Macrofaunal and foraminiferal community structure and their response to simulated phytodetrital food pulses

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Contents

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MAHALO …

Abstract

Deep-sea ecosystems are subjected to a variety of natural and/ or man-made perturbations such as disturbance events, pollution and climate change, and each of these stressors has the potential to substantially modify deep-sea biodiversity and ecosystem functioning. In order to elucidate the potential impacts of such stressors, it is important to first understand baseline ecosystem dynamics. To learn more about deep-sea ecosystem functioning, this thesis has focused on elucidating the role of macrofauna and Foraminifera in deep-sea C-cycling. Whilst the results presented and discussed are the outcome of only a relatively small set of experiments, they do reveal some interesting insights into the role of macrofauna and Foraminifera in deep-sea C-cycling and suggest avenues for further exploration.

The first manuscript describes the composition of, and for the first time, the response by macrofauna to a simulated organic matter (OM) pulse at an abyssal Station in the NE Pacific. In each experiment, 1.2 g C m^{-2} of ^{13}C-labelled *Skeletonema costatum* was deposited onto the seafloor using a benthic chamber lander. Macrofaunal abundance and biomass were found to be significantly higher at 0-5 cm depth compared to 5-10 cm, and were dominated by the Nematoda and Crustacea, respectively. Twenty-five percent of the macrofauna specimens showed ^{13}C-signatures indicative of label ingestion, but specific uptake ($\Delta\delta^{13}C$) and C-turnover rates varied strongly between and within taxa. Two organisms, a single cumacean from chamber two and a paraonid polychaete from chamber three, were responsible for the majority of C-turnover, and had ingested up to 2.3 % of their body weight in C. Macrofaunal C-turnover was much lower than recorded in the abyssal NE Atlantic, which is most likely due to differences in the timing of the

experiments relative to the spring/ summer bloom, different experimental durations and disparities in macrofaunal community structure. These results emphasize the degree of plasticity inherent in the macrofaunal response to a food pulse and stress the need for comprehensive *in-situ* investigations to further our understanding of deep-sea benthic ecosystem functioning. This chapter has now been published in Marine Ecology Progress Series, v 355, 73-84.

The second manuscript of this thesis describes the response by bathyal macrofauna from a deep western Norwegian fjord to a simulated OM pulse. In each experiment, 1 g C_{org} m^{-2} of ^{13}C-labelled *Skeletonema costatum* was deposited onto intact sediment cores collected from 688 m water depth and incubated *ex-situ* for 2, 7 and 14 d. Macrofaunal abundance and biomass estimates were comparable to other deep-sea continental margin sediments of similar depths but in contrast to previous fjord studies, the macrofaunal community was numerically dominated by ostracods. Tracer experiments revealed highest uptake of tracer after 7 and 14 d compared to 2 d. Of the 7 deposit feeding polychaete families, only the Paraonidae & Cirratulidae - together with the largely carnivorous Lumbrineridae - showed a significant response to our labelled C-source. The lack of response by the majority of deposit feeders, and the unexpected feeding mode of the Lumbrineridae may be attributable to species- rather than family-specific feeding-ecologies and/ or ontogenetic changes in diet/ feeding mode. Total macrofaunal C-turnover was much lower than recorded in the deep Sognefjord in a 3 d feeding experiment, and is most likely a result of 1) distinct differences in macrofaunal community composition between the two sites, with a predominantly sub-surface feeding macrofaunal assemblage in the Korsfjorden as opposed to a surface-feeding community

in the Sognefjord and/ or 2) variations in OM supply and demand. In conclusion, this investigation highlights the importance of ecological information on species level for a detailed understanding of C-cycling and early diagenesis in marine sediments. This manuscript has been revised for re-submission to Deep-Sea Research.

Finally, the third manuscript describes the response by Foraminifera to labile OM from the same study as that described in chapter 2. The Foraminiferal community (>250 μm) from the Korsfjordenen was largely dominated (91 %) by the deep-dwelling species *Globobulimina turgida* and *Melonis barleeanum*, aswell as the shallow infaunal species *Hyalinea balthica*. With the exception of *H. balthica*, Foraminiferal average living depths (ALD) were continuously deep, indicating that the majority of Foraminifera were not vertically migrating to the surface to feed on the fresh organic matter pulse. *Hyalinea balthica* did migrate towards the sediment surface, but did not feed on our ^{13}C-tracer, suggesting that migration was due to another factor, possibly microhabitat restabilization following initial sub-optimal living conditions. No Foraminifera were involved in C-turnover during the first 7 d. After 14 d, 3 % of the Foraminifera samples possessed δ^{13}C-signatures indicative of C-uptake, but uptake was confined to *G. turgida*. Foraminifera contributed 2.4 % to faunal C-turnover (Foraminifera plus macrofauna), despite them making up 24 % of the combined biomass. The dominance of deep-infaunal species such as *G. turgida* and *M. barleeanum* (68 %) that prefer degraded organic matter over more labile material, as well as the coarse size fraction of Foraminifera analysed, which are known to respond slower to phytodetritus deposition than smaller, more opportunistic taxa, are likely reasons for the retarded response to food input observed in

this study. This manuscript is undergoing revision for re-submission to The Journal of Foraminiferal Research.

In conclusion, this thesis highlights the extreme heterogeneity in the macrofaunal and foraminiferal response to phytodetritus deposition and the importance of biodiversity and benthic community structure in modifying benthic C-cycling rates in the deep-sea. For example, results from both macrofaunal feeding studies, when compared to previous abyssal and fjord investigations, suggest that low C-turnover rates may result from a lack of surface-deposit feeding animals. In addition, this thesis has provided evidence that foraminiferal communities dominated by large, deep-dwelling taxa generally respond slowly to phytodetritus deposition as a result of their deep-infaunal lifestyles, and possible preferences for recalcitrant organic material over fresh, more labile resources. Results from this thesis imply that changes in deep-sea biodiversity and benthic community structure as a result of natural and/ or man-made perturbations may have profound impacts on C-cycling and hence C-sequestration rates and emphasize the need for thorough biodiversity and ecosystem monitoring studies in deep-sea environments.

Chapter 1 – Introduction

1.1 - The marine carbon-cycle

The global carbon cycle is largely controlled by three biologically mediated processes; these being organic matter production, remineralisation and burial. The oceans comprise the largest reservoir of biologically active C and therefore take a leading role in global C-cycling (Figs. 1 & 2). Continuous gaseous exchange of CO_2 between the atmosphere and the oceans is largely controlled by 1) differences in the partial pressures of CO_2 (pCO_2) between these two environments, 2) water temperature, 3) wind velocity and 4) salinity. Most (~ 90 %) of the CO_2 in the oceans is in the form of dissolved bicarbonate (HCO_3^-), which is taken up by photoautotrophic nano- (2-20 μm) and picoplankton (0.2-2 μm) (hereafter referred to as phytoplankton) and assimilated or fixed into phytoplankton biomass during photosynthesis (Libes 1992). This biomass building process, which occurs in a relatively shallow sunlit surface layer termed the euphotic zone, can be represented by the following stoichiometry:

$$106\ CO_2 + 122\ H_2O + 16\ HNO_3 + H_3PO_4 \rightarrow (CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 138\ O_2$$

(Libes, 1992)

As can be seen in the above equation, in addition to dissolved inorganic C (DIC), and water, photosynthesis also requires dissolved inorganic nitrogen and phosphorus. Phytoplankton generally takes up these chemicals in the form of nitrate (NO_3^-), nitrite (NO_2^-) ammonium (NH_4^+) and phosphate (PO_4^{3-}). However, because of their relatively low concentrations in seawater, dissolved inorganic nitrogen and phosphate are usually

the limiting elements in primary production and their compounds are termed bio-limiting nutrients (Libes 1992).

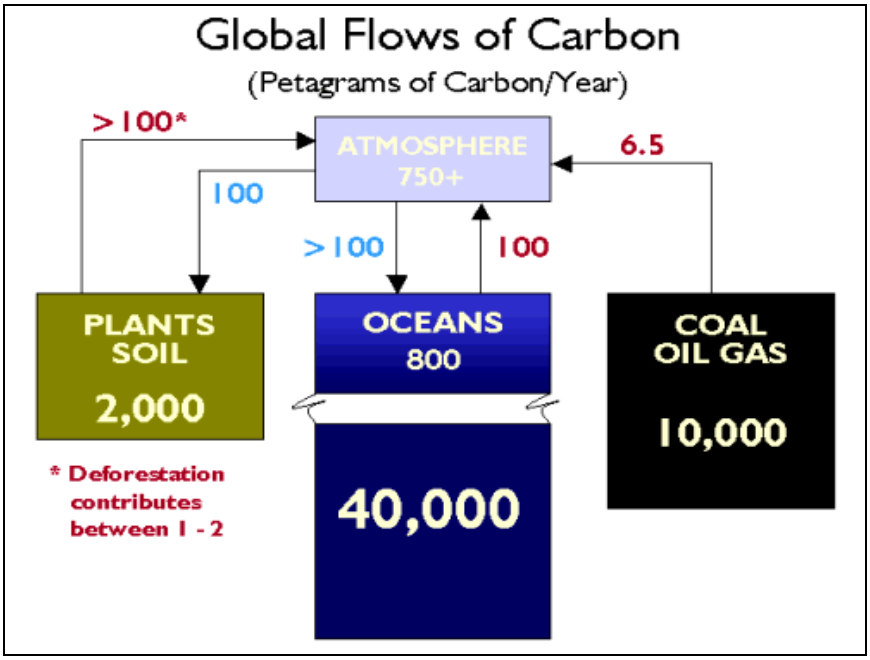

Figure 1. Global flows and reservoirs of carbon (www.whrc.org)

As primary production increases in the surface-lit euphotic zone, bio-limiting compounds generally decrease in concentration. Once these bio-limiting nutrients have been used up phytoplankton cells become nutrient limited and eventually die if nutrient concentrations are not replenished. Dead cells along with other biogenic particles such as molts and fecal pellets of phytoplankton consuming and carnivorous zooplankton, excreta, and other living and dead tissues, collectively termed particulate organic matter (POM) then begin to sink towards the seafloor either individually or as aggregates (Honjo 1982).

Since organic matter is the sole source of chemical energy for heterotrophic organisms, POM is rapidly decomposed as it sinks through the water-column. Sinking speeds of POM therefore dictate the concentration of labile, reactive material that reaches

the seafloor. Typical sinking rates are on the order of 1 - 100 m d^{-1}, but rates as high as 2200 m d^{-1} have been measured for sedimenting salp faeces (Madin 1982). However, despite a range of sinking speeds, remineralisation in the water column results in decreasing POM flux with depth and only a few percent of the actual primary production originating in the euphotic zone actually reaches the deep sea-floor (~ 1% at 4000 m depth).

