response, while incorporation and uptake play minor roles. Comparable bacterial growth efficiencies and relative contributions of the single benthic compartments to total processing suggest that timing plays an important role for the impact of phytodetritus quality in our study, and that both qualities are overall highly available to the benthic community. While our experiments clearly show the importance of OM quality for the short-term benthic response, they were not designed to investigate possible medium- and long-term effects. These should be addressed in future experiments combining the *in situ* and *ex situ*-addition of labelled complex substrates to a natural benthic community with detailed measurements of benthic total and tracer turnover specifically designed for longer time scales.

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Chapter 3

Microbial response to changing organic matter quality: pathways and timing of the benthic reaction investigated in medium-term labelling experiments

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Abstract

We investigated the microbial response pattern to two different qualities of phytodetritus in pulse-chase experiments carried out in surface sediments of the Benguela Upwelling Region. Isotopically (^{13}C -)labelled 'fresh' and 'altered' phytodetritus was supplied to the sediment and used to trace the pathways of organic matter (OM) turnover through the benthic microbial community on a time scale of a few days to weeks. The extent of mineralisation of the added material was distinctly higher in incubations with fresh compared to altered phytodetritus (2.2-3.8x). The same pattern - though less pronounced - was visible for bacterial secondary production (BSP). Conversely, incorporation of labelled OM into bacterial fatty acids was increased with altered compared to fresh OM additions. Calculations of bacterial growth efficiency (BGE) on the different qualities of OM displayed accordingly higher efficiencies on altered than on fresh OM (0.26 and 0.08, resp.), suggesting a higher utilisation of the altered phytodetritus. These results were explained by a time-lag effect in the incubations with fresh phytodetritus that - opposite to altered OM - still required initial break-up. Consequently, altered OM was taken up and incorporated faster than fresh OM, however it did not result in higher mineralisation or BSP. Even though bacterial incorporation and BGE suggest differently, fresh phytodetritus was shown to cause higher benthic carbon turnover than altered material on a medium time scale.

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Introduction

The food supply to sediment communities in slope and deep sea environments is subject to high spatial and temporal (e.g. seasonal) variability. The quantity of organic matter (OM) supply to the sediment has been subject to extensive research in the Benguela Upwelling System (Campillo-Campbell and Gordo 2004; Wefer and Fischer 1993). Comparatively little is known about the quality of OM arriving at the seafloor, which largely depends on its source and state of degradation (Minor et al. 2003; Wakeham et al. 1997). OM quality can be directly related to OM reactivity: while 'quality' indicates a given chemical composition, 'reactivity' is strongly dependent on the investigated time scale and the 'target' of this reactivity (e.g. microorganisms as decomposers of OM). Upon arrival at the sea floor, the quality of OM might be significantly altered from the initial state due to selective preservation (Minor et al. 2003; Wakeham et al. 1997). In this study, we investigate if and how the quality of OM arriving at the sea floor affects its reactivity and biological availability and the pathway and amplitude of its benthic utilisation.

Benthic organisms respire, assimilate, and redistribute OM arriving at the seafloor, and thereby play a major role in its early diagenesis. Total oxygen uptake (TOU) is mostly considered a reliable measure of total benthic carbon mineralisation in areas with well-oxygenated bottom waters. However, this method remains unable to track the pathways and specific rates of the reaction of the benthic community. Bacteria, being the most abundant and important biological component involved in the transformation and mineralisation of OM (Cho and Azam 1988; Deming and Baross 1993), perform two major functions: (1) respiration of organic carbon to inorganic carbon (bacterial mineralisation) and (2) production of new bacterial biomass (e.g. bacterial secondary production). Only the first could possibly be traced by TOU. In the last decade, *in situ*-pulse chase experiments with labelled substrates allowed a more detailed tracing of the benthic response pattern, its speed and amplitude, and the description of single compartment reactions in intertidal (Middelburg et al. 2000) as well as deep sea environments (e.g. Blair et al. 1996; Witte et al. 2003b). Bühring et al. (in press) first demonstrated the presence of a gradually enhanced benthic reaction to increasing quantities of OM input in the deep Cretan Sea. However, the influence of OM quality on the benthic response patterns remains

an open question. Significant relationships between bacterial distribution and concentration of labile organic compounds (such as DNA and carbohydrates) have been found e.g. in the highly oligotrophic Eastern Mediterranean Sea (Danovaro et al. 1999; Danovaro et al. 1993). Still, definition and measurement of labile components in marine sediments are a complex subject-matter. Moreover, studies on seasonal dynamics indicate that other factors, such as protozoan grazing (Kemp 1994), might also affect microbial growth (Deming and Baross 1993).

In this study, the medium-term response of the benthic microbial community to different qualities of OM was investigated. In the Benguela Upwelling System, sediment from 360 to 2000 m water depth was retrieved with a multicorer. Cores were subsequently incubated with additions of fresh and altered ^{13}C -labelled phytodetritus. Utilisation of the added material was tracked via its mineralisation, incorporation into microbial biomass, and the corresponding bacterial productivity.

Study Area

The Benguela Upwelling System is one of the four major coastal upwelling systems in the world, with its principle upwelling centre situated near Lüderitz in Southern Namibia (e.g. Campillo-Campbell and Gordoia 2004). Circulating cells along upwelling fronts transport OM towards the seafloor, resulting in the formation of centres of high OM content below the circulating cells (Giraudeau et al. 2000). The spatial extension of the Benguela Upwelling System is moreover characterised by long and rather stable filaments of high OM content that can extend several hundred kilometers westwards into the open sea (see Campillo-Campbell and Gordoia, 2004). They transport high loads of OM to waters overlaying the continental slope and deep sea, and thereby constitute an important source to the underlying sediments. Sediments on the continental slope off southwest Africa consist of an organic-rich, marine, diatomaceous ooze with only little terrigenous material, as the adjacent coastal land mass is desert with no significant riverine input (Calvert and Price 1983).

Material and Methods

Cultivation of labelled algae

Cultures of the planktonic diatom *Skeletonema costatum* (CCAP, Argyll, Scotland) were grown at 16°C on F/2 medium (Guillard and Ryther 1962) with artificial, HEPES-buffered seawater (Grasshoff et al. 1999). The algae were labelled by substituting 25 % of NaHCO₃ by NaH¹³CO₃ (99 %; Cambridge Isotope Laboratories Inc.). Algae were harvested by centrifugation at 1500 × g for 4 min and the pellet washed with sterile NaCl. Samples were stored freeze-dried.

Ahead of each deployment, a fraction of the algae was dialysed to obtain two different qualities of OM, the so-called 'fresh' and 'altered' algal material, respectively. Freeze-dried, 'fresh' *S. costatum* were soaked in sterile filtered (0.2 µm) seawater, filled into dialysis tubings (pore size 1000 MWCO), and dialysed in boiled seawater (pH 7) at 4°C at a sample:solution ratio of 1:100 for 6 h in the dark. The dialysis solution was changed every 2 h. After dialysis, samples were centrifuged at 2500 × g for 7 min at room temperature and used as 'altered' algal material in our experiments. The resulting labelling was 15 % ¹³C of the total organic carbon for both fresh and altered algae. Both fresh and altered phytodetritus had a organic carbon content of approximately 20 % and a C/N-ratio of approximately 7.1, close to the Redfield Ratio (Redfield et al. 1963). Concentrations of phospholipid fatty acids and algal pigments were mostly decreased in altered compared to fresh phytodetritus.

Experimental Setup

Samples were taken during FS METEOR cruise M57/2 in February/March 2003 in the Benguela Upwelling Region. During the cruise, on board incubations were performed at three stations covering gradients of surface sediment organic carbon concentration and water depth (Tab. 1). Multicorer tubes with an overlaying water column of max. 20 cm were covered with lids carrying valves to allow airtight

Table 1: Locations and characteristics of the investigated stations.

Station #	Lat. [°S]	Long. [°E]	Incub. #	Water Depth [m]	TOC [wt%]	O ₂ [μM]	Alkalinity [mM]	Bact. biomass [μg g ⁻¹ d.w.]
GeoB 8429	-25.47	13.72	INCUI	360	13.10 ± 2.45	196.4 ± 53.3	2.57 ± 0.05	1180
GeoB 8463	-25.61	12.72	INCUI2	1300	10.32 ± 0.27	213.3 ± 20.1	2.68 ± 0.18	660
GeoB 8422	-24.46	12.72	INCUI3	2000	2.98 ± 0.40	295.0 ± 9.1	2.76 ± 0.02	1610

storage and regular sampling of the overlaying water. Cores were held at *in situ* temperature for the duration of the experiment. A magnetic stirrer was inserted below the lid to avoid stratification in the overlaying water column.

Cores were incubated with labelled algal material of fresh and altered quality (see above). The amount of added phytodetritus per core was equivalent to 12 mg algal carbon in the fresh and 24 mg algal carbon in the altered incubations, to account for losses of the low molecular weight (LMW) fraction in the altered material. Incubation periods were between 6 and 15 days. For logistical reasons, only altered algal material could be added in the experiment at station GeoB 8429 (INCUI). A control experiment without any addition was run for each time step and station.

At regular time intervals, the overlaying water was sampled for O₂, DI¹³C, and alkalinity. While DI¹³C samples were fixed with HgCl₂ for later analysis, O₂ and alkalinity were measured immediately using Winkler titration and an autoanalyser. The volume removed for sampling was replaced by sterile filtered bottom water obtained from each respective station. Oxygen concentrations were monitored during the course of the incubation; incubations were temporarily aerated if values decreased to 100 μM. This minimized the influence of changing oxygen concentration as a driving force behind changes in benthic activity.

Sediment sampling

At the end of the incubation, the cores were sliced under argon-saturated atmosphere, the sediment was homogenised for each depth interval, and subsampled for microbial analysis. The remaining sediment was centrifuged at 1500 x g for 15 min to separate the sediment from the pore water, which was removed and filtered (0.2 µm) after centrifugation. Sediment was then stored frozen for TOC analysis. An aliquot of pore water was fixed for DIC-analysis and the remainder immediately analysed for alkalinity.

Total Organic Carbon (TOC)

Sediments were freeze-dried and subsequently acidified with HCl and washed with MilliQ-water to remove all inorganic carbon. Analysis of sedimentary TOC concentration was performed aliquots of 80-90 mg of dry sediment with a LECO CS-200 IH analysis system. For $\delta^{13}\text{C}_{\text{TOC}}$ analyses, subsamples of approximately 3 mg were transferred into tin capsules. Stable isotope analysis was performed with a THERMO/Finnigan MAT Delta plus isotope ratio mass spectrometer, coupled to a THERMO NA 2500 elemental analyser via a THERMO/Finnigan Conflo II-interface. Stable isotope ratios are given in the conventional delta notation ($\delta^{13}\text{C}$) relative to PDB (PeeDee Belemnite standard). Standard deviation for repeated measurements of lab standard material (peptone) is better than 0.15 per mill (‰).

Dissolved Inorganic Carbon (DIC)

Pore water and bottom water samples for DI^{13}C analysis were filtered (0.2 µm) directly into 5 ml gas-tight vials sealed with a teflon septum, containing HgCl_2 to an end concentration of 0.2 % to stop all biologic activity. Samples were stored refrigerated until analysis.

For carbon isotope measurement of DIC samples approximately 30 μl of anhydrous phosphoric acid was pipetted into a clean 10 ml vial. After sealing the exetainer with a septum cap the remaining air was removed by flushing the exetainer with He. Subsequently, approximately 0.7 ml of sample water was injected through the septum into the sealed exetainer using a disposable syringe. After 1 h of reaction time, the sample was ready for isotope measurement. The $\delta^{13}\text{C}$ in the headspace was measured using a Thermo Finnigan GASBENCH II coupled online with a Thermo Finnigan Delta *plus* isotope ratio mass spectrometer. Reference gas was pure CO_2 from a cylinder calibrated against the PDB standard by using IAEA reference materials (NBS 18, NBS 19). Reproducibility of replicate measurements of lab standards (limestone) is generally better than 0.10‰.

Analysis of Phospholipid Fatty Acids (PLFAs)

The lipid extraction was performed on wet sediment using dichloromethane-methanol and lipids were esterified according to Elvert et al. (2003). Concentrations were determined by gas chromatography-flame ionisation detection (Hewlett Packard 5890, Series II), stable isotope composition by GC-*c*-IRMS (Finnigan Delta plus MS connected via a Finnigan Combustion Interface III to a HP 6890 Series GC) and unknown compounds were investigated using GC-MS (Thermoquest Trace GC interfaced to a Finnigan Trace MS). For detailed description see Bühring et al. (2005). The carbon isotopic ratios were corrected for the one methyl group inserted during derivatisation.

Bacterial Secondary Production (BSP)

Substrate saturation was tested by incubating sediment samples with [^{14}C]leucine (CFB183, Amersham, U.K.) with a specific activity (SA) of 1500 Bq nmol $^{-1}$ at increasing concentrations of 0, 0.5, 1, 5, 10 and 40 μM . According to the results of these incubations, a [^{14}C]leucine concentration of 20 μM was used for all our

measurements. An appropriate incubation time was determined in time course experiments from 30 min to 8 h duration.

For measurement of BSP, sediment subsamples were transferred into glass tubes under argon saturated atmosphere and sealed with rubber stoppers with the exclusion of any gas. On-board, [^{14}C]leucine (SA 1500 Bq nmol $^{-1}$, 20 μM) was added, the tubes were sealed again and incubated in the dark at *in situ*-temperatures for 8 h. Incubations were stopped with trichloroacetic acid (TCA) at a final concentration of 5 %, and precipitated proteins cleaned by multiple centrifugation and washing steps (2x 5 % TCA, 1x 40 mM leucine, 1x 80 % ethanol, 1x nanopure water) according to Buesing and Gessner (2003). The filter and pellet were combined and protein was dissolved in an alkaline solution (0.5 N NaOH, 25 mM EDTA, 0.1 % SDS) for 60 min at 95 °C. The samples were centrifuged (4 min at 16,000 x g) and an aliquot of 100 μl was added to 15 ml Ultima GoldTM XR (Packard BioScience) and radioassayed in a liquid scintillation analyser (Packard Tri-Carb 2500TR).

Bacterial protein production was calculated following Simon and Azam (1989). A conversion factor of 0.86, based on investigations on pelagic bacteria, was used to transfer bacterial protein production into bacterial carbon production (BSP). This conversion factor allows us to directly calculate bacterial carbon production without knowledge of bacterial cell volumes or abundances (Simon and Azam 1989).

Calculations of bacterial carbon uptake (BSP-uptake) and bacterial growth efficiency (BGE)

From the rates of bacterial carbon production based on [^{14}C]leucine-incorporation, we calculated the total uptake of carbon by bacteria due to BSP during the experiment as 'BSP-uptake'. For this purpose, BSP was integrated over each time step of the experiment and consecutive time steps were added up to yield the total BSP-uptake.

From the data on mineralisation rate and bacterial incorporation of labelled phytodetritus, the bacterial growth efficiency (BGE) was calculated for growth on the added OM. BGE describes the amount of new bacterial biomass produced per unit carbon assimilated, following the formula

$$BGE = \frac{(BI)}{(BI + MR)}$$

where BI describes the bacterial biomass production, which was calculated from the incorporation of added phytodetritus into bacterial PLFAs, and MR gives the mineralisation rate, being derived from the release of $DI^{13}C$.

Results

Alkalinity and $DI^{13}C$

Initial average alkalinity of the sampled stations is given in Table 1. Alkalinity usually increased throughout the experiments and total mineralisation slightly increased in the experimental treatments when compared to the controls. Release of ^{13}C -labelled DIC differed strongly between the treatments. While the addition of altered algal material resulted in a comparably slow rise in total mineralisation of labelled material over the whole incubation period, addition of fresh material led to a rapid increase of mineralisation of labelled phytodetritus (Fig. 1). Within less than 100 hours, $DI^{13}C$ in fresh incubations reached concentrations more than 5 times as high as in altered incubations. This steep increase in mineralised algal carbon subsequently levelled off. Those cores extending beyond two weeks of incubation time suggest that the high rates can not be maintained over the whole incubation period (Fig. 1).

The extent of mineralisation of added OM was consistently higher for fresh than for altered incubations (Fig. 1, Fig. 2). At termination, 2.2 to 3.8 times more algal carbon was mineralised in fresh incubations than in the corresponding altered ones (Fig. 3). At all stations, the major part of the mineralised label was recovered in the overlaying water, where it likewise was significantly higher in fresh than in altered incubations (3.9 to 5.7 times in INCU2, 2.6 to 3.3 times in INCU3). The enrichment of $DI^{13}C$ in the overlaying water of our experiments (Fig. 1) is attributed to diffusion from the pore water. Pore water profiles of $DI^{13}C$ revealed highest concentrations at

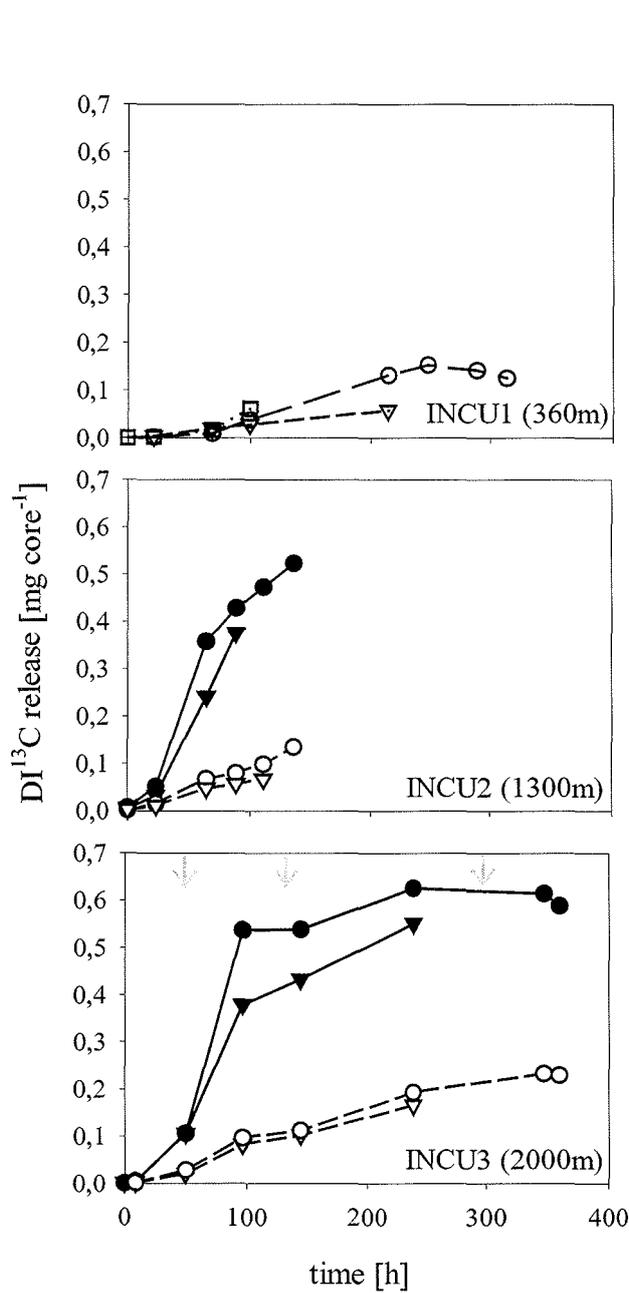


Fig. 1: $DI^{13}C$ release over time for fresh (closed symbols) and altered (open symbols) incubations. Squares, triangles and circles represent the short, medium and long incubations, respectively. The grey arrows for INCU3 mark time points when the incubation was aerated to assure oxic conditions.

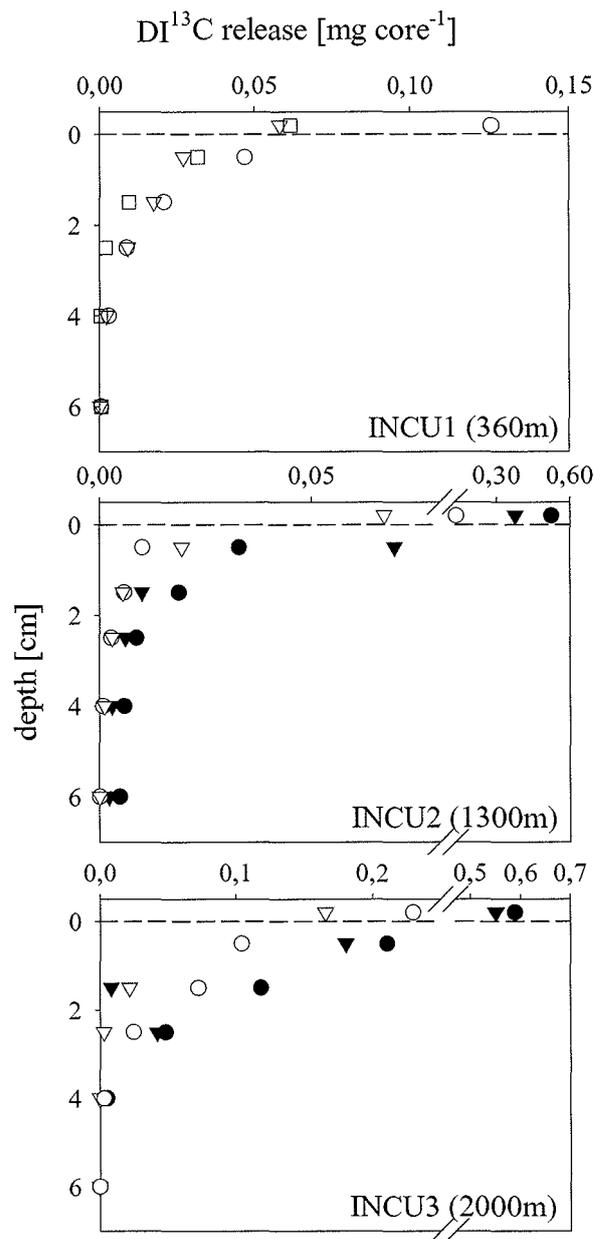


Fig. 2: $DI^{13}C$ concentrations in the pore water at end of the incubations. The dashed line indicates the sediment surface, above the line $DI^{13}C$ concentrations in the bottom water are plotted. Open symbols mark altered and closed symbols mark fresh incubations. Squares, triangles and circles represent the short, medium

the sediment surface, ranging between 0.01 and 0.21 mg ^{13}C core $^{-1}$ (Fig. 2). This could be expected, as most label was available to the sediment biota at the sediment surface (Fig. 4). DI^{13}C usually penetrated the pore water to 3 cm depth (Fig. 2).

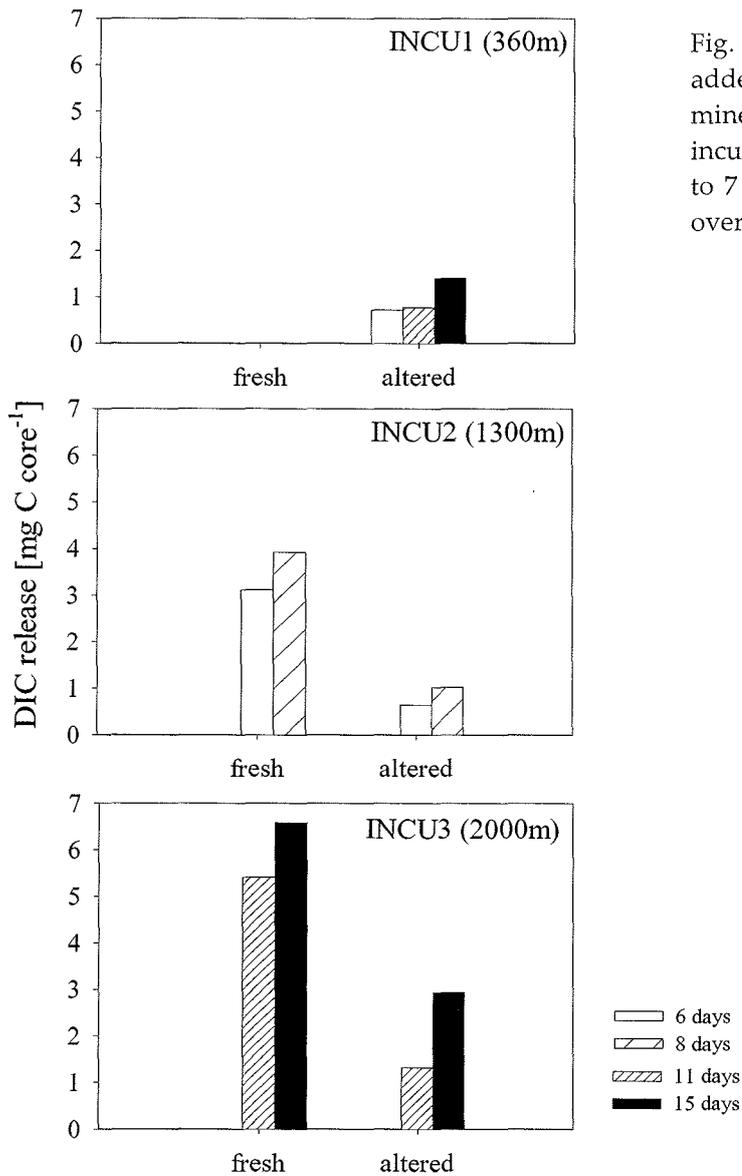


Fig. 3: Total amount of added algal carbon mineralised at the end of the incubation (pore water down to 7 cm sediment depth and overlaying water).

Total organic carbon (TOC) and TO¹³C

TOC concentrations of the investigated sediments are displayed in Table 1.

A similar pattern as for DI¹³C is found in profiles of TO¹³C (Fig. 4). Label penetrates to approximately 2 cm sediment depth. Again, highest concentrations of TO¹³C were measured at the sediment surface, ranging between 0.64 and 4.66 mg ¹³C core⁻¹.

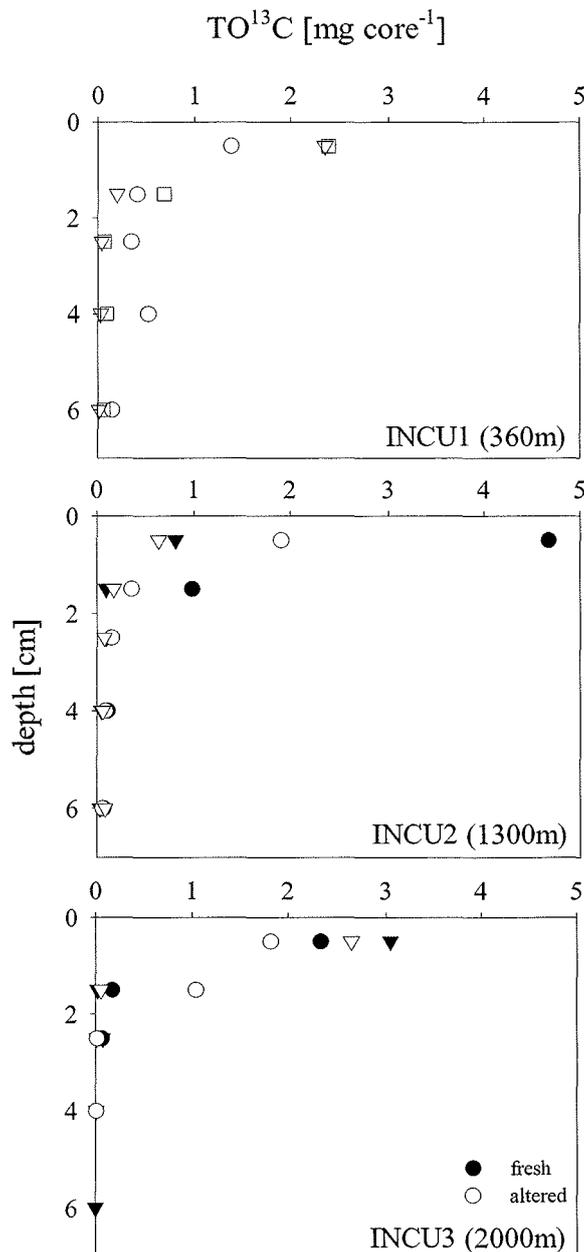


Fig. 4: TO¹³C concentrations in the sediment at the end of the incubations. Open symbols mark altered and closed symbols mark fresh incubations. Squares, triangles and circles represent the short, medium and long incubations, respectively.

Incorporation of ^{13}C into bacteria

The fatty acids *iso(i)C_{15:0}* and *anteiso(ai)C_{15:0}* were selected to examine label incorporation into bacteria, as they were considered to be representative of the entire bacterial community (Boschker and Middelburg 2002; Rütters et al. 2002). Concentration of these PLFAs as measured in an exemplary core for each station ranged from 1.90 to 4.33 $\mu\text{g g}^{-1}$ dry weight (d.w.) for *iC_{15:0}* and from 2.50 to 7.03 $\mu\text{g g}^{-1}$ d.w. for *aiC_{15:0}*. Total bacterial biomass amounted to 1180 $\mu\text{g g}^{-1}$ d.w. for INCU1, 660 $\mu\text{g g}^{-1}$ d.w. for INCU2 and 1610 $\mu\text{g g}^{-1}$ d.w. for INCU3 (Tab. 1), assuming an average of 0.056 g PLFA-carbon g^{-1} biomass (Brinch-Iversen and King 1990) and an average fraction-specific bacterial PLFA in bacteria-dominated sediments (0.19; calculated after Guezennec and Fiala-Medioni 1996; Rajendran et al. 1997). The incorporation of algal carbon ranged from 0.017 mg C core^{-1} (INCUI) to 0.177 mg C core^{-1} (INCUI3) (Fig. 5). Almost no label could be detected in one core (INCUI2, altered, 6 days). The amount of incorporated labelled phytodetritus into PLFAs clearly increased with increasing incubation time (Fig. 5) and was consistently higher in altered than in fresh incubations for all investigated PLFAs.