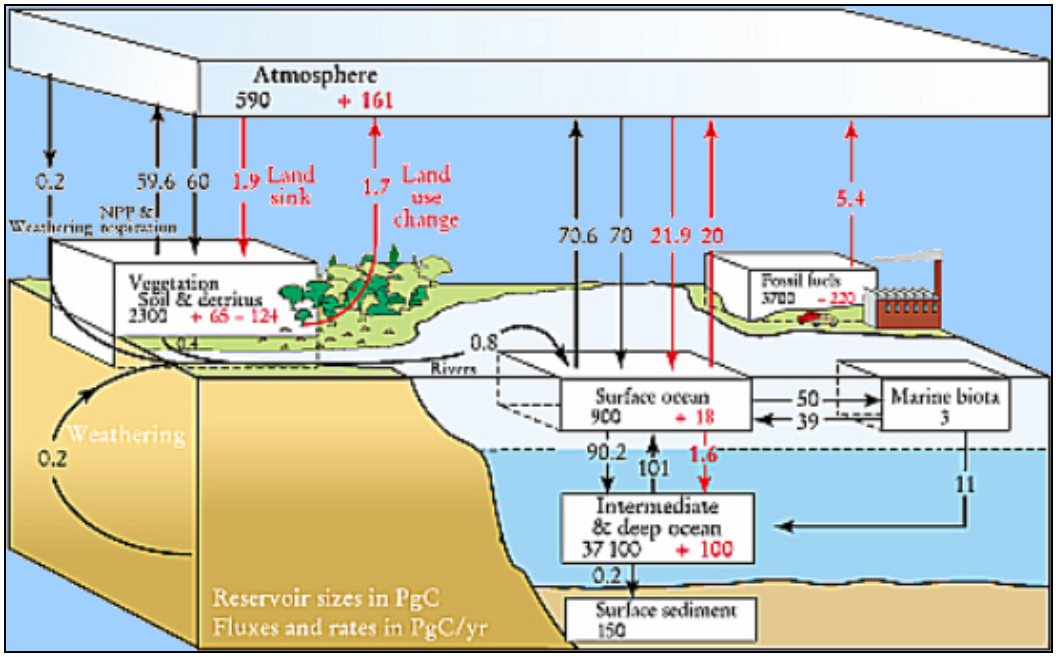

Figure 2. The C-cycle (www.archive.arm.gov)

The most active layer of organic matter remineralisation at the deep seafloor is normally the upper centimetres of sediment. Here, recently deposited organic matter forms a thin layer of phytodetritus (Fig. 3), which can be rapidly inhabited by small, opportunistic foraminifera (Gooday 1988), and/ or consumed by benthic organisms including microbes (Lochte & Turley 1988), meiofauna (Pfannkuche 1992, Danovaro et al. 1999), macrofauna (Witte et al. 2003a) and megafauna (Lauerman et al. 1997, Miller

et al. 2000). Respiration by deep-sea benthic communities accounts for most of the C-degradation (~ 80 - 95 %) followed by biomass production (~ 5 - 20%) (Pfannkuche 1992). As a result, very little (1 - 2 %) of the organic matter which does reach the sediment surface is actually buried. Exceptions do however occur in regions of very low oxygen concentrations such as within oxygen minimum zones and/ or under regions of high primary productivity (e.g. upwelling areas). The fraction of C which is buried in sediments and therefore sequestered for long periods of time (in the geological definition) therefore depends on benthic C-turnover rates, which are a function of the organisms that intercept and remineralize recently deposited phytodetritus and thus benthic community structure. Examining the role of two components of the benthic community- the macrofauna and foraminifera - in deep-sea C-cycling is the primary goal of the following thesis.

Figure 3 - Green phytodetritus at 600m depth on the Antarctic Shelf with feeding tracers of holothurians and ophiuroids clearly visible. Photo courtesy of Prof. Craig R. Smith

1.2 The importance of macrofauna and foraminifera in deep-sea C-cycling

Decomposition of organic matter by the deep-sea benthos is largely dominated by microbes (Pfannkuche 1992). However, even though macrofaunal density and biomass decrease with increasing water depth, in contrast to microbes (Rex et al. 2006), macrofaunal populations still play an important role in C-cycling in deep-sea sediments.

Dissolved oxygen is the strongest oxidising agent available for organic matter degradation, but in deep-sea regions where organic matter fluxes are high (e.g. upwelling areas), oxygen seldom penetrates more than a few millimetres into sediments (Glud et al. 1999). Therefore, any process which enhances oxygen penetration into sub-surface sediments is likely to have a profound effect on organic matter remineralisation and hence, C-cycling. Forster and Graf (1995) demonstrated at shallow water stations in the North Sea that decapod crustaceans and tube-building polychaetes, through burrowing and irrigation were able to modify and increase total oxygen uptake of the sediment by 85 % compared to the oxygen flux across the sediment-water interface, suggesting increased rates of organic matter and reduced compound oxidation. Jørgensen and Revsbech (1985) and Jørgensen et al (2005) have also shown the importance of macrofaunal activities/ burrow structures in enhancing O_2 flux into sediments.

Macrofauna not only enhance organic matter degradation by boosting O_2 flux into sediments, but also by increasing the volume of material susceptible to remineralisation through bioturbation (Levin et al. 1997) and 'hoeing' of labile surficial deposits (Dobbs & Whitlach 1982). In a study investigating pelagic-benthic coupling on the Vøring Plateau off the Norwegian continental margin (1430 m), Graf (1989) demonstrated from

chlorophyll-a profiles that sipunculans were able to mix pelagic material 7 cm into sub-surface geological strata in only a matter of days. Similar results were obtained by Levin et al. (1997) who reported that tube-building polychaetes of the family Maldanidae could, without ingestion, rapidly sub-duct recently deposited organic matter to depths of 10 cm thus, 1) making fresh, relatively labile, organic matter available to deep-dwelling microbes and other infauna and/ or 2) assisting in C-sequestration via organic matter burial.

Macrofauna also contribute to C-cycling by direct ingestion of organic matter. Selective feeding (e.g. preferential ingestion of small, organically coated particles) has been documented in a variety of macrofaunal taxa (e.g. Taghon 1982) and can result in substantial proportions of highly reactive organic matter being processed in favour of more recalcitrant material (Miller et al. 2000). Feeding experiments have also shown rapid ingestion of labile organic matter in deep-sea environments (e.g. Levin et al. 1997, 1999, Aberle & Witte 2003). For example, Witte et al. (2003 a) found that the macrofauna responded faster to a simulated food-pulse in the abyssal NE Atlantic compared to microbes and protozoan and metazoan meiofauna. In addition, in a study assessing the relative contribution of bacteria, foraminifera and macrofauna to C-cycling across the Arabian Sea oxygen minimum zone, Woulds et al. (2007) demonstrated that macrofauna were able to account for up to 83 % of the total C-turnover.

Benthic foraminifera are found in virtually every deep-sea sedimentary environment and can contribute a large fraction of the total sedimentary biomass (0-99 %). The widespread occurrence of foraminifera in deep-sea habitats together with their relatively large contribution to overall sedimentary biomass suggests that these

protozoans may play a pivotal role in deep-sea C-cycling (Gooday et al. 1992). Indeed a wide variety of studies at bathyal and abyssal depths have shown that benthic foraminifera are able to rapidly respond to and consume a large assortment of organic, nutrient-rich particles derived from rapidly settling POM (Gooday 1988, 1993, Ernst & van der Zwaan 2004). For example, Moodley et al. (2002) documented that foraminifera were extremely important to short-term C-turnover, and showed similar C-uptake rates to bacteria. Witte et al. (2003a) also demonstrated a dramatic, though delayed, response by foraminifera to a C-pulse in the abyssal NE Atlantic, which revealed that over the long-term (i.e. 3 weeks), foraminifera were more important to C-cycling than any other taxonomic group. Furthermore, feeding studies by Nomaki et al. (2005a & b) both described almost immediate responses to organic matter deposition by certain deep-sea foraminifera, in terms of rapid C-uptake and swarming behaviour towards elevated food-levels at the surface.

1.3 Stable isotope measurements and the pulse-chase approach

Measurements of the ratio between C- (^{12}C and ^{13}C) and N- (^{14}N and ^{15}N) stable isotopes within an organism can provide useful and powerful tools for studying trophic interactions within food-webs. Ratios are usually expressed in delta (δ) notation, and for C are based on the equation:

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

Where, R_{sample} and $R_{standard}$ denote the ratios of $^{13}C/^{12}C$ in the sample and standard (International Vienna PeeDee Belemnite). The stable isotopic signature of a heterotrophic organism depends on its trophic position within a food-web and the stable isotopic signature of the original food-source at the base of the food-chain, which is often a function of its specific source (e.g. marine vs. terrestrial) and metabolic pathway (e.g. a C3 vs. C4 plant). As heterotrophic organisms ingest a specific food-source, metabolic isotopic discrimination leads to a preferential loss of lighter isotopes during respiration (i.e. ^{12}C) and excretion (i.e. ^{14}N). The result is that the 'feeding organism' generally becomes 'enriched' in both ^{13}C (~ 1‰) and ^{15}N (~ 3-5‰) compared to the isotopic signature of the ingested food. The progressive enrichment in heavier isotopes with increasing trophic level can therefore help to unravel trophic structure in complex food-webs.

Whilst natural isotopic signatures can reveal much about basic trophic structure in marine and terrestrial ecosystems, they are unable to provide information on dynamic ecosystem functioning. The pulse-chase approach (as used in this study) is one method that is able to provide detailed information on ecosystem functioning and C-cycling rates in aquatic ecosystems. In short, an isotopically labelled substrate (e.g. ^{13}C-labelled algae) is deposited over an enclosed area of seafloor and the uptake of ^{13}C tracked into sediment-dwelling organisms (microbes through macrofauna) and abiotic components (e.g., dissolved inorganic carbon) (Fig. 4). When this technique is coupled to state-of-the-art molecular, geochemical and morphological methods, it is possible to quantify the uptake and turnover of C and assign the organisms and pathways responsible (e.g. Blair et al. 1996, Middelberg et al. 2000, Witte et al. 2003 a & b).

The pulse-chase approach was first used on the North Carolina continental slope by Blair et al (1996) who showed that certain species of macrofaunal polychaetes were capable of rapid (<1.5 days) C-uptake. Later, Levin et al (1997) demonstrated rapid subduction (<1.5 days) of labile organic matter to sediment depths of greater than 10 cm by tube-building polychaetes at an 850m deep site on the east coast of the USA. More recently, pulse-chase experiments carried out at bathyal depths and an abyssal site have first-hand revealed the potential importance and complexity of macrofaunal and foraminiferal communities in C-turnover in the deep-sea (e.g. Aberle & Witte 2003, Kitazato et al. 2003, Levin et al. 1999, Moodley et al. 2002, Nomaki et al. 2005a, 2006, Witte et al. 2003a, b, Woulds et al. 2007).

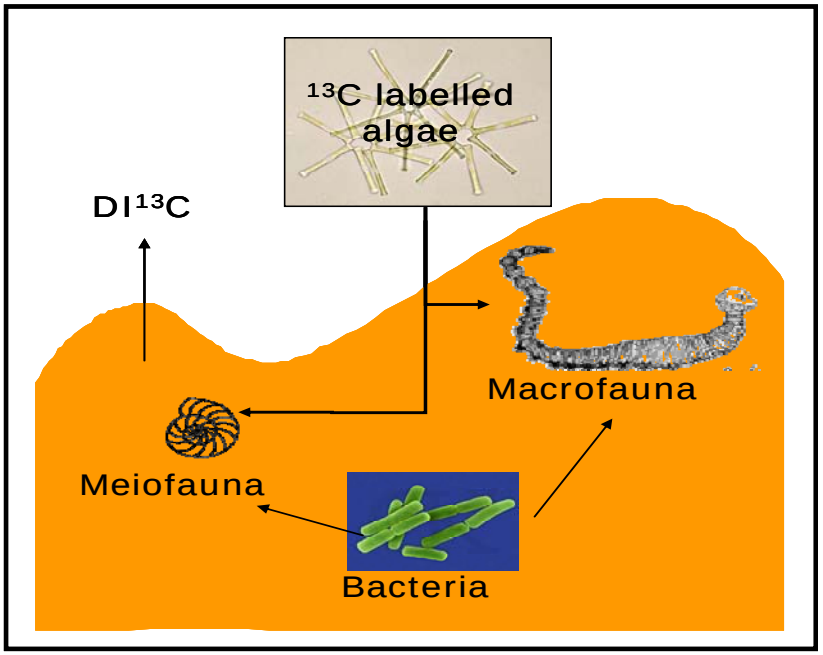

Figure 4 – The pulse-chase approach (diagram provided by Prof. Ursula Witte)

Although previous studies have partially highlighted the importance of macrofauna and foraminifera in deep-sea C-cycling via direct ingestion and processing and/ or simple

bioturbational activities, direct quantification of C-cycling rates are still few and far between. What's more, only a handful of studies have successfully shown the importance and complexity of macrofaunal and foraminiferal community structure in structuring rates and pathways of C-cycling in the deep-sea. With this in mind, studies (described in this thesis) were undertaken to elucidate the role of 1) macrofauna in benthic C-cycling at an abyssal site in the NE Pacific and 2) both macrofauna and foraminifera in C-cycling in an easily accessible bathyal Norwegian fjord.