BSP, BSP-uptake and BGE

BSP in the control cores ranged from 1.93 ± 0.27 to 3.64 ± 0.71 mg C $\text{m}^{-2} \text{d}^{-1}$. The response of BSP to our additions of phytodetritus varied between the different stations. At the shallow station (INCUI1), no effect on BSP could be detected following the addition of altered material. At the other stations, addition of fresh phytodetritus continuously increased BSP with final values reaching up to 5.93 ± 1.64 mg C $\text{m}^{-2} \text{d}^{-1}$ in INCUI2 and 7.16 ± 1.04 mg C $\text{m}^{-2} \text{d}^{-1}$ in INCUI3 (Fig. 6). Addition of altered material resulted in only slight increases in BSP in INCUI2 and INCUI3. At those stations extending beyond 11 days of incubation time, a decrease in BSP was noted in control cores and altered incubations (Fig. 6). Overall, BSP averaged 6.14 ± 0.74 mg C $\text{m}^{-2} \text{d}^{-1}$ in the fresh incubations and 3.42 ± 1.59 mg C $\text{m}^{-2} \text{d}^{-1}$ in the altered ones.

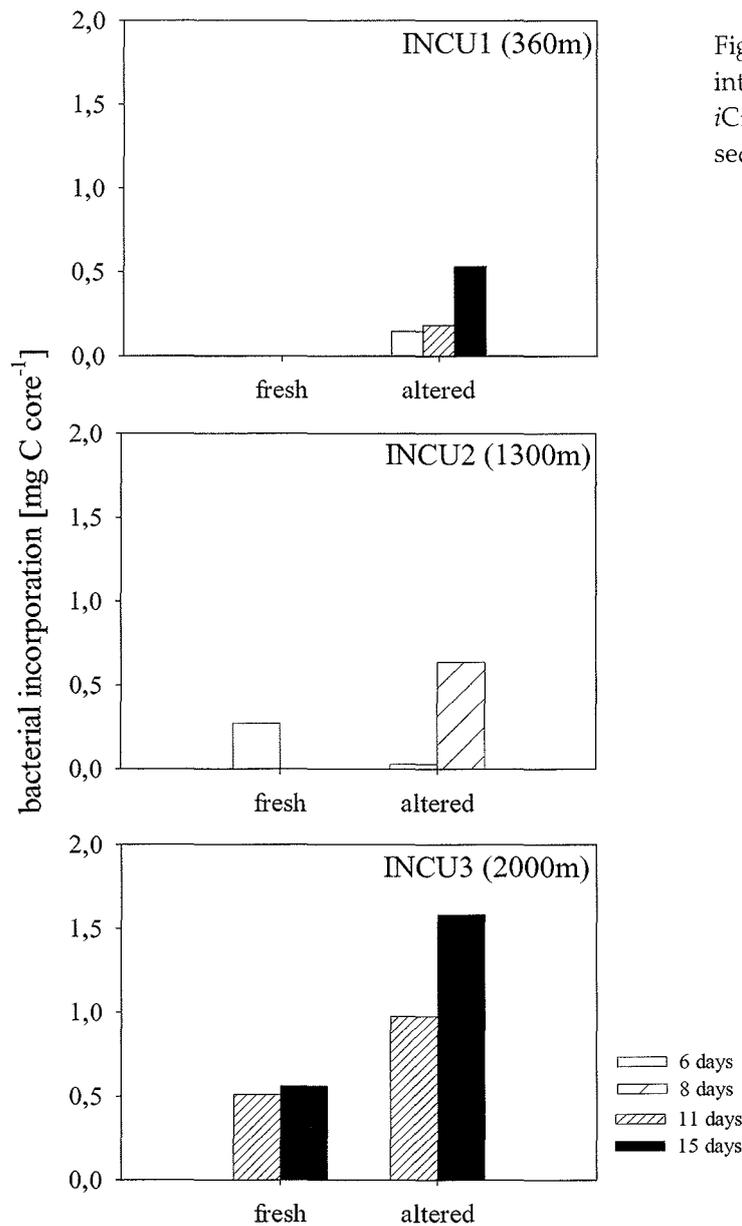


Fig. 5: Incorporation of label into the bacterial fatty acids *i*C_{15:0} and *ai*C_{15:0} at the sediment surface (0-1cm).

BSP-uptake displayed a pattern closely corresponding to that of total mineralisation of labelled material. At all stations, a continuous increase of bacterial carbon uptake was detected. BSP-uptake increased with water depth, reaching a maximum of 95.27 mg C m⁻² (0.75 mg C core⁻¹) after 15 days in the fresh INCU3 (Fig. 7). BSP-uptake was on average 1.4 times higher for the incubations with fresh than for those with altered phytodetritus (Fig. 7).

Average BGE was 0.21±0.13. BGE was uniform over all investigated water depths from 360 to 2000 m, amounting to 0.21±0.06, 0.17±0.19 and 0.23±0.18, respectively. Averaging BGE for each added quality of OM for all stations, fresh

phytodetritus supplied growth efficiencies of 0.08 ± 0.004 . BGE was significantly higher in the altered incubations, amounting to 0.26 ± 0.14 (see Fig. 8).

Discussion

Upwelling systems along the continental margins - such as the Benguela Upwelling System - represent areas of high export production to the sediment, resulting in locally high mineralisation and associated high degradation rates of OM (e.g. Hensen et al. 1998; Jahnke et al. 1990). However, the lack of a correlation between TOC concentration at the sediment surface and microbial parameters in our data shows that the quantity of OM present in the sediments is not the major determinant of benthic microbial activity (see also Chapter 4 of this thesis). Rather, the supply of labile OM primarily controls surface microbial biomass and activity in deep sea surface sediments (e.g. Boetius and Damm 1998; Smith Jr. et al. 1998). Bacterial secondary production in the control cores without organic enrichment was elevated compared to literature data available for deep sea environments (Alongi 1990; Boetius et al. 2000; Dixon and Turley 2001; Kemp 1994; Turley and Dixon 2002). The high secondary production is most probably the result of an intense and relatively continuous supply of labile substrate in this high productivity system. Bacterial growth efficiencies correspond to previous studies, reporting BGE values from 0.01 to 0.69 for marine planktonic bacteria (Del Giorgio and Cole 1998) and from 0.1 to 0.4 for lacustrine benthic bacteria (Bell and Ahlgren 1987; Goedkoop et al. 1997). In a study in sediments of the deep Arabian Sea, Boetius et al. (2000) found growth rates of 0.16 to 0.41. The uniformity of BGE from the upper slope to the deep sea sediments in the Benguela Upwelling System indicates comparable initial conditions for microbial communities and their growth at all investigated stations. Similar behaviour was found in the Middle Atlantic Bight by Kemp (1994), where consistent specific bacterial growth rates - which did not necessarily correlate with BSP - were measured all the way from 40 to 2000 m water depth.

Overall, the microbial community in the Benguela Upwelling System reacted fast to the addition of OM. The elevated BSP after 6 days and the steeply increasing

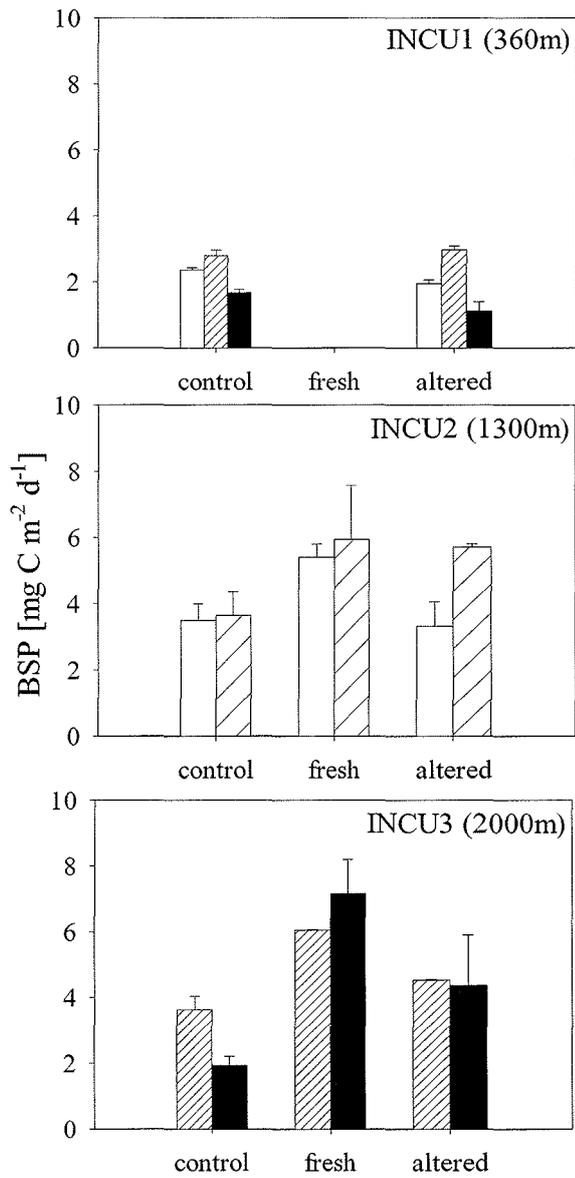


Fig. 6: Bacterial Secondary Production (average \pm s.d.) at the sediment surface (0-1cm) at the end of the incubation.

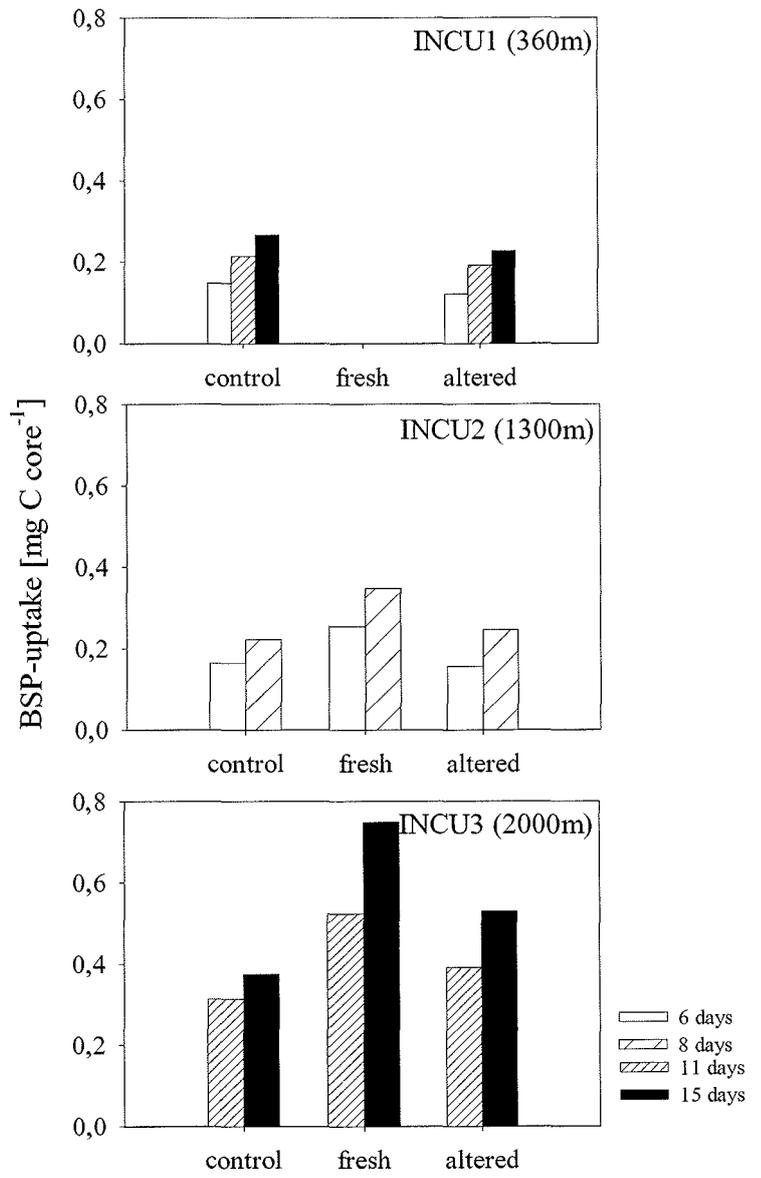


Fig. 7: Total amount of carbon taken up by bacteria at the sediment surface (0-1cm) at the end of the incubation.

amount of mineralised labelled material in the first 100 hours of incubation clearly show an instantaneous benthic microbial response. The decline in mineralisation and in some cases also BSP after approximately two weeks of incubation could be caused by depletion or transformation of the present OM or by increased grazing pressure towards the end of the incubation. Yet, reports on a retarded response of meiofauna to inputs of OM (e.g. Witte et al. 2003b) and a rare presence of macrofauna in our incubations makes a significant involvement of other groups of organisms than bacteria unlikely. Consistent results of fast benthic processing of phytodetritus have also been reported from *in situ* experiments in the Benguela Upwelling system in Chapter 2 of this thesis, showing a benthic response to an input of labelled phytodetritus within 6 hours and bacterial incorporation within 1.5 days after the addition. Also in an investigation on the Norwegian continental shelf, bacteria reacted to a pulse of OM within 36 hours (Witte et al. 2003a). At the Porcupine Abyssal Plain in the Northeast Atlantic, however, a delay of 8 days in response of the microbial and the foraminiferal community was observed by Witte et al. (2003b). The differences between the cited studies could be caused by the different adaptation of the bacterial community to varying availability of food at the study sites. Differences in benthic carbon processing between slope and deep sea sites have previously been reported from *in situ* experiments, as described in Chapter 2 of this thesis. The generally high supply of food to the community in the Benguela sediments, causing a high activity already at the onset of the experiment, could explain its fast reaction.

Impact of OM quality

The varying qualities of OM added in our experiments resulted in clearly different benthic carbon processing patterns: Total mineralisation of labelled phytodetritus was distinctly higher in fresh than in altered incubations (Fig. 3). Accordingly, BSP increased within a few days after the OM addition (Fig. 6). The reaction of benthic mineralisation to the addition of fresh phytodetritus was very fast (Fig. 1) and most probably resulted from assimilation of the LMW compounds smaller than 1000 Dalton. This LMW compounds increased total bacterial activity, emphasising the high bioavailability of the fresh material. The major part of the LMW material was respired within the first approximately 100 hours of the

incubation and only a minor fraction was incorporated (Fig. 5). In contrast, altered phytodetritus was preferentially incorporated into bacterial biomass (Fig. 5), while its mineralisation remained much lower with less dramatic rates (Fig. 1). That resulted in a BGE that was on average more than 3 times higher in altered than in fresh incubations. According to Del Giorgio and Cole (1998), two mechanisms can control BGE: the supply rate of OM and the nature of the available OM. Evidence from lab experiments indicates that if the supply of OM is low, it will be used for maintenance energy requirements of the cell rather than for growth, resulting in low BGE (Harder 1997; Russell and Cook 1979). Since the amount of added OM was even higher in altered than in fresh incubations, this is unlikely to cause the high BGE in altered incubations. Generally, in a high productivity region such as the Benguela Upwelling System with overall high input of OM to the sediments, it is very probable that OM quantity is not a limiting factor. Under a large supply of organic substrates, the relative nutritious content of the OM and its availability to the bacteria determine the degree of incorporation.

From these results, no straight-forward conclusions can be drawn on which of the added materials is of a generally higher reactivity for the benthic community. To resolve this question, a detailed look at the timing of the benthic reaction in combination with the time scales covered in this study is required.

Timing of the benthic reaction

Both added qualities of OM trigger an immediate benthic response (Fig. 1), but the pathways of this response through the benthic community seem to vary. While fresh phytodetritus is mineralised to a higher degree and induces increased rates of BSP (Fig. 3, Fig. 6), altered material becomes preferably incorporated into bacterial fatty acids and results in elevated BGE (Fig. 5, Fig. 8). On closer examination, it is not so much the pathways of the benthic reaction but rather its timing that varies between the different experimental treatments. This different timing is most probably the result of different points of departure, as the addition of the two qualities of OM sets up unequal initial situations. A schematic representation of the processes driving the benthic reaction is given in Figure 9. Addition of fresh

phytodetritus supplied the benthic community with algal material that had not been subjected to any further treatment than freeze-drying. Altered phytodetritus, on the other hand, had been soaked in seawater for dialysis for several hours, where it was subjected to removal of the size fraction smaller than 1000 Dalton, and presumably also to further degradation and break-up of some of its compounds. The fresh material comprised the LMW fraction, but its higher molecular weight compounds still required this initial break-up when it was supplied to the sediment community. As becomes obvious from the mineralisation data (Fig. 1), the usage of the LMW fraction in the fresh phytodetritus takes place fast and instantaneously. After only 100 hours, this highly available fraction appears to be used up, as mineralisation rates strongly decrease. Once those LMW compounds have been assimilated, the bacteria most probably start to depolymerise the larger compounds of the added OM. There is some experimental evidence that BGE correlates negatively to exoenzyme activity (Middelboe and Sondergaard 1993). The demand for exoenzymes after exhaustion of the LMW compounds together with their low incorporation resulted in decreased BGE in the fresh incubations. Altered incubations were supplied with pre-broken compounds, which were more readily available for incorporation and therefore supported high BGE. However, this effect of an early start does not necessarily indicate a better bioavailability of the altered material. Overall, the fresh phytodetritus appears to be of a higher nutritional value for the microbial community than the altered material, as indicated by an elevated BSP (Fig. 6). Other than BGE, BSP depicts not only the reaction to the added material – with its associated time-effect – but includes the production on OM already present in the sediment independent of the addition. It thereby presents a measure of the enhancement of total benthic activity following the addition of OM. This enhancement is clearly higher in fresh than altered incubations. In spite of a high incorporation of altered phytodetritus, benthic mineralisation as well as bacterial production can not be raised to the same degree as with fresh phytodetritus. Therefore, even though data on bacterial incorporation and growth efficiency suggest differently, the short- and medium-term reactivity of fresh material is higher than that of altered material.

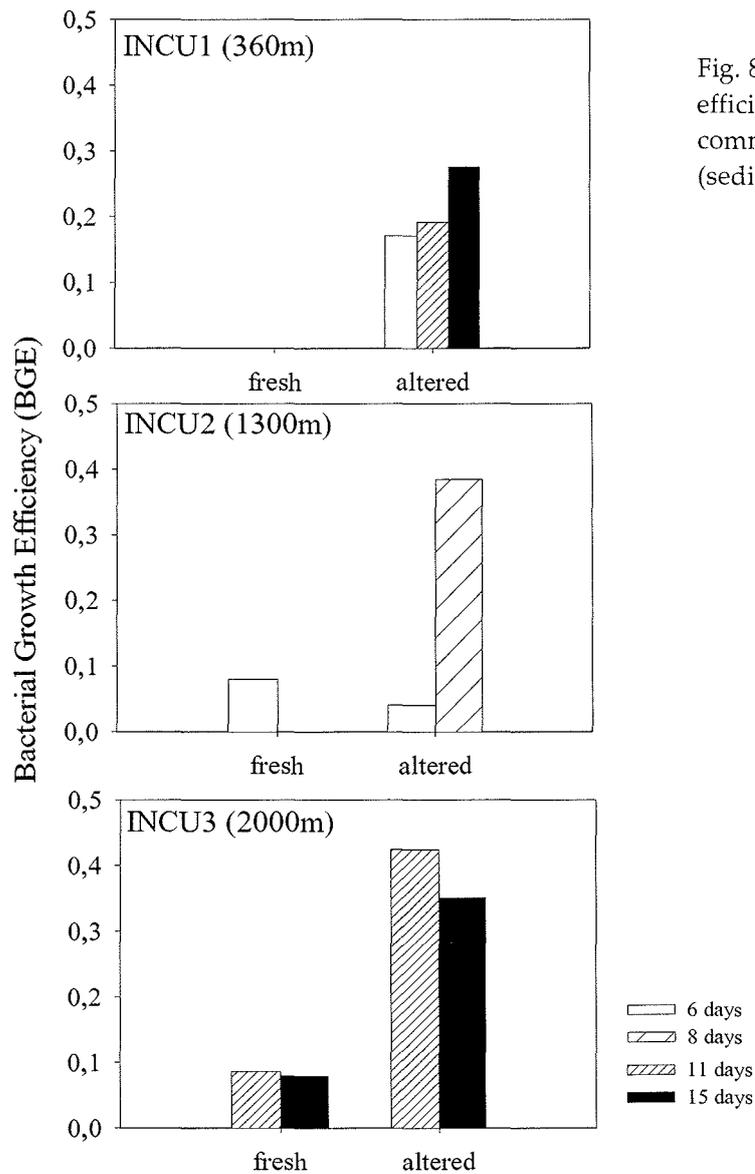


Fig. 8: Bacterial growth efficiency of the bacterial community on algal carbon (sediment depth 0-1cm).

Methodological considerations

Our experimental systems removed the sediment with its organisms from the sea floor and simulated *in situ* conditions only in terms of temperature but not of pressure. Core recovery has been shown to affect rates of BGE (Turley and Lochte 1990) and benthic activity due to e.g. disturbance, decompression, or transient heating (Glud et al. 1994; Wenzhöfer and Glud 2002). Therefore, the rates presented

here should always be regarded as potential rates and do not necessarily represent *in situ* benthic activity. Nevertheless, the fact that the benthic community in our experiments was not entirely uncoupled from their natural sources of OM and their natural environment results in a high ecological relevance of our results.

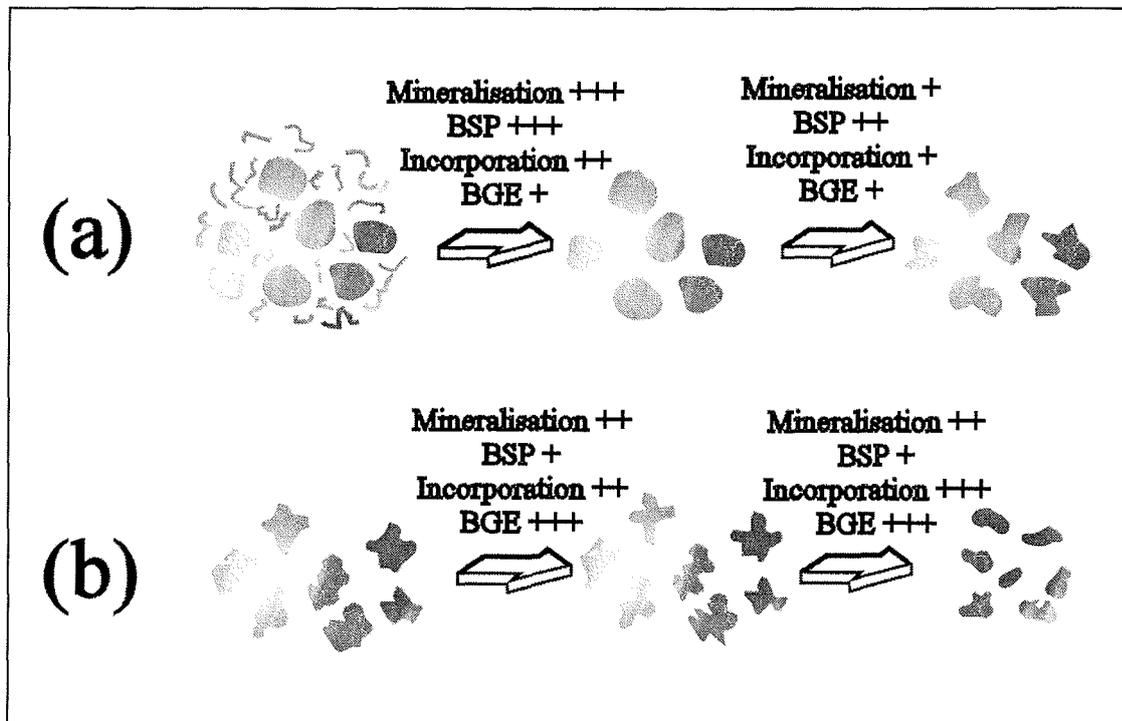


Fig. 9: (a) Fresh phytodetritus comprising LMW compounds (< 1000 Dalton) initially leads to a high mineralisation and BSP. Bacterial incorporation into fatty acids and BGE are not increased to the same degree. Once the LMW fraction is used up, mineralisation and BSP level off, while incorporation and BGE stay low. (b) Altered phytodetritus lacks the LMW fraction and the corresponding fast increase in mineralisation and BSP. Instead, the 'pre-soaked' material is rapidly incorporated into bacterial fatty acids and leads to a high BGE. Continuous degradation of the altered material results in relatively constant rates of phytodetritus processing.

Measurements of BSP in combination with respiration rates, the latter not relying on biochemical conversion factors and being less sensitive to sediment characteristics (Bastviken et al. 2003), has widely been used to calculate BGE that provides a direct measure of microbial substrate utilisation. Studies on the bacterial utilisation of specific organic substrates, such as glucose or cellulose (e.g. Boetius and

Lochte 1996), revealing fundamental but isolated details, do not provide much information on the ecosystem level, as individual compounds may be incorporated with very different efficiencies. Calculating BGE from mineralisation and incorporation of a ^{13}C -labelled complex substrate (i.e. phytodetritus) and in a natural assemblage, as done in this study, presents a specific, yet integrated measure of the efficiency of utilisation of a mixture of organic compounds as it has to our knowledge not been applied before.

The results gained from the measurement of BSP and BGE in this study point out the importance of integrated investigations of a variety of independent parameters when studying benthic carbon turnover. OM quality can exert very diverse influence on different cell components and their synthesis, in this case the biosynthesis of lipids (incorporation into fatty acids) opposed to proteins (BSP). Moreover, BSP and BGE access different pools of OM in our experiments: While BSP bases upon the entirety of present OM, BGE is calculated solely for processing of added phytodetritus. After addition to an active microbial community, the altered phytodetritus becomes incorporated faster, however it does not increase total rates of benthic activity as much as the fresh phytodetritus. Apparently, the incorporation of the added phytodetritus is determined by the setup of the experiment rather than the overall reactivity of the OM, while the rates and total amounts of mineralisation and BSP are indeed driven by the quality of OM. The potential of this study lies in the simultaneous surveying of both bulk activity and experimental labelling parameters, allowing for much deeper insights into the benthic microbial carbon cycle than the application of single approaches.

Conclusions

In our medium-term experiments in the Benguela Upwelling System, added fresh phytodetritus was mineralised more rapidly and increased benthic microbial activity to a higher degree than the addition of altered phytodetritus. Altered phytodetritus was preferentially incorporated by the microbial community, however it did not enhance bacterial productivity as much as fresh phytodetritus. Higher

growth efficiencies measured on altered phytodetritus were caused by a timing effect rather than better utilisation. The effects of timing and the different pathways of benthic carbon processing are very complex and detailed conclusions were only possible due to the application of a variety of independent parameters: combining pulse chase labelling experiments with measurements of BSP and calculation of BGE on an added complex substrate - as they have not been presented to date.

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Chapter 4

Organic matter reactivity driving diffusive benthic fluxes in the Benguela Upwelling System

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Abstract

Diffusive benthic fluxes of phosphate, nitrate and ammonium were calculated from pore water concentration profiles and related to the quantity and quality of deposited organic matter (OM) in sediments of the Benguela Upwelling System at water depths from 400 to 2500 m. The cross-slope distribution of the investigated fluxes revealed rates that increase with water depth to a depth of approximately 600 m and subsequently decrease again towards the deep sea, indicating the presence of a major depocentre of OM at the upper continental slope. Benthic flux rates are independent of water depth and sediment OM concentration, but they are closely coupled to the parameters of OM quality included in this study (e.g. total hydrolysable amino acids, labile hydrocarbons). An enhanced proportion of labile compounds in the sedimentary OM usually coincided with high benthic flux rates of nitrate and ammonium. Phosphate profiles were decoupled from this connection due to interactions with the benthic iron cycle. Oxidative respiration contributes up to 88 % of the total OM oxidation, with sulphate reduction being the second most important. Corresponding to the changes in OM quality, the contribution of oxidative respiration to total OM degradation reaches its maximum slightly below the shelf break and subsequently decreases downslope. Oxygen exposure times of the sediment, varying between 11 and 17 years, are not connected to benthic flux rates, indicating that the reactive fraction steering these rates is decomposed at time-scales well below the oxygen exposure times. The reactivity of OM is shown to be a major driving force behind benthic flux rates in the Benguela Upwelling System, clearly outrunning OM quantity.

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Introduction

The mineralisation and burial of organic matter (OM) in the ocean is decisive for the role of the world's oceans as a source or sink in the global cycles of bioactive elements, above all carbon. Up to 99 % of the OM produced in surface waters is regenerated in the upper water column (e.g. Bishop et al. 1977; De Baar and Suess 1993). The long-term fate of settling OM is determined by processes within the benthic boundary layer, and more than 90 % of the organic carbon in deposited OM may be recycled in surficial sediments (e.g. Berelson et al. 1987; Martin et al. 1991; Müller and Suess 1979). The remainder becomes buried and fixed in the sediment – and thereby removed from the present carbon cycle – on geological time scales. Processes at the benthic boundary layer might therefore ultimately affect atmospheric CO₂-concentrations.

Benthic mineralisation depends significantly on the concentration of oxidants in the bottom and pore water. The major part of sedimentary OM is degraded with oxygen as electron acceptor (Canfield 1989, 1993), amounting to more than 90 % in deep sea sediments due to the mostly oligotrophic conditions and low OM rain rate (Canfield 1989; Middelburg et al. 1993). In some sediments, however, sulphate may be just as or even more important than oxygen. This is the case e.g. in coastal sediments or in sediments under oxygen depleted conditions (e.g. when the oxygen minimum zone impinges on a continental margin).

Benthic microbial activity (and thereby benthic mineralisation) has long been thought to be mainly dependent on the amount of existing OM as well as the supply of material from surface waters, following a function of water depth (Hargrave 1984; Suess 1980). However, imbalances between the flux of OM to the sediment and corresponding benthic carbon oxidation rates have evoked discussion on the superposing mechanisms determining benthic activity (Jahnke et al. 1990; Rowe et al. 1994; Smith Jr. 1987; Walsh 1991). Obviously, a simple water depth-relation is often unrealistic, particularly in areas adjacent to continental margins (Cai and Reimers 1995; Seiter et al. 2005). Regionally, intense water circulation and strong bottom water currents can cause considerable lateral transport of suspended matter, especially across the shelf breaks and down the slopes (Hensen et al. 2000; Jahnke et

al. 1990; Mollenhauer et al. 2002; Rowe et al. 1994). These alternative transport pathways not only impact the quantity of OM arriving at the sea floor, they also have a significant impact on its composition, as they deliver OM from very different and variable sources, with probably complex preceding degradational histories.