1.4 The abyssal North East Pacific – Station M

Station M (Fig. 5) lies at 4100 m depth near the base of the Monterey deep-sea fan

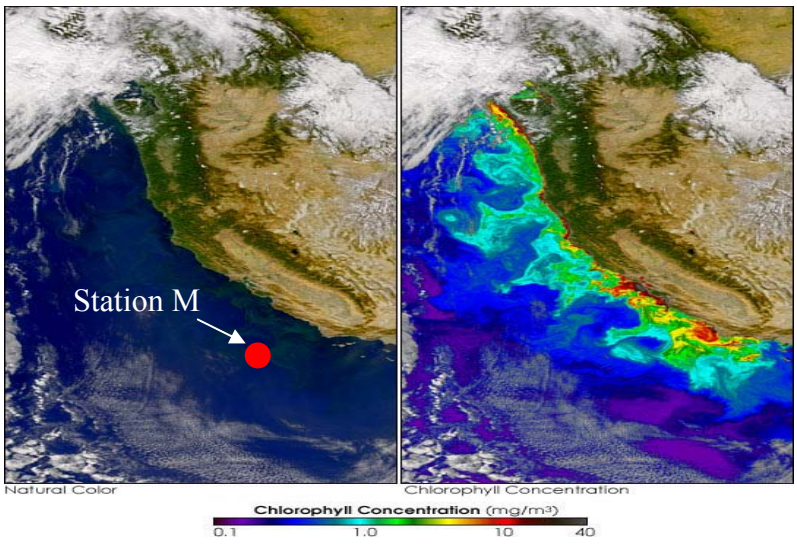

Figure 5 – Location of Station M in the NE Pacific. Elevated chlorophyll concentrations can be seen. (http://veimages.gsfc.nasa.gov/19597/California_SEA_2004265.jpg)

off the central California Coast and has been studied repeatedly since June 1989 to investigate the coupling of pelagic and benthic processes at abyssal depths (Smith & Druffel 1998).

Station M is located beneath the California Current where surface primary production is subjected to high variability as a result of upwelling along the California coastline (Fig. 5). Variability in surface processes results in large intra- and interannual fluctuations in the supply of POM (Fig. 6) to the seafloor (Baldwin et al. 1998, Smith et al. 1994, Smith & Kaufmann 1999, Smith et al. 2001, Smith et al. 2006).

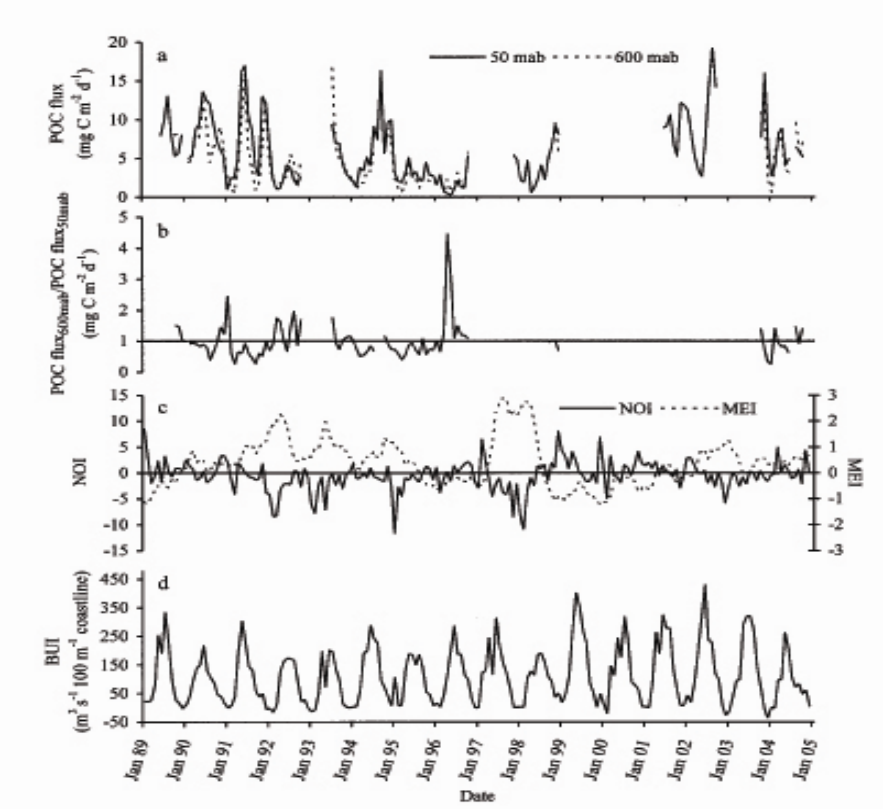

Figure 6 – (a) Long-term measurements of the supply of POC to 50 and 600 mab at Station M. (b) Ratio of POC sampled at 50 and 600 mab when synchronous measurements were available. (c) Northern Oscillation Index (NOI) and multivariate ENSO index (MEI) calculated monthly. (d) Bakun Upwelling Index (BUI) calculated for a 3^{o} x 3^{o} area at 36^{o}N, 122^{o}W. Figure from Smith et al. (2006).

Large seasonal inputs of POC to the seafloor at Station M normally result in concomitant increases in sediment community oxygen consumption (SCOC) rates (Drazen et al. 1998, Smith and Kaufmann 1999, Smith et al. 2001), similar to patterns reported from the abyssal NE Atlantic (Pfannkuche 1993) and bathyal Norwegian Sea (Graf 1989). However, since 1951 climatic warming and increased stratification of surface waters has led to reduced primary productivity in waters off southern California, which has resulted in reduced macro-zooplankton biomasses by approximately 80% (Roemmich & McGowan 1995). Impacts from changing climatic regimes have also propagated into the deep-sea environment at Station M. For example, a 7 yr study of food supply (POC flux) and demand (SCOC) at Station M by Smith and Kaufmann (1999) revealed decreasing POC: SCOC ratios from 1989 to 1996, synchronous with elevated sea surface temperatures and reduced phytoplankton biomasses. More recently, Ruhl and Smith (2004) reported a major change in community structure in epibenthic megafauna and found this change to be synchronous with the 1997-1999 El Nino/ La Niña event. The close coupling between shifting surface ocean processes – as a result of potential climate change – and the seafloor at Station M and possibly the deep-sea in general, highlights the need for a thorough analysis and understanding of pelagic-benthic coupling at this station and elsewhere. But, despite numerous studies of benthic O_2 consumption (i.e. SCOC) at Station M, no studies have ever addressed macrofaunal community structure or the importance of macrofauna in C-cycling at this station. The 2nd chapter of this thesis quantifies for the first time macrofaunal C-cycling rates in the abyssal Pacific at Station M.

1.5 The Korsfjord

Fjords are by definition, glacier-produced, coastally enclosed marine basins with restricted, shallow connections to the open sea, and are typically found in high-latitude regions (Pearson 1980). The topography and hydrography of fjords and the surrounding area regulate water movements/ stabilities and nutrient supplies (through advection and upwelling) and are therefore of up-most importance in structuring pelagic ecology, resulting C-flux to the seafloor and thus, benthic processes (Wassman 1991, Reigstad & Wassman 1996). West-Norwegian fjords are closely connected to continental shelf water masses and are therefore considered an integral part of the coastal zone, the Norwegian Coastal Current and the North Sea (Wassman 1991). The Korsfjord located roughly 25 km south of Bergen, Norway is approximately 690 m deep and possesses two arms, one of which runs WSW to the North sea and the other SSE where it connects with the northern end of the Hardanger fjord (Matthews & Sands 1973). Primary production estimates for the Korsfjord are on the order of greater than 100 g C m^{-2} yr^{-1}(Erga & Heimdal, 1984). However, although primary productivity estimates are known for the Korsfjord, no studies have ever been conducted to examine pelagic-benthic coupling in this deep-sea environment despite the fjord being very close (i.e. a 1 hour steam) to the University of Bergen's marine biological research station at Espeland. Given that Norwegian fjords are inhabited by typical deep-water communities (Brattegard 1979, Christiansen 1993, Witte et al. 2003b) and the Korsfjord's proximity to land, the fjord provided an ideal site for studies of deep-sea C-cycling by macrofaunal and foraminiferal communities – results of which are described in the third and forth chapters of this thesis.

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Response of an abyssal macrofaunal community to a phytodetrital pulse

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ABSTRACT: The majority of deep-sea benthic communities rely on organic matter (OM) sinking from the euphotic zone for energy, much of which is delivered in pulsed events. But we know little about abyssal plain macrofaunal communities, their response to such events or their role in deep-sea carbon-cycling. In this study, we examined the composition of the macrofaunal community at Station M in the deep NE Pacific and assessed their short-term response to a simulated OM pulse in two 36 hr *in-situ* enrichment experiments. In each experiment, 1.2 g C m^{-2} of ^{13}C-labelled *Skeletonema costatum* was deposited onto the seafloor using a benthic chamber lander. Macrofaunal abundance and biomass was significantly higher at 0-5 cm depth compared to 5-10 cm, and were dominated by the Nematoda and Crustacea, respectively. Twenty-five percent of the macrofauna specimens showed ^{13}C-signatures indicative of label ingestion, but specific uptake ($\Delta\delta^{13}C$) and C-turnover rates varied strongly between and within taxa. Two organisms, a single cumacean from one chamber and a paraonid polychaete from chamber 2, were responsible for the majority of C-turnover, and had ingested up to 2.3 % of their body weight in C. Macrofaunal C-turnover was much lower than recorded in the abyssal NE Atlantic, which is most likely due to differences in the timing of the experiments relative to the spring/ summer bloom, different experimental durations and disparities in macrofaunal community structure. These results emphasize the degree of plasticity inherent in the macrofaunal response to a food pulse and stress the need for comprehensive *in-situ* investigations to further our understanding of deep-sea benthic ecosystem functioning.

KEY WORDS: Abyssal plain ▪ North east Pacific ▪ Deep sea ▪ Pulse-chase experiments ▪ $\delta^{13}C$ ▪ $\delta^{15}N$ ▪ Natural isotopic signatures ▪ Benthic carbon remineralisation ▪ Macrofauna

INTRODUCTION

Prior to the early 1980s, it was thought that the majority of deep-sea communities derived their energy from a constant 'drizzle' of relatively refractory organic matter. However, within the last 25 years it has become apparent that this 'rain' of particulate organic matter (POM) can be punctuated by large, episodic, pulses of labile POM to the seafloor (Deuser & Ross 1980, Billet et al. 1983). It is from these downpours of organic matter that the majority of deep-sea communities obtain most of their energy (Gooday 1988, Graf 1989, Pfannkuche 1993), with the exception of reducing systems. Recent studies have additionally shown from both time-lapse camera systems and sediment trap moorings that large inter-annual variations in the supply of POM to the deep-seafloor do exist, and are regular features of this environment (Baldwin et al. 1998, Smith et al. 1994, Smith et al. 2001, Smith et al. 2006). Furthermore, rapid responses to POM input by a number of deep-sea benthic taxonomic groups from microbes (Pfannkuche 1993, Lochte & Turley 1988) and protozoa (Gooday 1988, Drazen et al. 1998), to megafauna (Tyler et al. 1982, Smith et al. 1994, Lauerman et al. 1997, Bett et al. 2001) have been identified.

Macrofaunal communities can provide helpful information about the quality and quantity of OM arriving at the seafloor, and can assist in predicting its overall fate within the sediment. For example, the vast majority of macrofauna found at abyssal depths are considered deposit feeders (Hessler & Jumars 1974) that, through bioturbation and feeding, considerably re-work sediment thus affecting the early diagenesis of recently

deposited organic matter (Levin et al. 1997). However, owing to the inherent costs and difficulties associated with sampling deep-sea environments, especially abyssal habitats, detailed knowledge of deep-sea macrofaunal trophic interactions, including their access to and ingestion rates of POM have yet to be established.

Conventional analysis using gut-contents to infer food-web structure in the deep-sea has proved successful for the megafauna (Lauerman et al. 1997), but is almost impossible to carry-out on small-sized biota, such as macrofauna. Recently, the establishment of stable isotope techniques has created numerous opportunities for studying macrofaunal trophic interactions (Iken et al. 2001), and the development of the pulse-chase approach has allowed direct quantification of C-flow through benthic food-webs (Middelberg et al. 2000, Witte et al. 2003a). In *in-situ* pulse-chase experiments at abyssal depths, Witte et al. (2003a) found during a 60 h experiment that of the bacteria, foraminifera, nematoda and macrofauna, the macrofauna responded and processed C faster when incubated with fresh phytodetritus. Witte et al. (2003b) reported a similar reaction by infaunal macrofauna from the deep Norwegian Sognefjord (1265m) during a 3 d experiment. Furthermore, a detailed study by Aberle & Witte (2003) revealed that, of the dominant taxa, crustaceans were of minor importance in C-cycling in the abyssal NE Atlantic, but cirratulid and spionid polychaetes played a leading role in re-working freshly deposited material, in a similar manner to the maldanid and paraonid polychaetes on the Carolina continental slope (Levin et al. 1997, 1999).

The coupling of pelagic and benthic processes has been studied repeatedly since 1989 in the abyssal NE Pacific at Station M (Smith & Druffel 1998, see Deep-Sea Research II, v. 45 for a review), however, detailed information on macrofaunal

community structure and trophic interactions is lacking for this site and for the abyssal Pacific in general. This study therefore examines macrofaunal community composition at Station M and explores food-web structure using natural C and N isotopic signatures. We also describe for the first time, the short-term response of an abyssal Pacific macrofaunal community to a simulated phytodetritus pulse. We present *in-situ* data from two replicate enrichment experiments carried out at Station M using a benthic chamber lander in October 2004. Diatoms, labeled with ^{13}C, were incubated for a period of 36 h over a known area of seafloor, and uptake of labelled C into the metazoan macrofauna was subsequently measured. We specifically focused our attention on the polychaetes, since this group comprises a number of dominant functional groups whose diversity is known to affect biogeochemical fluxes (e.g. PO_4^{3-} and O_2), profiles, (e.g. O_2 and pH) and transport rates in addition to rates of organic matter remineralisation (Levin et al. 1997, 1999, Aberle & Witte 2003, Waldbusser et al. 2004, Waldbusser & Marinelli 2006).

MATERIALS AND METHODS

In late October 2004, during cruise PULSE 45 of the RV 'NEW HORIZON', *in-situ* pulse-chase experiments were carried out at Station M (Fig. 1 - centered at 34°50'N, 123°00'W; ca. 4100 m water depth), located approximately 220 nm west of Point Conception, California at the base of the Monterey Deep-Sea Fan. The seafloor at Station M is characterised by silty-clay sediments with an organic C-content of approximately 17 mg C g^{-1} and possesses little topographical relief (<100 m over 1600 km^2) (Smith et al. 1994, Smith & Druffel 1998, Smith et al. 2001).

A non-axenic clone of the diatom *Skeletonema costatum* (Bacillariophyta) was used as a labelled food source in our experiments. This diatom species was chosen as a suitable food source since it occurs within the vicinity of, and has been sampled in sediment traps moored above the seafloor at Station M (Venrick 1998, Beaulieu & Smith 1998). Algae were cultured in an artificial seawater medium modified with F/2 (Grasshoff et al. 1999). The culture medium was amended by replacing 25 % of ^{12}C bicarbonate with $NaH^{13}CO_3$. Diatoms were cultured for 3 wk at 15^{o}C under a 16:8 h light/dark cycle and harvested. To harvest, inoculums were concentrated by centrifugation (1500 rpm x 5 min), washed 4 times in a isotonic solution to remove excess labelled bicarbonate and freeze dried. Algae possessed a ^{13}C-content of 7.9 ± 0.4 atom % (n = 6) and a C: N ratio of 9 ± 1 (n = 6). Comparatively similar C:N ratios of added algae to seafloor phytodetrital aggregates (C: N = 11) sampled in September 1994 at Station M (Smith et al. 1998) suggest that the OM used was representative of natural phytodetritus entering the benthic boundary layer (BBL) in autumn.

Macrofaunal community structure was assessed from 3 multiple corer (MUC) and 3 benthic chamber sediment samples. Macrofauna from the MUC cores were additionally used for natural or 'background' $\delta^{13}C$ and $\delta^{15}N$ measurements. MUC cores were sampled at a depth of 4062 m, and processed in a cold-room once back onboard. All three cores (78.5 cm^2; 10 cm ø) were sectioned at 0-2 cm and 2-5 cm, but one core was additionally sampled at 5-10 cm. Sectioned sediment horizons were immediately sieved for metazoan macrofauna (>250 μm) and all sieved organisms transferred to 4 % buffered formaldehyde solution for long-term storage and refrigerated. Macrofauna from the 3 benthic chambers were sampled at 0-2 cm, 2-5 cm, and 5-10 cm sediment depth and

processed in the same way as above. The macrofaunal abundance and biomass determined from MUC cores and benthic chambers did not differ significantly with sampling technique (macrofaunal abundance: t-test, $t_4 = 0.693$, $p = 0.526$ and biomass: t-test, $t_4 = 0.953$, $p = 0.394$).

In-situ pulse-chase experiments were carried out during a single deployment of a deep-sea benthic chamber lander. The lander carried 3 independent, autonomous benthic chambers (400 cm^2) with each chamber separated from the other by approximately 0.5 m. For a description of the lander see Witte & Pfannkuche (2000). Two hours after arriving on the seafloor, approximately 250 mg of labile algal C, equivalent to 1.2 g C m^{-2} (or ~ 40 % of the annual C-supply to the BBL), was injected into two chambers and homogenously distributed by stirrers mounted in the chamber lids. Approximately 1 min after algal injection stirrers were switched off for 1 h to allow the labelled algae to sink. Stirrers were then turned on and the chamber waters gently mixed (without creating sediment resuspension) for the duration of the 36 h *in-situ* incubation. After 36 h, the lander was recalled to the surface. Unfortunately, the algal injector in the third chamber failed to work in concert with the other two and only fired during the recovery of the lander thus, contaminating this 'control' chamber. Once onboard, half of the enclosed sediment (200 cm^2) in each chamber was sectioned and processed as above. In an effort to gather greater numbers of animals for C-uptake measurements, an additional core (28.3 cm^2; 6 cm ø), initially sectioned and preserved unsieved for foraminifera (0-2 & 2-5 cm), was taken from the 2nd half of each chamber and later sieved in the laboratory for metazoan macrofauna (>250 µm). Sieved animals from both the 28.3 cm^2 core and 200 cm^2 sediment samples from 0-2 and 2-5 cm were then pooled.

In the laboratory, sieved samples were picked for macrofauna (>250 μm) in cooled artificial seawater (salinity 35) under a binocular microscope and transferred to 4 % buffered formaldehyde solution. To derive information from macrofaunal natural isotopic signatures about potential food sources at Station M, $\delta^{13}C$-signatures from 'background' macrofauna were corrected for formaldehyde preservation effects by adding 1 ‰ to each $\delta^{13}C$ value (Kaehler & Pakhomov 2001, Sarakinos et al. 2002). Only 13 of the 25 macrofaunal samples measured for background C and N signatures possessed enough biomass for natural $\delta^{15}N$ measurements. Preservation effects on stable isotope signatures were considered to be negligible (~0.5 - 1 ‰ – L. Levin & C.R. Smith pers. comm.) compared to tracer uptake and thus, no corrections were applied to 'background' or 'enriched' signatures when calculating specific uptake of ^{13}C and C-turnover. Separate picking utensils were used for background and labelled samples to avoid contamination of stable isotopes. Organisms were identified to major taxon, with polychaetes being identified to family or lowest taxonomic level possible. Crustacea were identified to class or order. Single organisms were cleaned of attached organic debris in cooled, clean artificial seawater (salinity 35), placed in silver caps and dried at 35-40^{o}C for a period of 2 wk. Calcareous shelled organisms were decalcified with 2M HCl in double boated silver caps and dried as above. In order to obtain sufficient biomass for isotope measurements, some individual organisms (See Table 1) were combined as in Aberle & Witte (2003) and Kamp & Witte (2005). Prior to isotopic analysis, all organisms were weighed on an electronic microbalance (Sartorius) for biomass determinations (mg dw).

From the 2nd half of each benthic chamber, a 6 cm (ø) core was taken for determination of total organic (TO) ^{13}C-signatures of the sediment ($\Delta\delta$TO ^{13}C). Each core was extruded at 1 cm intervals from 0 to 5 cm, 2 cm from 5 to 7 cm, and 3 cm from 7 to 10 cm. Cutlets were placed in brown glass bottles and immediately frozen at -20 ^{o}C. Background sediment samples were collected from a 4th MUC core (78.5 cm^2; 10 cm ø; 4062 m depth) and processed in the same way. Upon return to the laboratory, each cutlet was freeze dried for 4 d and homogenized using a pestle and mortar. From each homogenized horizon, approximately 50-100 mg of freeze dried sediment was transferred to a pre-combusted glass tube (550^{o}C for 5 h) and decalcified overnight with 10 % HCl. Decalcified sediment was vigorously washed 4 times with Milli-Q water, concentrated by centrifugation and dried at 50^{o}C for 3 d. Approximately 30 mg of post-acidified sediment was then transferred to tin caps for isotope ratio mass spectrometry analysis.

The isotopic ratios of the macrofaunal organisms were measured using a Finnigan Delta plus XP (Thermo) Isotope Ratio Mass Spectrometer (IRMS) at MPI Bremen (reproducibility: $\delta^{13}C$ = 0.2 ‰, $\delta^{15}N$ = 0.8 ‰) and those of the sediment samples analysed using a Europa Integra (enriched isotopes) and Hydra 20/20 (natural isotopes) IRMS at UC Davis (reproducibility: $\delta^{13}C$ = 0.02 ‰, $\delta^{15}N$ = 0.06 ‰). Macrofaunal C-isotopic ratios ($^{13}C/^{12}C$) were measured against a PDB-standard and are expressed as delta notation ($\delta^{13}C$) as relative difference between sample and standard: $\delta^{13}C$ (‰) = $(^{13}C/^{12}C_{sample})/ (^{13}C/^{12}C_{standard})$ -1] x 10^3. Specific uptake of ^{13}C by macrofaunal organisms was calculated as excess (above background) and is expressed in $\Delta\delta^{13}C$ notation: $\Delta\delta^{13}C = \delta^{13}C_{sample} - \delta^{13}C_{background}$. Turnover of ^{13}C was calculated as the product of the excess atom % ^{13}C (difference in atom % ^{13}C between sample and

background) and C-content (expressed as unit weight): C-turnover (unit wt C) = [(atom % $^{13}C_{sample}$ – atom % $^{13}C_{background}$) x (unit wt C of organism). Specific labelling ($\Delta\delta TO^{13}C$) of sediment was measured relative to a PDB standard and expressed as excess above background as $\Delta\delta TO^{13}C = \delta TO^{13}C_{sample} - \delta TO^{13}C_{background\ sediment}$.