In the Benguela Upwelling System, Inthorn et al. (in prep.) describe the importance of lateral transport processes in the supply of OM to the sediment: Benthic nepheloid layers close to the seafloor as well as intermediate nepheloid layers in the water column can transport high loads of OM to regions far off their original production (Inthorn et al. in prep.; Jahnke 1990; McCave et al. 2001), influencing the local sediment OM signal both in terms of quantity and quality. Moreover, Mollenhauer et al. (2003) points out that the aging of particles transported within these nepheloid layers is decoupled from aging during vertical transport and laterally transported particles can therefore distinctly alter the age-signature of a certain sediment body. A major part of the OM transported in the nepheloid layers in the Benguela Upwelling System is thought to be deposited at a major depocentre situated between 600 and 1500 m water depth at approximately 25.5° S (Inthorn et al. in prep.). However, to date there is little knowledge concerning origin and composition of the OM in this depocentre.

Even though the composition of OM is widely recognised to affect the rate and extent of its mineralisation (Westrich and Berner 1984), the specific features which define quality remain elusive. Moreover, compositional characteristics of OM have rarely been linked to its biological availability or its degradation dynamics, and direct flux measurements - indicating specific degradational processes - are complex to obtain and are therefore not available for many regions. In this study, we investigate the influence of quantity as well as quality of OM on benthic mineralisation and the corresponding benthic fluxes of phosphate, nitrate and ammonium. While the quantity is recorded by the total amount of organic carbon in surface sediments, information on the concentrations of chlorins and THAAs together with their accompanying indices of OM degradation (Ahke et al. in prep.) and results from Rock-Eval pyrolysis (Inthorn et al. in prep.) are used as indicators of the quality of OM. Additionally, the importance of different pathways of carbon oxidation (oxic respiration, sulphate reduction, denitrification and iron oxidation) for

total carbon turnover is evaluated. Radiocarbon ages of sediments from selected stations were used to calculate sedimentation rates and oxygen exposure time.

Material and Methods

Study area and oceanographic setting

The Benguela Upwelling System is one of the four major coastal upwelling systems on earth, extending from southern Angola along the west coast of Namibia and South Africa. Several distinct upwelling cells build up its latitudinal extension, with the strongest one being the Lüderitz cell situated near Lüderitz in southern Namibia (Giraudeau et al. 2000; Lutjeharms and Meeuwis 1987). Productivity measured along the Lüderitz and Walvis coasts is reported to reach up to $350 \text{ g C m}^{-2} \text{ a}^{-1}$ (Behrenfeld and Falkowski 1997). Due to varying mixing intensities following varying seasonality and to bottom water currents, the upwelling cells of the surface waters do not necessarily reproduce in the sediment. In sediments underlying the Lüderitz cell, for example, rates of OM accumulation as well as rates of benthic activity are comparably low (Brüchert et al. *subm.*).

The transition from the shelf to the continental slope off the Namibian coast is characterised by a main shelf break at 360 to 400 m water depth, and a second, minor shelf break at about 180 m water depth (Inthorn et al. *in prep.*). A map of the organic carbon content of surface sediments of the Benguela Upwelling System from coastal waters down towards the continental rise at 4000 m depth recently compiled by Inthorn et al. (*in prep.*) (Fig. 1) reveals a very heterogeneous distribution pattern of total organic carbon (TOC). A prominent depocentre of organic carbon is situated on the upper continental slope from 24° S to 26.5° S in water depths of 600 to 1500 m. Within this depocentre, TOC-contents reach up to 9 %.

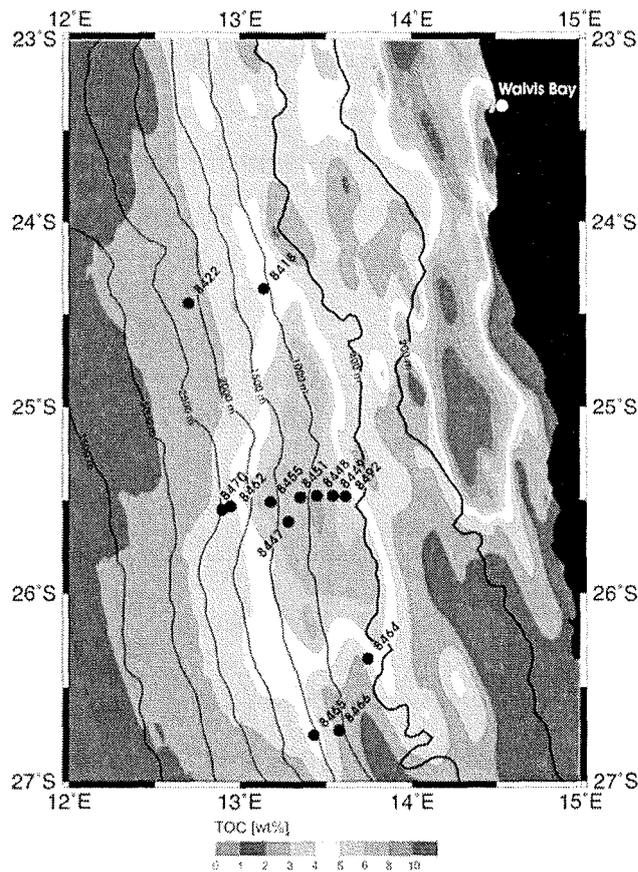


Figure 1: Study area and locations of the investigated GeoB-stations. Underlying a map of the surface sediment TOC-contents (Inthorn et al. in prep.). For further information on the sampled stations see Table 1.

Sampling

Samples were retrieved on FS METEOR cruise M57/2 in February/March 2003 along three major transects from below the major shelf break across the continental slope at approximately 24.5° S (Transect 1; T1), 25.5° S (Transect 2; T2) and 26.7° S (Transect 3; T3). These transects cover the area of the most intense upwelling in the Benguela System (Fig 1). Details on the sampled stations are given in Table 1. Sediment was sampled using a multicorer (diameter ~10 cm) with a usually very low disturbance of the sediment–water interface. Recovered cores were immediately

transferred to a refrigerated on-board laboratory (4 °C) to avoid warming on deck and were processed within a few hours. After careful siphoning of the bottom water the samples were processed within a glove box under argon atmosphere. Pore water was extracted using teflon squeezers for pressure filtration with 0.2 µm cellulose acetate membrane filters. The squeezers were operated with argon at a pressure that was gradually increased to a maximum of 5 bar.

Table 1: Geographical position and TOC content of the surface sediment (0-1 cm) at the investigated stations and the corresponding bottom water oxygen concentrations.

Station #	Lat. [°S]	Long. [°E]	Transect	Depth [m]	TOC [%]	O ₂ [µM]
GeoB 8418	24.36	13.14	T1	1005	4.88	164.84
GeoB 8422	24.46	12.72	T1	2000	1.83	216.67
GeoB 8492	25.47	13.61	T2	500	4.68	181.30
GeoB 8449	25.48	13.55	T2	600	7.05	144.82
GeoB 8448	25.48	13.45	T2	800	3.91	160.43
GeoB 8451	25.48	13.36	T2	1040	7.87	167.34
GeoB 8447	25.61	13.28	T2	1300	8.11	194.86
GeoB 8455	25.51	13.19	T2	1500	7.35	220.95
GeoB 8462	25.54	12.95	T2	2300	3.65	108.16
GeoB 8470	25.55	12.86	T2	2500	3.10	187.41
GeoB 8464	26.34	13.73	T3	429	2.95	168.50
GeoB 8466	26.72	13.64	T3	935	2.79	227.95
GeoB 8465	26.75	13.43	T3	1320	4.27	108.47

Analytical methods

Pore water analysis was carried out on board the ship. Ammonium was measured applying the flow injection technique described by Hall and Aller (1992). Nitrate and phosphate concentrations were analysed photometrically using a continuous flow system. Dissolved iron (Fe²⁺) was also determined photometrically. Details on the applied methods can be found at <http://www.geochemie.uni-bremen.de/koelling/onboard.html>.

Estimation of diffusive fluxes

Assuming steady state conditions, Fick's first law of diffusion was applied to calculate the diffusive flux rates of phosphate, nitrate, ammonium and ferrous iron (Boudreau 1997; Schulz and Zabel 2000). Diffusion coefficients were recalculated for *in situ* temperatures (3-8 °C) after Li and Gregory (1974) and Lerman (1979). Porosity was assumed to be 0.9 in all investigated cores. With this approach, factors that can influence solute transport such as bioirrigation (e.g. Glud et al. 1994; Kamp-Nielsen et al. 1982; Liere and Mur 1982), decompression, or warming effects associated with core recovery (e.g. Jahnke et al. 1982) were neglected.

Total Oxygen Uptake

Total oxygen uptake (TOU) of the sediment was determined using benthic chambers that were deployed over a period of 18 to 36 hours (for details on the chambers see Witte and Pfannkuche 2000). Oxygen concentrations were determined by Winkler titration. TOU was calculated from the decrease in oxygen concentration over time.

Sulphate Reduction Rates

Sulphate reduction rates (SRR) were determined using the whole-core $^{35}\text{SO}_4^{2-}$ method (Jørgensen 1978). For that purpose, sub-cores (inner diameter 26 mm) of the multicores were injected with 5 μL radiolabelled sulphate (Amersham, approximately 200 Bq per injection) via silicon-filled ports spaced at 1 cm intervals along the tube. Incubation took place in the dark at *in situ* temperature. After an incubation period of 8-12 hours, the samples were sliced in 1-2 cm intervals into an equal volume of 20 % (w/v) zinc acetate solution and kept frozen until further analysis in the home lab. ^{35}S -incorporation into total reducible inorganic sulphur

(TRIS) was determined using the one-step acidic Cr-II method (Kallmeyer et al. 2004). Samples were counted in a liquid scintillation counter (Packard Tri-Carb 2500TR) using Ultima Gold™ XR (Packard Bioscience) as the scintillation mixture. An average sulphate concentration of 25.2 mmol L⁻¹ was used for the calculations. The presented rates are areal SRR integrated to a sediment depth of 15 cm.

Results

Pore water profiles and diffusive benthic fluxes

Selected representative pore water profiles are depicted in Figure 2. Iron and phosphate profiles usually show a rapid downward increase of pore water concentrations from the sediment surface, whereas ammonium is completely depleted above 1.5 cm sediment depth. Distinct subsurface peaks of phosphate and iron concentrations show maxima between 1.75 and 4.5 cm sediment depth. Down to a water depth of approximately 1300 m, nitrate concentrations in the pore water are always lower than in the bottom water, which indicates that nitrification already takes place in the overlying water. Thus we only regard nitrate consumption (denitrification) for flux calculations. However, at greater water depths, maximum concentrations are usually measured in the uppermost 0.5 cm interval and nitrate is usually completely depleted below 3-5 cm sediment depth.

Diffusive benthic fluxes for the investigated parameters are given in Table 2 and Figure 3. For nitrate and phosphate, maximal flux rates are found at T2 (~25.5° S). Regarding cross-slope transects, highest fluxes were usually measured between 600 m and 1000 m water depth (Fig. 3a-c). At stations shallower than 600 m, fluxes of nitrate, phosphate and ammonium were lower than between 600 and 1000 m. Also below 1000 m benthic fluxes generally decrease towards greater water depths.

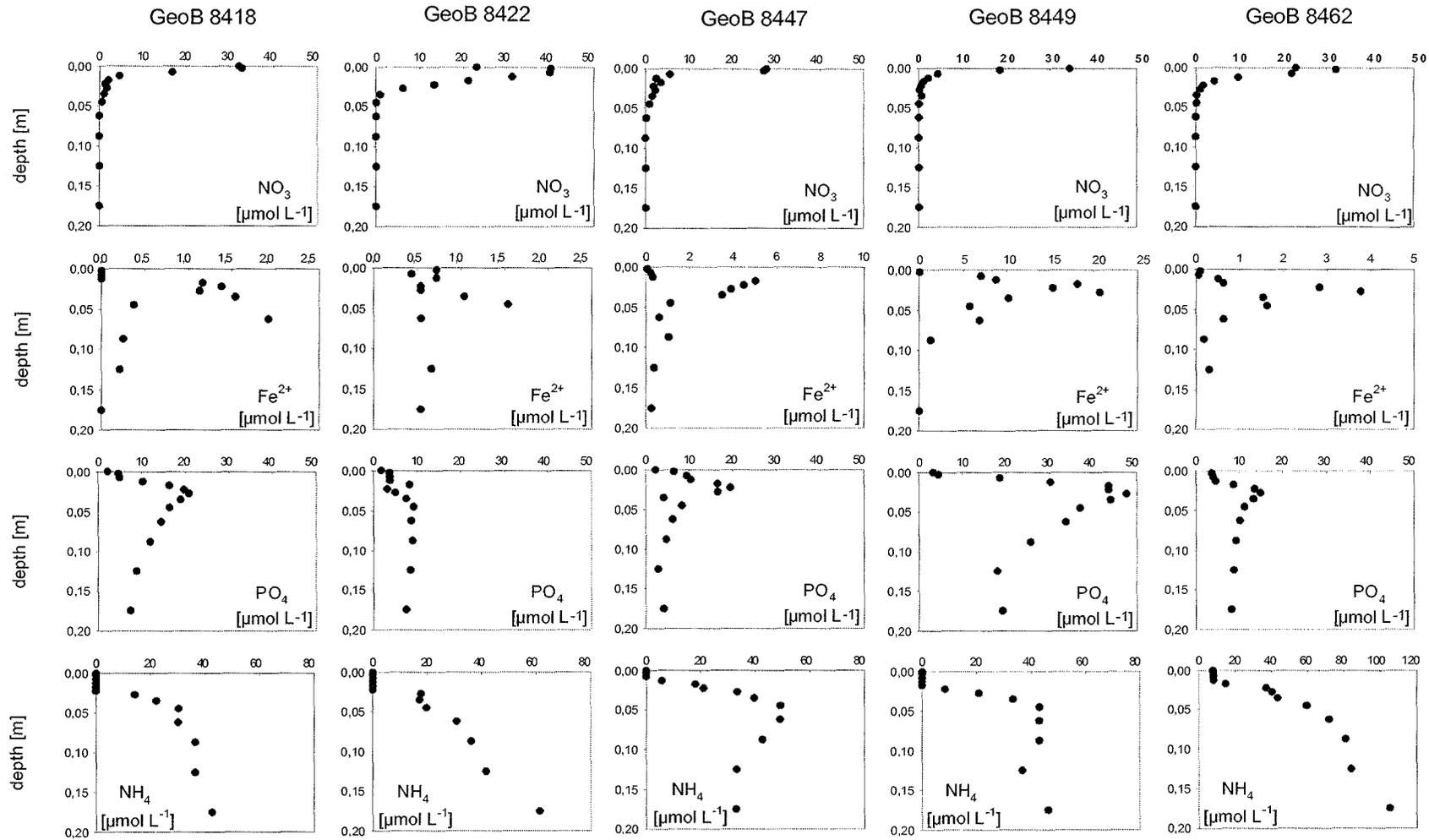


Figure 2: Selected pore water profiles (GeoB 8418, 8422, 8447, 8449, 8462) of nitrate, ferrous iron, phosphate and ammonium.

Table 2: Diffusive benthic flux rates of nitrate, phosphate, ammonium and ferrous iron across the sediment-water interface and rates of total oxygen uptake (TOU) and sulphate reduction (SRR).