RESULTS

Macrofaunal abundance and biomass

Total macrofaunal density was 6165 ± 3751 ind. m^{-2}/ 2462 ± 396 ind. m^{-2} (SD, n = 4, incl./ exc. nematodes). Total biomass was 509 ± 226 mg dw m^{-2}/ 485 ± 227 mg dw m^{-2} (SD, n = 4, incl./ exc. nematodes), respectively. The top 2 cm of sediment at Station M comprised the greatest concentration (53 %) of macrofauna with 4350 ± 2270 ind. m^{-2} (n = 6, incl. nematodes, Fig. 2a). Macrofaunal abundance decreased below 2 cm sediment depth with 42 % (3419 ± 1986 ind. m^{-2}, n = 6, incl. nematodes) and 5 % (432 ± 390 ind. m^{-2}, n = 4, incl. nematodes) found within the 2-5 cm and 5-10 cm horizons, respectively (Fig. 2a). Significantly higher abundances were found in the 0-5 cm horizon compared to the 5-10 cm layer (t-test, $t_6 = 3.132$, $p = 0.020$) when adjusted for multiple testing (Holm 1979). Maximum biomass values were observed at 0-2 cm (Fig. 2b). After correcting for multiple testing (Holm 1979), biomass values were significantly different between 0-5 and 5-10cm depth (t-test, $t_6 = 2.998$, $p = 0.024$). The majority of organisms (95 %) and biomass (82 %) were found within the top 5 cm (Figs. 2a & b). Due to the presence of a single large opheliid polychaete (1172 mg dw m^{-2}) in chamber BC1 drastically altering biomass estimates, this animal was removed from further analysis. Macrofaunal community composition is given in figures 3 to 5. Altogether, ten

major macrofaunal taxa were found at Station M. The nematoda contributed 60 % to macrofaunal abundance, but only 6 % to overall biomass. The crustacea were the second most abundant taxon (23 %) and made up 43 % of the biomass, followed by the polychaeta, which contributed 8 % to overall abundance and 29 % to biomass. Although the Harpacticoida were the most abundant (56 %) crustacean group, the Ostracoda made up for most of the crustacean biomass (40 %). Members of the family Paraonidae (20 %) and Pilargidae (15 %) were the most common polychaete families found, but the Capitellidae contributed by far the most biomass (65 %), followed by the Paraonidae (10 %).

Natural isotopic signatures and ^{13}C labelling experiments

Natural $\delta^{13}C$- and $\delta^{15}N$-signatures are summarized in figure 6 a & b, respectively. Delta ^{13}C-signatures showed negative values and ranged from -15.8 to -27.8 ‰. The highest and lowest $\delta^{13}C$-signatures were measured for an ostracod (-15.8 ‰) and a syllid polychaete (-27.8 ‰), respectively. Natural $\delta^{13}C$ signatures of polychaetes (n = 14) and crustaceans (n = 7) were -20.2 ± 2.7 ‰ and -19.1 ± 2.1 ‰, respectively. Delta ^{13}C- and ^{15}N-signatures of surface ($\delta^{13}C$ = -19.5 ‰, n = 2, $\delta^{15}N$ = 16.5 ‰, n = 2) and sub-surface deposit feeding polychaetes ($\delta^{13}C$ = -19.6 ± 1.1 ‰, n = 7, $\delta^{15}N$ = 17.8 ± 1.2 ‰, n = 4) showed little variation amongst functional groups. Carnivorous polychaete families were on average slightly lighter, but comparable (-20.8 ‰, n = 4), although they displayed far more variability (range: -17.2 to -27.8 ‰) in ^{13}C over deposit feeding polychaetes. Mean $\delta^{15}N$-signatures of carnivorous (18.1 ‰, n = 2) vs. sub-surface deposit feeding polychaetes were approximately identical. Amongst the polychaetes, a pilargid of the species *Ancistrosyllis homata*, showed the highest $\delta^{13}C$-signature (-17.2 ‰), and a syllid

polychaete of the genus *Brania* sp. possessed the lowest (-27.8 ‰), whilst δ^{15}N-signatures ranged from 15.6 ‰ for the Ampharetidae to 19.4 ‰ for the Opheliidae. Natural δ^{13}C measurements for the crustaceans ranged from -15.8 ‰ (Ostracoda) to -21.4 ‰ (Tanaidacea), and δ^{15}N-signatures for the harpacticoida and isopoda were 14.3 ‰ and 15.7 ‰, respectively. We did not observe background δ^{13}C-signatures higher than -15.8 ‰. Thus, in our enrichment experiments we considered signatures > -14 ‰ as evidence of uptake of ^{13}C from our labelled algae (Aberle & Witte 2003). Delta^{13}C- and δ^{15}N-signatures of decalcified sediment at Station M were -22 ± 0.1 ‰ (n = 7) and 9 ± 0.1 ‰ (n = 7), respectively.

The isotopic signatures of macrofaunal organisms retrieved from both experimental chambers are shown in table 1. A number of macrofaunal organisms rapidly incorporated the ^{13}C-labelled phytodetritus with 37 % (BC2) and 13 % (BC3) of the macrofauna showing δ^{13}C-signatures indicative of phytodetritus ingestion after 36 h (Table 1). Enrichment was modest in most organisms with only 3 individuals, a cumacean ($\Delta\delta^{13}$C = 127 ‰) from chamber 2 and an isopod ($\Delta\delta^{13}$C = 295 ‰) and paraonid polychaete ($\Delta\delta^{13}$C = 165 ‰) from chamber 3, showing $\Delta\delta^{13}$C-signatures greater than 100 ‰. At the same time, a large degree of variation was observed in enrichment between related taxa within and between each chamber. For example, a single paraonid polychaete from chamber 3 showed a $\Delta\delta^{13}$C-signature of 165 ‰, whilst additional paranoids in BC3 possessed δ^{13}C-signatures of < -14 ‰. Similar patterns were also seen amongst the paranoids in BC2 and the isopods in BC3. Highest enrichment occurred in the top 5cm of sediment (Fig. 7).

C-turnover rates are shown in table 1. Mean metazoan macrofaunal C-uptake was 3.4 x 10^{-3} % of the C added. Highest turnover rates were found at 0-2 cm where 96 % (BC2) and 70 % (BC3) of the C was processed. However, there was an order of magnitude difference in C-uptake between chambers BC2 and BC3. Counting the two amphipods in chamber 2, 1.7 % (BC2) and 3.1 % (BC3) of the combined biomass (C) measured by IRMS analysis was directly involved in C-turnover. Profiles of sedimentary $\Delta\delta TO^{13}C$ profiles are shown in fig. 8.

DISCUSSION

Metazoan macrofaunal abundance decreases exponentially with increasing water depth (Flach & Heip 1996, Cosson et al. 1997). Macrofaunal abundance was similar to macrofaunal densities observed in previous investigations at Station M (Drazen et al. 1998, mesh size 300 µm), and higher than those observed at the Porcupine Abyssal Plain (PAP - Aberle & Witte 2003), the Goban Spur (Flach & Heip 1996), and the southern Arabian Sea (Witte 2000). Previous investigations have noted a linear relationship between organic carbon flux and macrofaunal density (e.g. Cosson et al. 1997). Higher particulate organic carbon fluxes to the seafloor at Station M (~ 2.4 g C m^{-2} yr^{-1}, Baldwin et al. 1998) in contrast to the NE Atlantic (~ 1.3 g C m^{-2} yr^{-1} at PAP, Lampitt et al. 2001) and the southern Arabian Sea (~ 1.3 g C m^{-2} yr^{-1}, Honjo et al. 1999), probably account for the higher densities we observed at Station M. Assuming an annual POC flux of 2.4 g C m^{-2} yr^{-1} at Station M (Baldwin et al. 1998), our mean macrofaunal abundance estimates fit well into the regression published by Cosson et al. (1997).

The majority of metazoan macrofauna density and biomass was found in the top-most 5 cm thus, adhering to profiles observed in previously studied continental slope (Blake 1994, Blair et al. 1996) and abyssal habitats including Station M (Drazen et al. 1998) and the Porcupine Abyssal Plain (Aberle & Witte 2003). Metazoan macrofaunal biomass profiles with depth echoed those of abundance and were comparable to previous abyssal studies undertaken by Drazen et al. (1998) and Aberle & Witte (2003).

The standard deviations of our macrofaunal density and biomass estimates were extremely large, suggesting high spatial heterogeneity amongst the macrofaunal community - a pattern also noted by Drazen et al. (1998). Like Drazen and his co-workers, we found no significant difference in macrofaunal abundance or biomass in relation to sampling technique [multicorer (78.5 cm^2) and benthic chamber lander (400 cm^2)]. Processes that drive macrofaunal community spatial structure such as the presence or absence of biogenic structures (Thistle 1979, Shaff & Levin 1994, Levin et al. 1986) must therefore function at scales different from the area difference enclosed by both sampling devices.

Previous publications point to the dominance of either polychaetes (Shaff & Levin 1994, Flach & Heip 1996, Cosson et al. 1997, Galeron et al. 2001) or crustaceans at deep-sea environments (Drazen et al. 1998, Witte 2000, Aberle & Witte 2003). In the present study, the crustaceans were the most abundant group (exc. nematodes) and contributed most to overall biomass. However in an earlier investigation at Station M, Drazen et al. (1998) found the polychaetes to contribute more to community biomass - a discrepancy most likely due to the high spatial heterogeneity of macrofauna previously discussed.

As already stated, crustaceans were numerically dominated by the Harpacticoida but by the Ostracoda in terms of biomass. Drazen et al. (1998) also reported that the Harpacticoida were the most dominant crustacean group in their study but found the Isopoda to contribute more to overall crustacean biomass. Of the polychaetes sampled, the Paraonidae were most abundant. In a study carried out on the central equatorial Pacific abyssal plain, Glover et al. (2002) reported that the polychaete assemblage was highly dominated by members of the Paraonidae (~ 17 %). Paterson et al. (1998) found relatively high densities of paraonid polychaetes (range: 8.5 - 15.2 %) from three sites in the equatorial Pacific, and Shaff & Levin (1994) reported elevated densities of the paraonid *Levinsenia gracilis* in the vicinity of biogenic structures such as tubes, pits and mounds. Furthermore, in a feeding study conducted on the continental slope off the east coast of the USA, Levin et al. (1999) noted that paraonids were very active sediment and diatom ingesters, leading the authors to postulate that paraonids were opportunistic/ flexible feeders. It is this opportunistic lifestyle that probably allows the paraonids to reach high densities in relation to other polychaetes at the food-limited seafloor of Station M.

Lack of accessibility to, and the high costs and risks associated with conducting research in the deep-sea means that relatively little is still known about macrofaunal feeding ecology. Very often, inferences on deep-water feeding guilds are drawn based on animal mouth morphologies and/ or feeding-modes of shallow-water analogues. In recent years the use of natural stable C and N isotope measurements and more recently, the pulse-chase approach have provided insightful information about macrofaunal feeding ecology and C-flow through deep-sea food-webs (Fry & Sheer 1984, Levin et al. 1999,

Iken et al. 2001, Aberle & Witte 2003, Witte et al. 2003a). Natural δ^{13}C-signatures of the macrofauna at Sta. M (-19.9 ± 2.4 ‰) suggested a dependency on a phytoplankton-based food web (Fry & Sherr 1984). Natural ^{13}C-isotopic signatures measured in the present study were comparable to those measured from two bathyal sites located off the Carolina margin by Levin et al. (1999). In comparison to the PAP where polychaetes and crustaceans showed average δ^{13}C-signatures of -25 and -24 ‰, respectively (Aberle & Witte 2003), polychaetes and crustaceans from Station M exhibited heavier signatures, suggesting more recent ingestion of a fresh C source. Aberle & Witte (2003) conducted their experiments in May/ June 2000 before the pulse of exported phytodetritus had settled to the abyssal plain, in contrast to the present investigation that was carried out in late October 2004 - a mere 3 - 4 mo after the peak POM pulse, around the same time as the autumn POM pulse event (Baldwin et al. 1998, Drazen et al. 1998, Smith et al. 2001). Druffel et al. (1998) showed that POC settling at a depth of 3450 m in the water column at Station M in September 1994 possessed a δ^{13}C-signature of ~ 21 ‰. Thus, if we assume a ^{13}C-enrichment of 1 ‰ per trophic step (Fry & Sheer 1984), it seems plausible that the heavier signatures measured in our study were the result of fauna assimilating a fresher, more labile food source than those sampled by Aberle & Witte (2003). This assertion is further supported by the results of Iken et al. (2001) who measured natural ^{13}C-signatures in polychaetes and crustaceans at the PAP in September 1996 and July 1997 (immediately after the peak POM pulse) and found lower δ^{13}C-signatures of -17.4 ± 1.4 ‰ and -17.9 ± 1.2 ‰, respectively. Mean natural δ^{13}C- and δ^{15}N-signatures of deposit feeding and carnivorous polychaetes were surprisingly similar (Fig. 6 a & b), despite carnivores generally living at higher trophic levels and thus exhibiting heavier

isotopic signatures compared to deposit-feeding animals. Nevertheless, a large degree of variability was evident in $\delta^{13}C$-signatures of carnivorous polychaetes owing to a very lightly labelled syllid of the genus *Brania* sp. The majority of the Syllidae have been classified as carnivores by Fauchald and Jumars (1979) and Gaston (1987), but based on the $\delta^{13}C$-signature found for *Brania* sp., we postulate that this particular genus ingests highly refractory detritus, but may alter its diet serving as a carrion feeder and/ or carnivore when the opportunity occurs (Fauchald & Jumars 1979). Due to the small size of this animal we were unable to measure its $\delta^{15}N$-signature and as such this statement must remain a postulation until further studies are conducted. Surprisingly, of all the taxa measured for $\delta^{15}N$, none appeared to feed directly on sediment and associated phytodetritus, assuming a ^{15}N-enrichment of 3.5 ‰ per trophic level (Fry & Sherr 1984, Fry 1988) and a sediment plus POM $\delta^{15}N$-signature of 9 ± 0.1 ‰ that is in good agreement with previous $\delta^{15}N$-signatures for POM (Iken et al. 2001). Rather, the Harpacticoida, Isopoda, Aplacophora, and Ampharetidae appeared to be feeding in the 2^{nd} trophic level ($\delta^{15}N > 12.5$ ‰, Fig. 6b) with the remaining polychaetes, nematodes and those unclassified animals feeding in the 3^{rd} ($\delta^{15}N > 16$ ‰, Fig. 6b). Since trichobranchid and paraonid polychaetes have been previously classified as surface and sub-surface deposit feeders, respectively (e.g. Fauchald & Jumars 1979, Gaston 1987, Levin et al. 1997, 1999), it is possible that the large $\delta^{15}N$-signatures measured for these two taxa ($\delta^{15}N > 17$ ‰) resulted from IRMS sample reproducibility error. Additionally surprising was the extremely large $\delta^{15}N$-signature of the opheliid polychaetes analyzed that suggested a carnivorous, as opposed to a detritivore lifestyle, which has been previously proposed in the literature (Fauchald & Jumars 1979). The opheliid

polychaetes sampled may have instead been preying on protozoans (Fauchald & Jumars 1979).

Remarkably, only a small fraction of the macrofauna sampled from both chambers showed $\delta^{13}C$-signatures indicative of ^{13}C-ingestion. This differs sharply with *in-situ* pulse-chase experiments carried out at the PAP by Aberle and Witte (2003) who found after only 2.5 d, approximately 77 % of the polychaetes and crustaceans (ca. 95 % of the macrofauna) were already labelled. Vertical $\Delta\delta^{13}C$ profiles highlighted the relative importance of the top sediment layers (0 - 5 cm) in abyssal C-cycling, and indicated that deeper-dwelling macrofauna had far less access to the labelled food source than those living within the top 5 cm. These findings concur with earlier invesitigations carried out in the abyssal NE Atlantic (Aberle & Witte 2003, Witte et al. 2003a), deep Sognefjord (Witte et al. 2003b) and a shallow shelf habitat (Kamp & Witte 2005). Jumars et al. (1990) hypothesized that in environments characterized by highly sporadic food-supply and scarce food resources (e.g. abyssal regions), fauna bury with food to deeper sediment layers in an effort to store food out of reach of competitors. Despite only a single ostracod from a single chamber showing $\Delta\delta^{13}C$ values greater than -14 ‰ at 5 - 10 cm depth (Table 1), $\Delta\delta TO^{13}C$ profiles did reveal the presence of small amounts of labelled material at 7 to 10 cm depth in both chambers. Although we cannot specifically assign a subduction mechanism for the $\Delta\delta TO^{13}C$ profiles observed it is possible that the presence of capitellid and paraonid polychaetes (Table 1) - families known for their burrowing lifestyles (Fauchald & Jumars 1979) – contributed to these distributions. If true, faunal-mediated burial of organic matter to deeper sediment layers provided highly reactive,

labile resources to fauna and microbes living beneath the surficial sediments (Levin et al. 1997, Witte et al. 2003b).

As stated before, both specific uptake ($\Delta\delta^{13}C$) and C-turnover rates varied between and within taxa and were almost negligible with the exception of 4 individual organisms. Of the 6 paraonids analysed, 4 showed background isotope signatures indicating no ingestion of our tracer, one had ingested a minor amount, whilst another individual was heavily labelled. In chamber 2, while ^{13}C uptake was detectable in one third of organisms, only one cumacean was heavily labelled and responsible for 85 % of C-turnover. In chamber 3, a total of 3 individuals were significantly labelled with the above mentioned paranoid being responsible for 57 % of C-turnover. This is especially noteworthy when one considers that these animals accounted for only 0.4 and 1.2 % of the total biomass (C), respectively, and had ingested up to 2.3% of their body weight in C.

Total C-turnover rates for the whole macrofaunal community at Station M were approximately two orders of magnitude lower than at the PAP (Witte et al. 2003a) in the NE Atlantic. When normalized to both the amount of C added and incubation time, the average C-turnover rate at Station M was 1.3 % of that in the NE Atlantic, with 2.3×10^{-3} % of algal C added being processed at Sta. M (in 24 h) compared to 0.18 % at PAP. While it is important to bear in mind the highly variable response in this study (total C-turnover by the macrofaunal community varied by an order of magnitude between replicates despite similar overall biomass in both chambers), this is likely to be due to the different fractions of the macrofauna community that had ingested significant amounts of ^{13}C-labelled OM (6.7 vs. 55 % of specimens, representing 1.4 vs. 97 % of the biomass at

Station M and PAP, respectively) and indicates that macrofaunal response patterns to fresh OM may vary seasonally. Witte et al. (2003a) carried out their investigation immediately prior to the maximum POM pulse settlement, whilst our experiments were carried out at approximately the same time as the autumn POM pulse event (Baldwin et al. 1998, Drazen et al. 1998). Also, sedimentary C_{org} content during the experiment was 4 times higher at Station M than at PAP (1.7 vs. 0.4 wt %). Therefore, an immediate response by the entire macrofaunal community coupled with elevated C-turnover rates at the PAP would be a reasonable trait of a severely food-limited community as opposed to a macrofaunal population that had very recently ingested fresh bloom C. Had our experiments been carried out at a similar time of year (i.e. immediately prior to the main POM pulse event when the fauna should naturally be more food-starved), and/ or for a similar duration (i.e. 60 instead of 36 h), we may have observed a reaction by the Station M macrofaunal community, both in terms of percentage labelled and macrofaunal C-turnover, that was similar to that measured at the PAP (Aberle & Witte 2003, Witte et al. 2003a).

Dissimilarities in macrofaunal community structure may also help to explain the different response patterns between Station M and the PAP. Aberle and Witte (2003) documented that surface deposit feeding cirratulid polychaetes: (1) were the most abundant polychaete family, (2) contributed most to polychaete biomass, and (3) showed some of the highest ^{13}C-signals measured, allowing them to speculate that this particular family plays a leading role in reworking freshly deposited POM in the NE Atlantic. At Station M however, the sub-surface deposit feeding Paraonidae and carnivorous Pilargidae were the most abundant polychaete families found, with the Cirratulidae

making up less than 10 %. Members of the Paraonidae and sub-surface deposit feeding Capitellidae also made up the largest fraction of polychaetes in our two replicate experiments, making it reasonable to assume that they had far less access to our fresh food source than would surface-deposit feeding polychaetes. Thus, the larger assemblage of sub-surface deposit feeding polychaetes and smaller, sometimes absent (chamber 2), surface-deposit feeding polychaete community in our two replicate experiments may additionally explain the comparatively small amount of C processed at Station M.

All of these findings emphasize the amount of heterogeneity and plasticity in the response to a food pulse on the family, taxon and community levels. Reasons for this variability may stem from variations in OM supply and demand (Aspetsberger 2005, Bühring et al. 2006), particle size (Wheatcroft 1992), age (Smith et al. 1993) and density (Mayer et al. 1993), as well as from variations in metabolic state, infaunal life history (Whitlach & Weinberg 1982), the degree of selective ingestion, assimilation and feeding modes of the taxa (Aberle & Witte 2003, Fauchald & Jumars 1979). Finally, our results stress the need for long-term, time-series pulse-chase experiments with multiple replication in order to reliably quantify, and identify reasons for temporal and spatial variations in macrofaunal C-cycling at abyssal depths.

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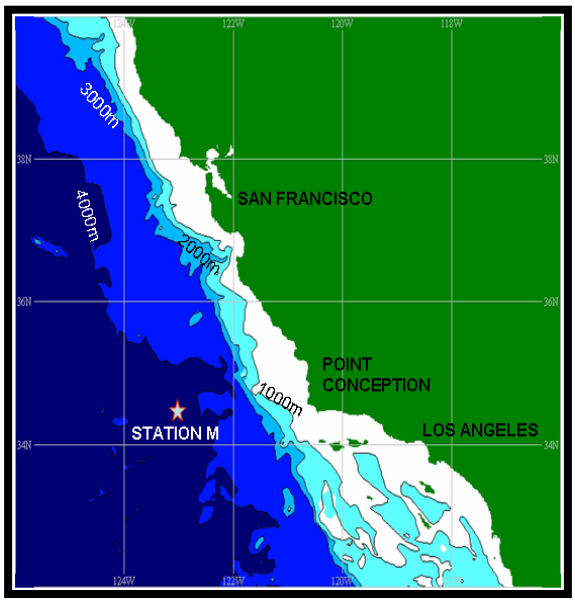