Station #	Transect	$J(\text{NO}_3)$ [mmol m ⁻² a ⁻¹]	$J(\text{PO}_4)$ [mmol m ⁻² a ⁻¹]	$J(\text{NH}_4)$ [mmol m ⁻² a ⁻¹]	$J(\text{Fe}^{2+})$ [mmol m ⁻² a ⁻¹]	TOU [mmol m ⁻² a ⁻¹]	SRR [mmol m ⁻² a ⁻¹]
GeoB 8418	T1	70.83	9.08	69.73	0.97	3070*	208
GeoB 8422	T1	46.83	6.57	101.35	0.91	1726*	73
GeoB 8492	T2	175.46	6.01	55.62	5.07		307
GeoB 8449	T2	183.17	4.57	74.16	16.62	5990*	544
GeoB 8448	T2	207.94	16.16	74.71	3.42		
GeoB 8451	T2	99.55	4.61	64.36	0.82		
GeoB 8447	T2	102.76	15.12	68.65	9.83	1453	318
GeoB 8455	T2	125.88	3.29	49.03	0.67		
GeoB 8462	T2	55.03	6.27	42.82	3.90	416*	88
GeoB 8470	T2	41.47	2.53	22.52	0.85		
GeoB 8464	T3	172.07	6.59	45.40	4.21		
GeoB 8466	T3	125.2	9.08	130.75	3.49		
GeoB 8465	T3	57.22	6.77	31.68	0.37		

*From Aspetsberger et al. (subm.)

Total Oxygen Uptake and Sulphate Reduction Rates

Total oxygen uptake (TOU) continuously decreases with increasing water depth at both investigated transects (T1 and T2) and varies between $1.14 \text{ mmol m}^{-2} \text{ d}^{-1}$ (at 2300 m) and $16.41 \text{ mmol m}^{-2} \text{ d}^{-1}$ (at 600 m) (Tab. 2, taken from Chapter 2 of this thesis).

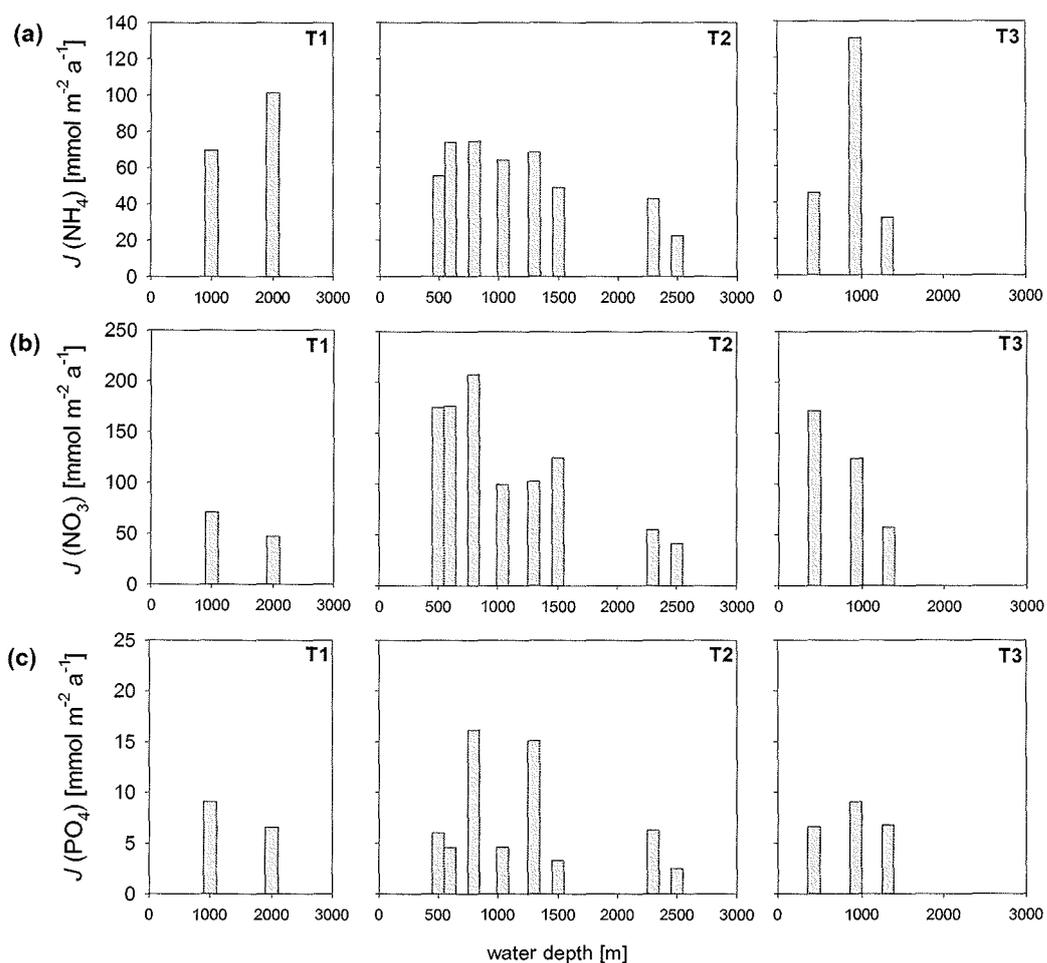


Figure 3: Cross-slope transects of benthic nutrient fluxes of (a) ammonium, (b) nitrate (denitrification only) and (c) phosphate across the sediment-water interface calculated following Fick's first law of diffusion.

The same trend is visible for the sulphate reduction rates (SRR), which decrease from 0.57 to $0.20 \text{ mmol m}^{-2} \text{ d}^{-1}$ at T1 and from 1.49 to $0.24 \text{ mmol m}^{-2} \text{ d}^{-1}$ at T2.

At the latter transect we additionally measured sulphate reduction (SR) at a shallower station at 500 m ($0.84 \text{ mmol m}^{-2} \text{ d}^{-1}$) that revealed that rates decrease at this depth compared to the 600 m-station (Tab. 2).

Carbon oxidation

From stoichiometric relationships, carbon oxidation equivalents can be calculated for TOU as well as SR and denitrification, with conversion factors amounting to 1, 2, and 1.12 equivalents of carbon per unit substrate, respectively. With these conversion factors, total sediment carbon oxidation rates have been calculated for stations GeoB 8418, 8422, 8447, 8449 and 8462 (Tab. 3, Fig. 4). These rates reveal a clear maximum of total carbon oxidation at the shallowest station (GeoB 8449: $19.93 \text{ mmol C m}^{-2} \text{ d}^{-1}$). Subsequently, total carbon oxidation gradually decreases towards greater depths, reaching minimal rates of $1.79 \text{ mmol C m}^{-2} \text{ d}^{-1}$ at station GeoB 8462 (Fig. 4).

Table 3: Total carbon oxidation rates and single oxidation rates for the single degradational pathways (oxic respiration, sulphate reduction, denitrification) and rates of iron reduction (note the different unit).

Station #	Total [$\text{mol C m}^{-2} \text{ a}^{-1}$]	from oxic resp. [$\text{mol C m}^{-2} \text{ a}^{-1}$]	from SR [$\text{mol C m}^{-2} \text{ a}^{-1}$]	from denitrif. [$\text{mol C m}^{-2} \text{ a}^{-1}$]	Iron reduction [$\text{mmol m}^{-2} \text{ a}^{-1}$]
GeoB 8418	3.57	3.07	0.42	0.08	0.35
GeoB 8422	1.92	1.73	0.15	0.05	0.40
GeoB 8449	7.28	5.99	1.09	0.20	8.20
GeoB 8447	2.20	1.45	0.64	0.12	8.54
GeoB 8462	0.65	0.42	0.18	0.06	2.81

Sedimentation Rates and Oxygen Exposure Time

At selected stations (GeoB 8418, 8422, 8451, 8462), radiocarbon ($^{14}\text{C}_{\text{org}}$)-ages of sediment (M. Inthorn, pers. comm.) were used to calculate sedimentation rates

between the surface and sediment at 15-20 cm depth, which lie between 14.58 and 39.09 cm kyr⁻¹ (Tab. 4). Total organic carbon burial amounts to 358.7 (GeoB 8418), 193.9 (GeoB 8422) and 67.7 (GeoB 8462) $\mu\text{mol cm}^{-2} \text{a}^{-1}$, calculated after Hartnett et al. (1998) as the sum of organic carbon burial as estimated from sedimentation rates and carbon oxidation (see above). No such calculation was possible for GeoB 8451, as no data were available on the carbon oxidation rates.

To estimate the oxygen exposure time (OET) without pore water oxygen profiles, nitrate concentrations were used. With the assumption that the maximum in nitrate concentration indicates oxygen penetration depth, we calculated OET using sedimentation rates. OET amounts to 17.2, 11.9 and 11.5 years for GeoB 8418, 8422 and 8462, respectively (Tab. 4).

Table 4: Sedimentation rates and oxygen exposure times (OETs) calculated from radiocarbon ages (M. Inthorn, pers. comm.).

Station #	Sedimentation Rate [cm ka ⁻¹]	OET [a]
GeoB 8418	14.58	17.2
GeoB 8422	20.98	11.9
GeoB 8451	39.09	6.4
GeoB 8462	21.77	11.5

Discussion

The various pathways of OM degradation, such as oxic respiration, denitrification, sulphate reduction and iron reduction, all rely on one major prerequisite – the presence of OM in the form of $n(\text{CH}_2\text{O})$, which can be oxidised to gain the free energy contained in the reaction. The complexity of different control mechanisms acting upon benthic flux rates often hampers definite conclusions about

the forces driving these rates. The amount of OM available for benthic degradation might be a decisive factor, yet that is only true if the OM is also utilisable for the benthic decomposers, i.e. if the quality of the present OM makes it susceptible to benthic degradation. OM quality can moreover be directly related to OM reactivity. While quality indicates a given chemical composition, reactivity is strongly dependent on the investigated time-scale and the reactant or organism interacting with the OM (e.g. microorganisms as decomposers of OM). Criteria characterising OM reactivity are yet hard to define. Nevertheless, the multitude of parameters describing OM quality, which have been evaluated in the context of this study, allow some inferences about the importance of the quantity of OM versus its quality in our study area.

Pore water profiles and diffusive benthic fluxes

The measured benthic flux rates correspond well with rates from previous investigations in the same area (Hensen et al. 1998; Zabel et al. 1998), which found phosphate release of 1.55 to 16.94 mmol m⁻² a⁻¹ and nitrate fluxes of 46 to 229 mmol m⁻² a⁻¹ at water depths between 600 and 3000 m. Highest values were also observed at approximately 600 m. The finding of lower flux rates in sediments from the uppermost slope in this study (Fig. 3) can most probably be attributed to local erosion patterns (Bremner and Willis 1993). Along the shelf edge, significant winnowing of sediment results in locally low TOC contents (Inthorn et al. in prep.) and correspondingly low benthic nutrient fluxes. Down from the depocentre at the upper slope, which is rich in organic carbon, flux rates generally decrease with increasing water depth (Fig. 3).

Very prominent are the maxima of dissolved phosphate concentrations a few cm below the sediment surface (Fig. 2). Similar features were recently observed in Namibian shelf sediments, where they were caused by a concentrated occurrence of the giant sulphur bacterium *Thiomargarita namibiensis* and were connected with the authigenic formation of phosphorites (Schulz and Schulz 2005). However, concentrations were ten times higher on the shelf than in our study (up to 300 μmol L⁻¹), and the occurrence of *T. namibiensis* is restricted to areas of at least temporarily

oxygen-depleted conditions (Schulz 1999). Therefore, the phosphorus cycle at deeper waters may rather be controlled by a link to the iron cycle (e.g. Slomp et al. 1996), which is also indicated by the similarity of phosphate and ferrous iron pore water profiles (Fig. 2). Consequently, the phosphate release cannot solely be attributed to OM degradation because this process is most probably masked by iron-related effects like iron reduction (Tab. 3) and inorganic sorption of phosphate to iron (oxyhydr)oxides in the oxic zone (e.g. Froelich et al. 1982).

Carbon oxidation pathways

Considering the major pathways for bacterial organic carbon mineralisation, oxic respiration contributes between 57.0 and 87.8 % of the total organic carbon oxidation in our data (Fig. 4). As expected, the second biggest contribution stems from sulphate reduction with 7.6 - 28.8 %, followed by denitrification accounting for 2.2 to 9.4 % of the total oxidation (Fig. 4). The contribution of iron oxidation to TOU is almost negligible, amounting to 0.01 to 0.34 %. Rates of total carbon oxidation strongly decrease with water depth, from 3.57 to 1.92 mol C m⁻² a⁻¹ at T1 and from 7.28 to 0.65 mol C m⁻² a⁻¹ at T2 (Fig. 4). Data for comparison of absolute rates of total carbon oxidation are rare and often problematic due to different modes of calculation. Nevertheless, for the North Carolina continental slope, Jahnke and Jahnke (2000) report OM mineralisation rates of 0.97 - 3.9 mol C m⁻² a⁻¹ at a depocentre site, which are a factor of 3 to 10 greater than rates in adjacent continental rise and upper slope areas. The North Carolina continental slope exhibits high OM deposition rates, significant input from lateral transport and high bottom water oxygen concentrations - just as our study area. Oxygen fluxes amount to 1.1 to 4.9 mol O₂ m⁻² a⁻¹ on the North Carolina continental slope (Jahnke and Jahnke 2000). These rates - albeit calculated with a different approach - are very similar to the ones obtained in our study (Tab. 3), underlining the importance of the sedimentary setting for total carbon turnover.

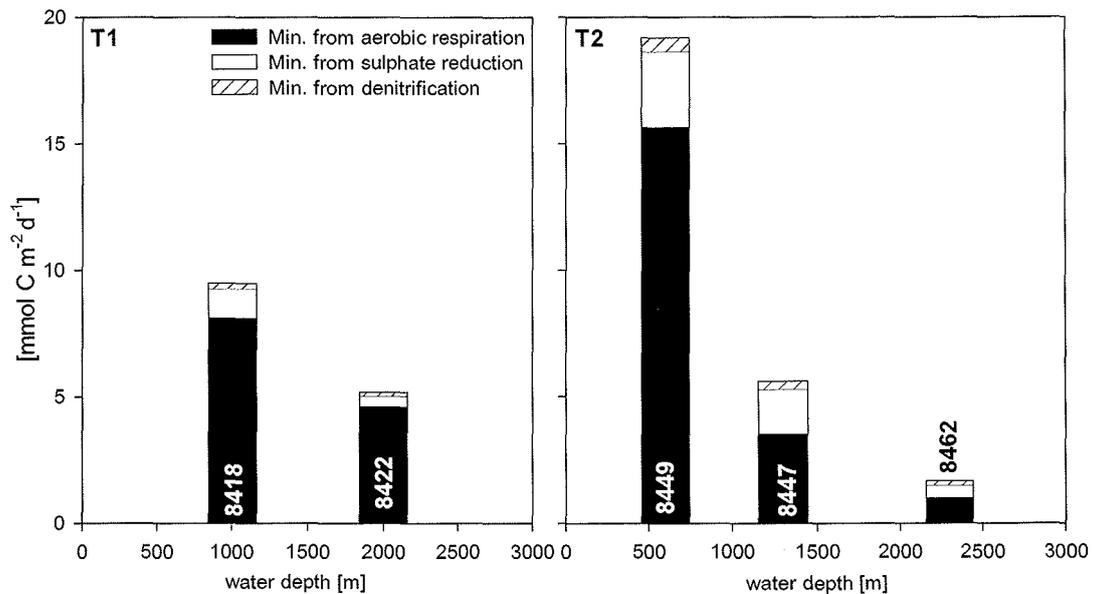


Figure 4: Carbon mineralisation by the different investigated carbon oxidation pathways: oxic respiration (black bars), sulphate reduction (white bars) and denitrification (hatched bars).