Figure 1. Location of Station M in the NE Pacific

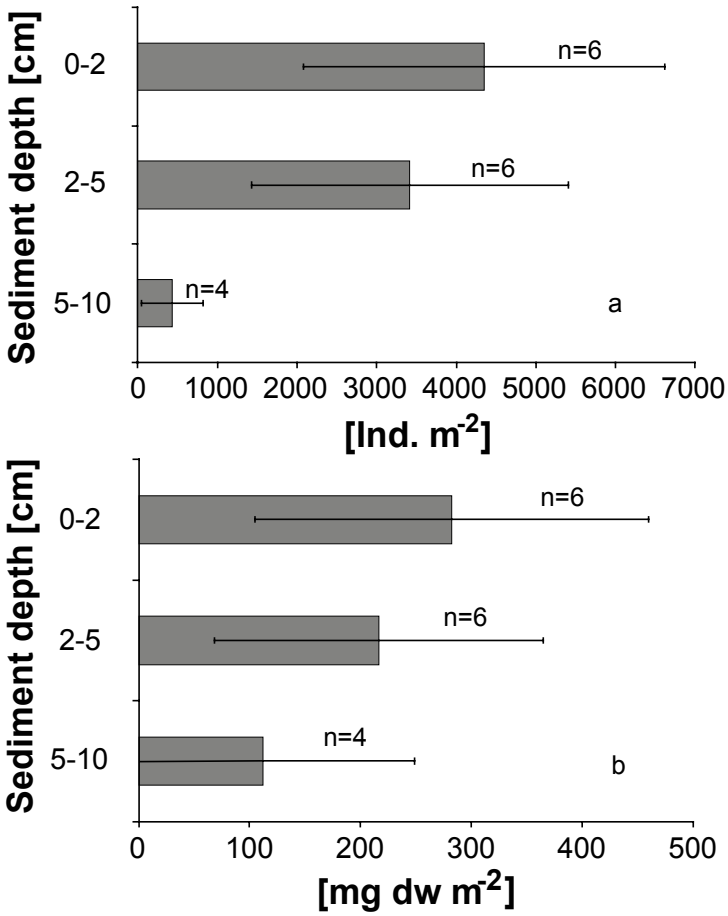
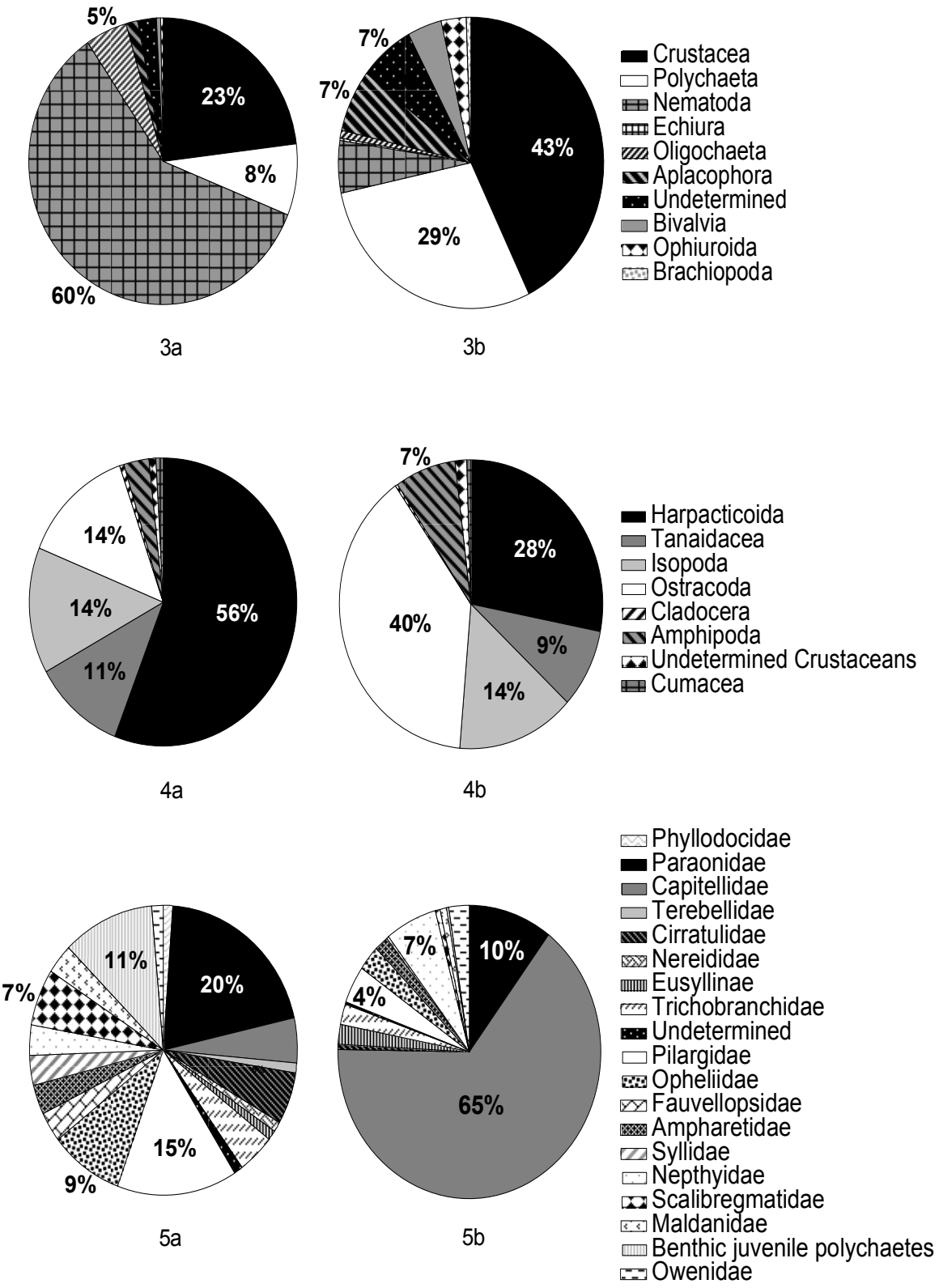


Figure 2. Vertical distribution of (a) total macrofaunal abundance and (b) biomass within the sediment column (0 - 10 cm) at Station M (±1 SD). n = 6 denotes samples from 3 x benthic chambers and 3 x MUC cores; n = 4 denotes samples from 3 x benthic chambers and 1 x MUC core.



Figures 3-5. Figure 3(a) Relative abundance (ind. m^{-2}) and (b) biomass (mg dw m^{-2}) of major macrofaunal taxa (incl. nematodes) at Station M (data from 3 x benthic chambers, 3 x MUC cores). Figure 4 (a) Relative abundance (ind. m^{-2}) and (b) biomass (mg dw m^{-2}) of major crustacean taxa at Station M (data from 3 x benthic chambers, 3 x MUC cores). Figure 5 (a) Relative abundance (ind. m^{-2}) and (b) biomass (mg dw m^{-2}) of major polychaete families at Station M (data from 3 x benthic chambers, 3 x MUC cores).

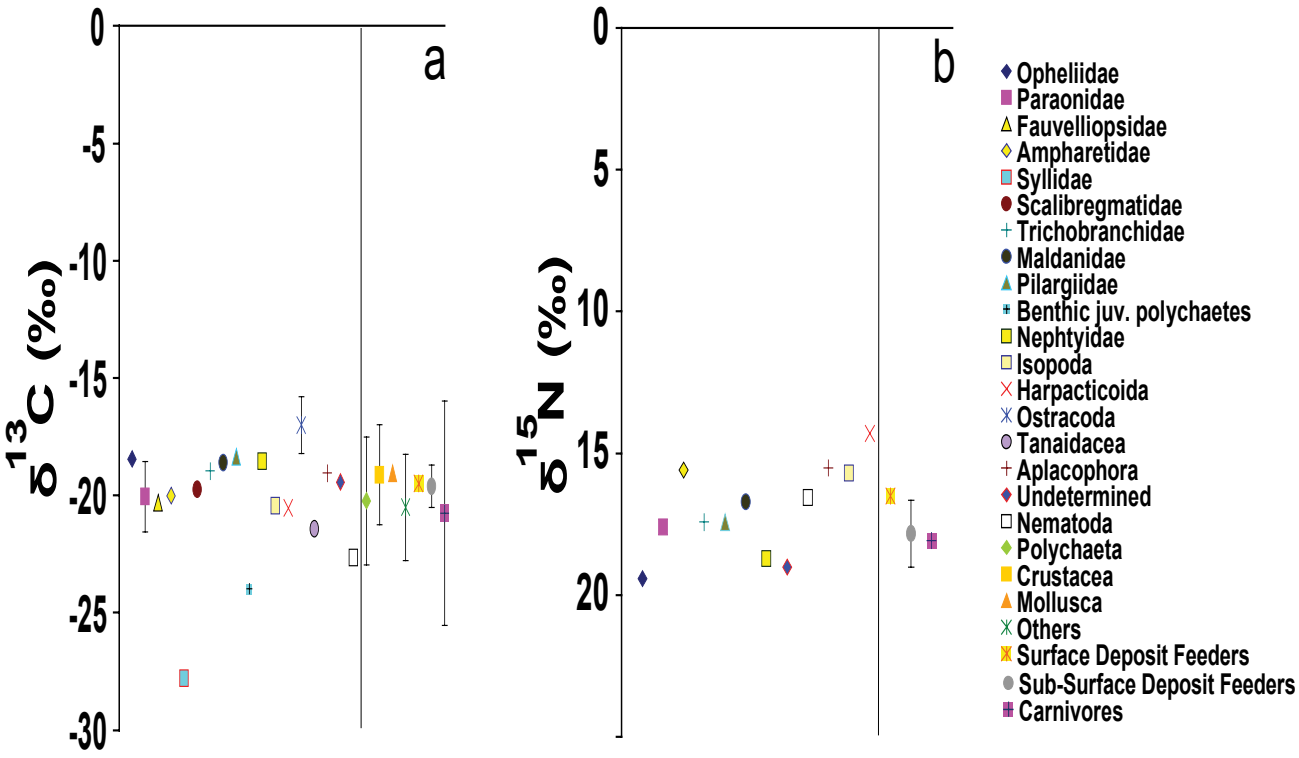


Figure 6. Natural (a) δ^{13}C-signatures and (b) δ^{15}N-signatures of MUC collected macrofauna taxa at Station M. Legends/ data points 'Polychaeta', 'Crustacea', and 'Mollusca', Surface- and Sub-Surface Deposit Feeders and Carnivores denote mean of natural isotopic signatures of all polychaetes, crustaceans, molluscs, surface deposit feeding, sub-surface deposit feeding and carnivorous polychaetes, respectively. 'Others' refers to mean of δ^{13}C-signatures of undetermined taxa and nematodes. Feeding guilds of polychaetes were determined from Fauchald & Jumars (1979). Vertical lines separate individual taxa and aforementioned groups. Bars denote ± 1 SD.

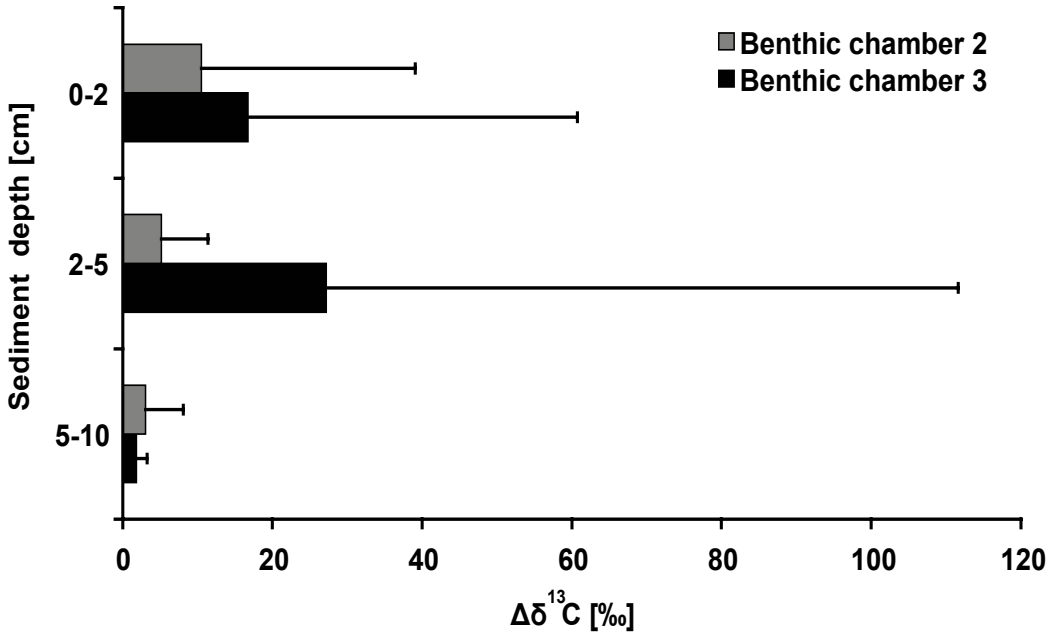


Figure 7. Vertical distribution of mean $\Delta\delta^{13}C$-signatures of macrofaunal taxa with sediment depth (0 - 10cm) at Station M. Bars denote +1 SD.