While our values of carbon mineralisation generally agree well with an estimation of the global capacity of terminal electron acceptors for organic carbon oxidation (Zabel and Hensen 2003), significant differences in weighting become obvious when looking at the single locations. In our data, the relative importance of TOU does not increase with water depth, especially at T2 (Fig. 4). Such an increase should be expected if the organic carbon rain rate would be continuous. Similar features were already reported from other continental margins (e.g. Cai and Reimers 1995; Jahnke 1990), where they were attributed to e.g. variations in the oxygen concentration of bottom waters. However, on closer examination of oceanic and sedimentological conditions in our study area, these differences down the slope cannot be explained by only looking at the quantity of the organic carbon and the availability of oxygen (Tab. 1). Obviously, there is at least one additional factor that controls the microbially catalysed transfer rates in these sediments. The most obvious may be the quality of the accumulated organic substance.

Importance of OM quantity and quality for benthic transfer rates

Sediments in our study area are predominantly influenced by lateral, cross-slope particle transport (e.g. Inthorn et al. in prep.; Mollenhauer et al. 2002). This has resulted in the development of a distinct mid-water depocentre, which is clearly reflected in the distribution pattern of TOC in surface sediments (Fig. 1). Neither benthic flux rates nor carbon oxidation rates correlate with surface sediment TOC contents, clearly showing that TOC alone can not explain the distinct cross-slope distribution of flux rates. Similarly, no correlation exists between the flux rates and bottom water oxygen concentrations, as has been described for other continental slopes by Cai and Reimers (1995). In our study area, oxygen in the bottom water is generally near saturation and very uniformly distributed (Tab. 1).

In contrast to the TOC content as a simple measure of OM quantity, the use of sediment parameters indicating the quality of OM encloses the degradational history the OM has undergone prior to deposition. In this study, a number of different parameters for OM quality were combined to try to establish an integrated picture of the driving forces behind the calculated benthic fluxes.

Two recently presented molecular degradation indices have been applied to our sediments by Ahke et al. (in prep.) to elucidate the diagenetic state of the deposited OM and to characterise its geochemical reactivity:

- (1) Total chlorins, comprising chlorophyll and its degradation products, can be used to calculate a chlorin index (CI) (Tab. 5), which represents the ratio of chlorophyll and its degradation products deposited in the sediments that could still be chemically transformed and those that are inert to chemical attack (Schubert et al. 2005).
- (2) The degradation index (DI), which can be derived from the evaluation of the concentration of a variety of amino acids (THAAs – total hydrolysable amino acids) (Tab. 5), is directly linked to the reactivity of OM as indicated by its lability to enzymatic degradation and its first-order degradation rate constant (Dauwe and Middelburg 1998).

Both chlorin as well as THAA concentrations show a tight, quasi-linear connection to the rates of denitrification (Fig. 5a). Similar connections exist between

Chlorins and THAAs and ammonium release rates (Fig. 5b). Moreover, SRR and TOU are comparatively high at stations with high chlorin and THAA concentrations.

More detailed information on the reactivity of both chlorins and THAAs can be obtained from their associated indices. The CI shows little fluctuation throughout the investigated sediments. Values between 0.70 and 0.85 (Tab. 5) identify the OM as fairly refractory (Ahke et al. in prep.). Correspondingly, its relationship to rates of denitrification and ammonium release is little distinct. This lack of a correlation indicates that it is not the composition of the present chlorins that impacts benthic fluxes but obviously some other compartment of OM. DI values correspond to results reported for coastal and ocean margin sediments (Dauwe et al. 1999) (Tab. 5). In contrast to CIs, calculated DIs do not suggest refractory and progressively altered material. High positive values, indicating easy enzymatic degradation, usually coincide with high rates of denitrification and ammonium release (Fig. 5). This suggests that it is mainly the easily degradable fraction of the present OM that causes variations in benthic flux rates. At the continental slope deeper than 800 m as well as directly below the shelf break, the easily degradable fraction is reduced (lower DI), accompanied by decreased benthic flux rates. The sedimentary setting in the study area provides an explanation for this distribution: Slightly below the shelf break is an area of very low accumulation of reactive organic matter, while refractory material is repeatedly resuspended and deposited (Inthorn et al. in prep.). The remaining sediment is less reactive or rather of minor quality, which is reflected in lower reactivities and rates compared to those at adjacent deeper stations.

Table 5: Parameters of OM quality.

Station #	Transect	Total chlorins* [$\mu\text{g g}^{-1}$ sed.]	Chlorin Index*	THAA fluff* [mg g^{-1} sed.]	THAA sed.* [mg g^{-1} sed.]	DI fluff*	DI sed.*	%(S1+S2') ^o
GeoB 8418	T1	19.71	0.82	-	12.41	-	0.06	28
GeoB 8422	T1	4.75	0.76	7.66	-	-0.70	-	23
GeoB 8492	T2	-	-	-	-	-	-	29
GeoB 8449	T2	79.59	0.76	27.85	17.78	-0.13	0.48	32
GeoB 8448	T2	100.70	0.77	34.68	29.64	0.65	-	32
GeoB 8451	T2	42.12	0.75	27.06	24.15	0.50	-	29
GeoB 8447	T2	-	-	-	-	-	-	30
GeoB 8455	T2	24.94	0.77	26.24	21.06	-0.03	0.37	30
GeoB 8462	T2	10.41	0.77	13.34	14.14	-0.48	0.09	24
GeoB 8470	T2	15.91	0.73	12.34	11.19	-0.50	-	22
GeoB 8464	T3	10.95	0.83	19.56	9.89	0.44	-	23
GeoB 8466	T3	-	-	-	-	-	-	25
GeoB 8465	T3	16.84	0.81	20.79	19.12	-0.55	-	27

taken from *Ahke et al. (in prep.) and ^oInthorn et al. (in prep.).

As a third approach to characterise the sedimentary OM, Rock-Eval pyrolysis was applied to surface sediments by Inthorn et al. (in prep.), which also allows a qualitative assessment of OM composition and enables us to relate benthic fluxes to the presence of a labile fraction of hydrocarbons. The cross-slope distribution of the fraction of labile hydrocarbons in total hydrocarbons ($\%(S1+S2')$) resembles that of the other OM quality parameters, showing a decrease in OM reactivity (decreasing $\%(S1+S2')$) at the shelf break compared to the upper slope stations and another decrease from there towards the deep sea (Tab. 5). If benthic transfer rates are mainly controlled by the easily degradable fraction of OM, as deduced from the correlations with THAA-data, they can also be expected to correlate with the labile hydrocarbon fraction. A close correspondence indeed exists between this labile fraction and rates of denitrification, which contemporaneously increase (Fig. 5a). The same correspondence is seen for ammonium release rates (Fig. 5b), further supporting our findings from the THAA analysis and underlining the importance of OM quality for the regulation of benthic flux rates.

The tight connection between benthic flux rates and most sediment OM quality parameters clearly shows that the reactivity of deposited OM is to a high degree decisive for benthic turnover and the related benthic fluxes. Different quality parameters exert different influence on benthic transfer rates, e.g. the CI is of little explanatory power compared to the DI or the labile fraction of hydrocarbons. This supports the picture that microbial communities tend to oxidise organic substrates sequentially, consuming the more reactive substrates first (Middelburg et al. 1993). A CI showing a generally refractory chlorin composition of the sediment probably indicates that chlorin degradation is already advanced at or shortly after arrival of the OM at the sediment surface. The DI, on the other hand, still has a significant impact on benthic transfer rates. The time that a certain sediment is in contact with oxygenated bottom or pore water, termed the oxygen exposure time (OET), is further thought to affect OM reactivity by influencing its degree of processing before final burial (e.g. Hartnett et al. 1998; Hedges et al. 1999; Hedges and Keil 1995). For instance for the Namibian slope, Schulz et al. (1994) showed that settling OM is likely to experience varying degrees of biochemical transformation under oxic, sub-oxic and/or anoxic conditions, depending on the flux of labile OM that reaches the sea floor.

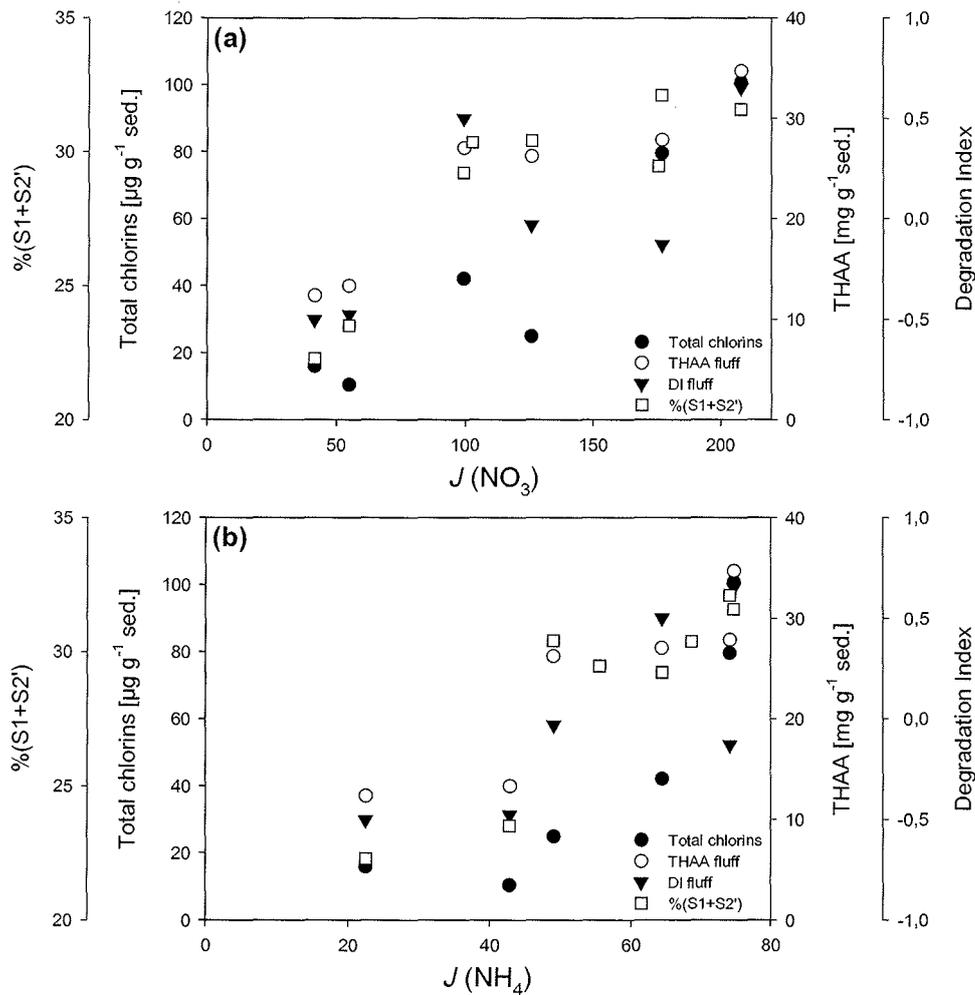


Figure 5: Rates of denitrification (a) and ammonium release (b) plotted against quality parameters of OM: labile fraction of hydrocarbons (%(S1+S2')), concentration of total chlorins and concentration of THAAs as well the associated degradation index (DI) in fluff samples.

Influence of oxygen exposure history

There are strong indications that OET exerts a major influence on carbon burial efficiency of a sediment (Hartnett et al. 1998; Hedges and Keil 1995; Keil et al.

2004) and consequently affects the reactivity of the existing sedimentary OM: The higher the OET, the higher the processing and thus the lower the reactivity of OM. Table 4 shows the calculated OETs, which have to be treated as maximum estimates due to the indirect estimation of oxygen penetration depth. However, this considerable uncertainty also applied to calculations given in Hartnett et al. (1998), who presented an OET of 6.42 yr for upper slope sediments of the Washington margin. Moreover, our estimates do not account for lateral transport of OM to the sediment, which has been shown to be important in the Benguela Upwelling System (Inthorn et al. in prep.). As Keil et al. (2004) point out, the quantitative impact of laterally transported OM on sediment OET is hard to assess. Lateral transport and resuspension events increase OET, however the magnitude of that influence remains to be elucidated in our study area.

As expected, concentrations of THAAs decrease with increasing OET in this study. That supports the hypothesis that – at a given primary production rate – biomarker accumulation strongly depends on OET in the water column and particularly in the pore water (e.g. Hartnett et al. 1998; Sinninghe Damsté et al. 2002). Still, neither rates of denitrification nor ammonium release can be easily correlated to OET, indicating that the benthic fluxes are not primarily driven by OET. One has to keep in mind that total concentrations of THAAs do not contain any information on the composition of these THAAs, and the relative degree of preservation varies between different classes of biomarkers on changing exposure to oxygen. The lack of a correlation of OET and DI indicates that – even though total THAA-concentration appears connected to OET - the share of easily degraded components of THAAs is mainly independent of the contact time with oxygen.

Bioturbation and -irrigation can further complicate interpretations of oxygen exposure histories. Macrofauna distribution at the investigated stations, as presented in Chapter 2 of this thesis, indicates that bioturbation depth can be substantially deeper than oxygen penetration depth in our study area. Therefore the number of times an individual particle passes between oxic and anoxic zones will be much greater with bioturbation than without (Aller 1994). Periodic irrigation of anoxic pore waters with oxygenated bottom water should have the same local effect. Given evidence that re-exposure of OM from anoxic sediments to oxygenated conditions facilitates biodegradation (Hulthe et al. 1998), OET calculations based on steady state

conditions – as done in this study - may substantially underestimate cumulative degradation under oscillating redox conditions (Aller 1994).

Overall, a variety of factors influences OET in our study area, complicating a linking to benthic flux rates. No direct correlation between these parameters could be detected. Rather, benthic fluxes in the Benguela slope sediments appear to be primarily driven by an easily degradable fraction of OM, whose decomposition probably takes place at the time scale of days to months, well below the time-scale recorded by OET.

Conclusions

This study shows that OM degradation and associated benthic fluxes and transfer rates are clearly controlled by the quality of OM rather than its quantity. Accompanying changes in OM quality, the contribution of oxic respiration to total OM degradation and the benthic flux rates of nitrate and ammonium reach their maximum in the upper part of a prominent depocentre at the upper slope and subsequently decrease towards the deep sea. As deduced from carbon oxidation rates, total benthic activity is highest in the upper slope area as well. Parameters indicating a labile and easily available quality of OM are closely connected to the rates of denitrification and the benthic release of ammonium. Similarly, TOU and SRR are coupled to these benthic fluxes. Obviously, a small but highly reactive fraction of the total OM accounts for the bulk of OM degradation in the investigated sediments and thereby drives benthic fluxes, while the refractory part of the deposited OM remains without much effect. Describing sediments with the conventional bulk parameters such as TOC-content, C/N-ratio, etc. can therefore not sufficiently specify the factors driving microbial benthic activity.

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Synopsis and Outlook

This thesis intends to elucidate the fate of settling organic matter in deep sea sediments underlying a high-productivity system and the importance of organic matter quality for the benthic response. The study area was located off Namibia in the Benguela Upwelling System, representing one of the most productive ocean areas in the world, and was visited on a cruise with FS METEOR in February/March 2003. A benthic community adapted to year-round high organic matter input to the sediment was expected to react fast and selectively to varying additions of organic matter. The study covers the benthic response to changing organic matter quality at three different time-scales, from hours and days to months and years:

- Short-term experiments were carried out *in situ* using a benthic chamber lander. Isotopically (^{13}C) labelled phytodetritus of 'fresh' and 'altered' quality was supplied to the sediment community and its benthic processing was traced over 18 to 36 hours via label mineralisation and incorporation into bacteria and macrofauna.
- Medium-term on board-experiments were conducted as whole core-incubations in a comparable set-up to the *in situ*-experiments that allowed for longer incubation times of up to 15 days. Additional to the mineralisation and bacterial incorporation of label, bacterial productivity was investigated and allowed the calculation of bacterial growth efficiencies.
- The long-term impact of organic matter quality on benthic activities was investigated by comparing different quality parameters of the sediment with benthic fluxes of phosphate, nitrate and ammonium and sedimentary carbon oxidation rates.

On all investigated time-scales, a strong impact of organic matter quality on benthic activity was found. The most important results from the *in situ*- and on board-experiments are summarized in Table 1. In both experimental set-ups, fresh phytodetritus was mineralised to a distinctly higher degree than altered

phytodetritus. Similarly, in the *in situ*-experiments incorporation into bacteria and uptake by macrofauna was increased in fresh incubations. The *in situ*-experiments, carried out at four stations of increasing water depth, moreover allowed conclusions about spatial patterns in the benthic response to varying qualities of organic matter. Obviously, the importance of an input of easily available organic matter for benthic processing rates is increased in the deep sea compared to shelf and slope stations. This was attributed to changes in the benthic community composition, with higher abundances of macrofauna both in absolute numbers as well as relative compared to microorganisms at the shallower stations. As macrofauna is reported to be less sensitive to the quality of organic matter, their high abundance at the upper continental slope results in a less pronounced difference in total processing rates of both fresh and altered phytodetritus at the upper slope stations. More microbially dominated communities in deep sea sediments show a higher sensitivity to organic matter quality, resulting in a higher discrepancy in total processing rates. Moreover, benthic processing of phytodetritus was increased in stations situated within a major centre of organic matter deposition at 25.5 °S compared to northward stations at 24.5 °S.

Tab. 1: Summary of the most important results from our ¹³C-pulse-chase experiments. While mineralisation shows the same trend in both experimental set-ups, results on bacterial incorporation differ.

<i>in situ</i> -experiments		on board-experiments	
fresh	altered	fresh	altered
Higher mineralisation	Lower mineralisation	Higher mineralisation	Lower mineralisation
Higher bacterial incorporation	Lower bacterial incorporation	Higher bacterial production	Lower bacterial production
Higher macrofaunal uptake	Lower macrofaunal uptake	Lower bacterial incorporation	Higher bacterial incorporation
Higher total carbon processing	Lower total carbon processing	Lower bacterial growth efficiency	Higher bacterial growth efficiency

The on board-experiments, allowing for incubation times of up to two weeks, revealed differences in the medium-term compared to the short-term benthic response. While mineralisation of added phytodetritus and bacterial productivity was distinctly higher in fresh incubations, an opposite picture was found when investigating bacterial incorporation of added phytodetritus. Bacterial fatty acids showed a clearly increased incorporation of altered compared to fresh phytodetritus. As a result, the addition of altered phytodetritus resulted in distinctly higher bacterial growth efficiencies. A timing effect explains these results: Fresh phytodetritus contained the low molecular weight fraction of organic matter smaller than 1000 Dalton, which rapidly increased mineralisation and bacterial secondary production but was not incorporated at an accordingly high rate. Altered phytodetritus lacked that low molecular weight fraction, but had been soaked on seawater for several hours prior to the experiment. This treatment resulted in a higher incorporation of altered compared to fresh organic matter and an accordingly higher bacterial growth efficiency. However fresh phytodetritus was shown to be more reactive for total carbon turnover than altered material on a medium time-scale.

Also on longer time-scales a distinct impact of organic matter quality on benthic activity could be shown. The Benguela Upwelling System constitutes an area of generally high concentrations and inputs of organic matter to the sediment. This organic matter input is to a significant degree supplied from lateral transport, especially in a depocentre situated at the upper continental slope. A complex system of vertical and lateral transport processes in combination with erosion and deposition related to near-bottom currents results in a high diversity of organic matter sources. This diversity is expressed in a highly variable quality of sedimentary organic matter, which is decoupled from surface water productivity. A comparison of sediment characteristics with rates of benthic denitrification and release of phosphate and ammonium revealed that it is not the quantity of organic matter, but mainly its quality that drives these rates.

The tracer approach followed in our experiments allows us to stretch beyond widely used bulk parameters of benthic activity, such as total oxygen uptake, and enables statements about single compartments of the benthic community and detailed analysis of the pathways of benthic carbon processing. In a high-

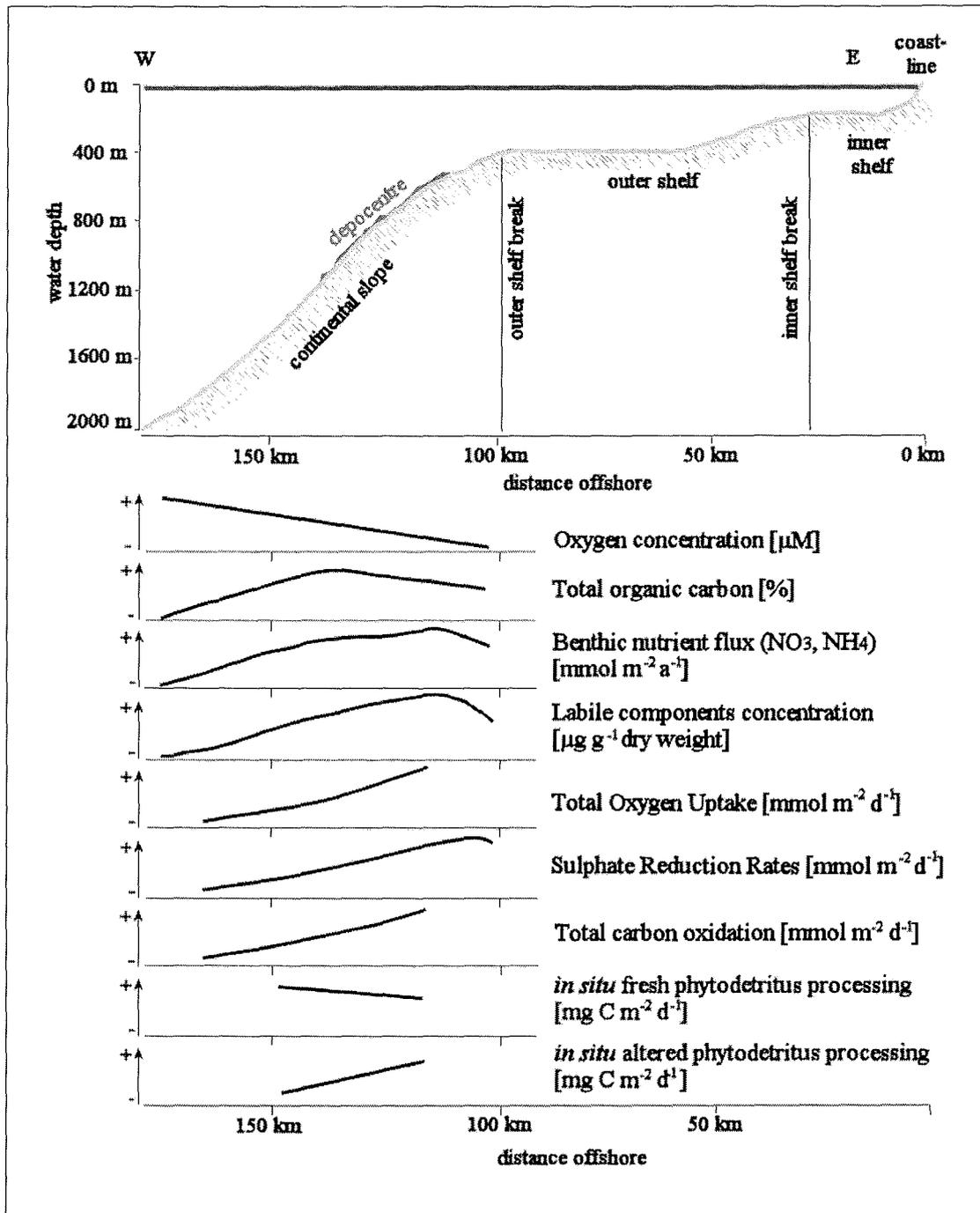


Fig. 1: Distribution pattern of the most important sediment characteristics and benthic rates on the Benguela continental shelf, as presented in Chapters 2 and 4 of this thesis. Total organic carbon content is uncoupled from benthic nutrient fluxes and benthic activity (e.g. TOU, SRR, total carbon oxidation, phytodetritus processing), that are rather driven by the concentration of labile components in the sediment.

productivity system like the Benguela Upwelling System, where natural rates as well as variance of total oxygen uptake are high, it presents a necessary and practical way to investigate benthic carbon turnover. The combination of *in situ*- and on board-experiments permitted us to cover a wide range of time-scales, which have a significant impact on amplitude and pathways of the benthic response. While the short-term response was similar for all benthic compartments in our experiments, the medium-term reaction appeared more differentiated. Thereby, the medium-term experiments also revealed the constraints associated with conventional measurements as indicators of total benthic activity. Total oxygen uptake has widely been used as such an indicator, however it is not only subjected to high spatial variability but also includes the ultimate oxidation of reduced compounds arising from anaerobic respiratory processes, e.g. sulphide. Mineralisation as measured from DI^{13}C release therefore presents a better measure for benthic activity. However, the results on bacterial growth efficiency from our on board-incubations revealed that this approach can not always trace the whole complexity of the benthic ecosystem. While mineralisation rates generally offer an appropriate way to investigate the activity of the benthic community, they do not yield any information about the actual momentary utilisation of the available material by the benthos. The combination of ^{13}C -tracer addition with measurements of bacterial productivity, as done in the on board-incubations, revealed that growth efficiencies of the bacterial community did not correspond to the mineralisation rates. The addition of altered phytodetritus resulted in distinctly higher bacterial growth efficiencies than the addition of fresh material. Individual compounds of organic matter may be incorporated with very different efficiencies, and perhaps the overall bacterial growth efficiency is related to, and indicative of, the proportion of broad qualitative classes of organic compounds available to bacteria. This, however, could not be clarified in our experiments and requires further investigations, e.g. by the addition of more specific labelled substrates to the benthic microbiota.

The findings of this thesis reveal the great importance of organic matter quality for the processing and turnover of organic matter in deep sea sediments. An overview of the most important sediment characteristics covered in this study and the related rates of benthic activity is given in Figure 1, emphasising the importance of organic matter quality. Detailed knowledge about the factors driving benthic carbon turnover and burial is of major importance on a global scale, as it is crucial to

the prediction of future levels of atmospheric carbon dioxide and the interpretation of organic carbon variations in marine sediments. Moreover, this thesis clearly underlines that only an integrated approach will allow deeper insights into the benthic carbon cycle, and that the strength of ecological investigations lies in the combination of a variety of methods which then hopefully lead to a detailed knowledge of the functioning of the benthic ecosystem.

Appendix I

Does the quality of organic material influence the macrofaunal community?: An experiment in the Benguela Upwelling System.

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Abstract

Continental slope and deep sea sediments under the Benguela Upwelling System were studied through investigations of the benthic boundary layer in high productivity systems undertaken by the Research Centre Ocean Margins in Bremen.

Benthic landers with chambers were used to undertake the experimental work whereby fresh and altered material was added to the chambers. The aim was to investigate the influence of different quality material on the benthic macrofaunal communities. ^{13}C -labelled phytodetritus was used as a tracer to follow its uptake into the macrofaunal community.

We found that in general stations situated at shallower depths, which had had fresh material added to the chamber, had a greater number of macrofauna present, particularly from the depth slice 0 – 2 cm. Stations situated at 2000 m and 2280 m, even with the addition of fresh material, did not appear to have a high number of macrofauna present.

Unsurprisingly polychaetes dominated macrofauna abundance. A total of 201 individuals from 25 different families were recorded. Of those families, the most abundant five were the Spionidae, Paraonidae, Lumbrineridae, Maldanidae and Ampharetidae, which accounted for almost 70 % of the total number of polychaetes collected. Information on the labelling of single organisms will be available in the near future.

Appendix II

Particulate organic matter dynamics in a river floodplain system: impact of hydrological connectivity

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The following manuscript was not included in this thesis, as it deals with a very different environment, a river-floodplain system in central Europe. However, in this study stable isotope analysis – in this case of natural abundances - is once more used to evaluate the quality and sources of organic matter, which is then linked to its biological availability as estimated e.g. from bacterial secondary production. Thereby it shows the almost universal applicability of the stable isotope approach for integrated ecosystem studies, linking the living to non-living compartments in the cycling of organic matter.

Reprints can be made available upon request.

Abstract

The retention efficiency of a specific reach is one key factor controlling the dynamics of particulate organic matter (POM) in running waters. Floodplains enhance the retention of riverine POM, thereby altering its structure and diagenetic state, and constitute a substantial autochthonous source. Hydrological connectivity between a river and its floodplains determines the impact of floodplains for the POM dynamics of the entire river. The elemental and isotopic ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) composition and microbial utilisation of POM was investigated in relation to hydrological connectivity in the River Danube and two floodplain segments, one of which was isolated, the other dynamically connected. The latter had been subjected to river restoration measures. An increased integration in the riverine network was the effect of the restoration. Within both floodplains, isolated, disconnected and connected conditions were distinguished depending on the location of inflow areas and the riverine water level. Carbon isotopic composition of POM clearly separated riverine and connected conditions from those disconnected and isolated, the latter representing autochthonous material mainly derived from plankton. At disconnection, the maximum contribution of phytoplankton to POC was determined ($54.5\% \pm 28.8\text{ SE}$), which also supported the highest bacterial productivity ($4.61\ \mu\text{g C l}^{-1}\ \text{h}^{-1} \pm 0.55\text{ SE}$). Connected conditions were characterised by relatively enriched, allochthonous POM ($\delta^{13}\text{C}$: $-23.27\text{ ‰} \pm 0.98\text{ SE}$). In the isolated floodplain, high standing stocks of aquatic macrophytes developed which act as 'sinks' of carbon for the river. Restoration efforts like the Danube restoration project, which increase hydrological connectivity, enhance the importance of autochthonous POM and its further transformation by re-establishing dynamically connected floodplains in regulated, temperate large rivers.

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