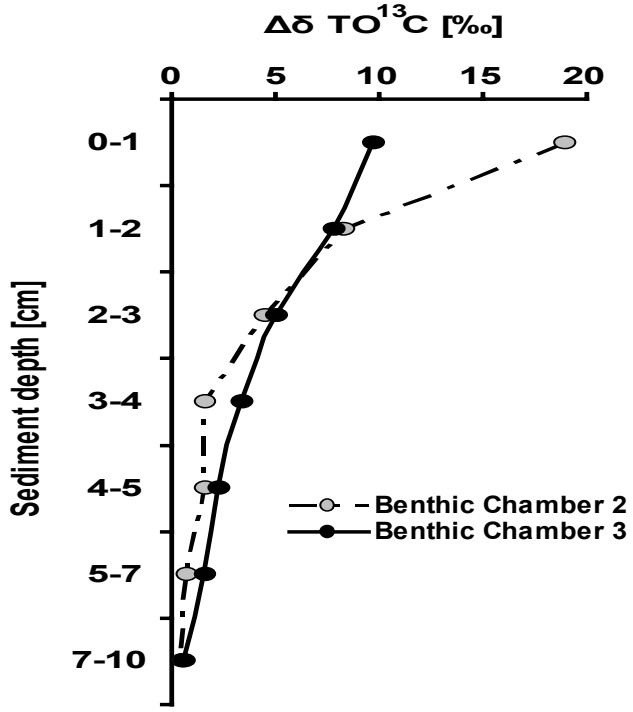


Figure 8. Specific labelling of total organic (TO) ^{13}C in the sediment ($\Delta\delta TO^{13}C$) in each replicate experimental chamber.

Table 1. Isotopic signatures and C-uptake of macrofaunal organisms within two replicate chambers (BC2 & 3) and their vertical position within the sediment column (0 - 10 cm) at Station M. n denotes number of organisms combined for 1 measurement. Undet.: undetermined. Note: in chamber 2, a single amphipod from the 0 - 2 cm was accidentally combined with an amphipod from 5 - 10 cm sediment depth prior to IRMS analysis. Since different areas of sediment were sampled from these two horizons (see Material and Methods); we were unable to calculate a value for C-uptake per unit area for these two pooled animals despite the sample showing a $\delta^{13}C$ signature of > -14 ‰.

TAXON	SEDIMENT DEPTH (cm)	BIOMASS (µg C)	n	$\delta^{13}C$ (‰)	$\Delta\delta^{13}C$ (‰)	C-TURNOVER (x 10^{-3} mg C m^{-2} d^{-1})	C-INGESTION (% of body wt C)
BENTHIC CHAMBER 2							
Crustacea							
Amphipoda	2-10	10.69	2	36.71	56.83	…	0.78
Harpacticoida	0-2	33.63	15	-20.93	…	…	…
Tanaidacea	0-2	30.36	5	-20.99	…	…	…
Cumacea	0-2	11.63	1	107.07	127.20	5.94	1.75
Cladocera	5-10	23.56	1	-21.56	…	…	…
Ostracoda	0-2	4.39	1	-20.57	…	…	…
Ostracoda	0-2	2.94	1	-12.36	5.64	0.06	0.07
Ostracoda	0-2	1.83	1	-11.56	6.44	0.05	0.08
Ostracoda	0-2	2.38	1	-12.03	5.97	0.05	0.08
Ostracoda	0-2	1.67	1	-5.73	12.27	0.08	0.17
Ostracoda	2-5	3.03	1	-13.95	4.05	0.05	0.05
Ostracoda	5-10	2.41	1	-9.55	8.45	0.09	0.11
Polychaeta							
Paraonidae	0-2	8.47	1	-8.08	12.97	0.44	0.18
Paraonidae	0-2	35.90	1	-19.29	…	…	…
Phyllodocidae	0-2	10.18	1	-18.96	…	…	…
Capitellidae	2-5	2510.37	1	-18.61	…	…	…
Other metazoa							
Bivalvia	0-2	7.06	1	-15.49	…	…	…
Bivalvia	0-2	3.12	1	-11.27	8.79	0.11	0.12
Bivalvia	2-5	8.93	1	-17.98	…	…	…
Bivalvia	5-10	26.88	1	-17.81	…	…	…
Nematoda	0-2	14.69	1	-19.28	…	…	…
Nematoda	0-2	18.07	10	-21.25	…	…	…
Nematoda	0-2	13.50	19	-20.85	…	…	…
Nematoda	2-5	23.19	8	-20.03	…	…	…
Nematoda	2-5	14.23	2	-19.74	…	…	…
Nematoda	2-5	19.31	24	-22.27	…	…	…
Brachiopoda	2-5	1.89	1	-2.45	19.06	0.15	0.26
Oligochaeta	0-2	13.09	6	-21.22	…	…	…
Undet.	0-2	8.07	1	-20.45	…	…	…
Undet.	0-2	7.66	1	-20.12	…	…	…

TAXON	SEDIMENT DEPTH (cm)	BIOMASS (µg C)	n	$\delta^{13}C$ (‰)	$\Delta\delta^{13}C$ (‰)	C-TURNOVER (x 10^{-3} mg C m^{-2} d^{-1})	C-INGESTION (% of body wt C)
BENTHIC CHAMBER 3							
Crustacea							
Amphipoda	0-2	811.42	1	-21.83	…	…	…
Harpacticoida	0-2	30.84	6	-21.33	…	…	…
Harpacticoida	0-2	26.30	13	-22.05	…	…	…
Tanaidacea	0-2	421.25	1	-16.22	…	…	…
Tanaidacea	0-2	20.15	1	-16.66	…	…	…
Tanaidacea	0-2	19.57	3	-20.21	…	…	…
Cumacea	2-5	25.21	1	-11.18	8.95	0.92	0.12
Isopoda	0-2	22.46	1	-17.02	…	…	…
Isopoda	0-2	14.16	1	-19.62	…	…	…
Isopoda	2-5	5.69	1	-22.38	…	…	…
Isopoda	2-5	11.66	1	273.75	295.19	13.84	4.06
Polychaeta							
Paraonidae	0-2	41.85	1	143.97	165.02	27.82	2.28
Paraonidae	2-5	79.12	1	-21.07	…	…	…
Paraonidae	2-5	21.15	1	-19.06	…	…	…
Paraonidae	5-10	50.43	1	-19.93	…	…	…
Trichobranchidae	0-2	26.56	1	-19.95	…	…	…
Cirratulidae	2-5	25.45	1	-20.31	…	…	…
Capitellidae	5-10	47.27	1	-20.05	…	…	…
Capitellidae	5-10	1522.89	1	-18.72	…	…	…
Undet. polychaete	2-5	14.81	1	-20.38	…	…	…
Other metazoa							
Ophiuroida	0-2	34.26	1	20.57	42.07	5.83	0.58
Nematoda	0-2	52.06	8	-19.40	…	…	…
Nematoda	0-2	43.58	45	-20.18	…	…	…
Nematoda	0-2	25.03	34	-22.83	…	…	…
Nematoda	2-5	63.62	1	-18.50	…	…	…
Nematoda	2-5	46.36	15	-21.37	…	…	…
Nematoda	2-5	33.72	29	-17.39	…	…	…
Nematoda	2-5	24.43	39	-20.68	…	…	…
Nematoda	2-5	18.04	12	-19.95	…	…	…
Nematoda	5-10	36.84	16	-19.86	…	…	…

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In revision for Deep-Sea Research

Macrofaunal community structure and response to a simulated phytodetrital input in a deep Norwegian fjord

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ABSTRACT: The continental margin constitutes approximately 1/10th of the surface area of the oceans but between 80 – 90 % of all organic matter is remineralised here. Recent evidence has suggested that macrofauna may play an important role in organic matter remineralisation in deep-sea continental margin sediments, and the deep fjords of Western Norway provide a relatively easily accessible opportunity for detailed studies of continental margin macrofaunal communities and their role in C-cycling. We examined the macrofaunal community and assessed their response to a simulated OM pulse in a fjord environment using pulse-chase tracer experiments. In each experiment, 1 g C_{org} m^{-2} of ^{13}C-labelled *Skeletonema costatum* was deposited onto intact sediment cores collected from 688 m water depth and incubated *ex-situ* for 2, 7 and 14 d. Macrofaunal abundance and biomass estimates were comparable to other deep-sea continental margin sediments of similar depths but in contrast to previous fjord studies, the macrofaunal community was numerically dominated by ostracods. Tracer experiments revealed highest uptake of tracer after 7 and 14 d compared to 2 d. Of the 7 deposit feeding polychaete families, only the Paraonidae & Cirratulidae - together with the largely carnivorous Lumbrineridae - showed a significant response to our labelled C-source. The lack of response by the majority of deposit feeders, and the unexpected feeding mode of the Lumbrineridae may be attributable to species- rather than family-specific feeding-ecologies and/ or ontogenetic changes in diet/ feeding mode. Total macrofaunal C-turnover was much lower than recorded in the deep Sognefjord in a 3 d feeding experiment, and is most likely a result of distinct differences in macrofaunal community composition between the two sites, with a predominantly sub-surface feeding macrofaunal assemblage in the Korsfjord as opposed to a surface-feeding community in

the Sognefjord. In conclusion, this investigation highlights the importance of ecological information on species level for a detailed understanding of C-cycling and early diagenesis in marine sediments.

Keywords: Macrofauna; Stable isotopes; Pulse-chase experiments; $\delta^{13}C$; Deep-sea fjord; Feeding

1. Introduction

The continental margins constitute 11 % of the surface area of the oceans, but 80 – 90 % of all organic matter remineralisation occurs here (Jørgensen, 1983; Middleburg et al., 1997). The majority of benthic communities which inhabit deep-sea continental margin sediments are reliant on the export of phytodetritus, and its more labile components from the euphotic zone for food. This export flux is by no means constant in time and can arrive at the seafloor in large, episodic, pulse-like events (Deuser and Ross, 1980; Billet et al., 1983). Once at the seafloor, a variety of organisms from microbes to megafauna feed on and process this phytodetritus, thereby affecting its early diagenesis (Gooday, 1988; Pfannkuche, 1993; Levin et al., 1997; Drazen et al., 1998; Bett et al., 2001). Therefore, to better understand early diagenetic processes at the deep-sea floor and the global C-cycle in general, we need to know how sedimentary organisms influence and shape these processes.

Although macrofauna are among the best studied faunal group in the deep-sea, very little is known about their trophic ecology. Traditional food-web analysis using gut-contents to deduce trophic structure has proven successful for the megafauna (e.g.

Lauerman et al., 1997; Ginger et al., 2001), but is very difficult to carry-out on small-sized biota, such as macrofauna. As a result, deductions about feeding mechanisms of macrofauna are often drawn based on mouth part morphologies and/ or information on feeding of shallow-water representatives of a certain taxon. Stable isotope techniques have provided an alternate approach and have allowed numerous insights into macrofaunal trophic interactions (Blair et al., 1996; Middelberg et al., 2000; Iken et al., 2001; Aberle and Witte, 2003; Witte et al., 2003a; Demopoulos et al., 2007; Sweetman and Witte, in press). Furthermore, tracer experiments using stable isotopically labelled phytodetritus have demonstrated that macrofauna are capable of 1) fast subduction (Blair et al., 1996; Levin et al., 1997) and 2) rapid ingestion (Witte et al., 2003a & b) of organic matter and are therefore important agents of C-turnover. In a short-term experiment in the deep NE Atlantic, the macrofauna responded and processed C faster when incubated with fresh phytodetritus than bacteria, foraminifera or nematoda (Witte et al. 2003a).

The relatively sheltered, and easily accessible deep-water fjords of western Norway are inhabited by typical deep-water benthic communities (Brattegard, 1979; Christiansen, 1993) and therefore provide a good setting to study how deep-sea macrofaunal communities respond to a food pulse. In this study, the response of a bathyal fjord macrofaunal community to a simulated food pulse is described over a 2 week period. We present data from a series of tracer addition experiments carried out *ex-situ* using sediment cores collected from 688 m in the Korsfjord, western Norway. Sediment cores were spiked with diatoms labeled with ^{13}C, and incubated for 2, 7, and 14 d and macrofaunal uptake of labelled C subsequently measured. We also describe the general macrofaunal community composition in this fjord, since structural characteristics

of macrofaunal communities may in future be used as proxies for the quality and quantity of OM arriving at the seafloor, and its subsequent degradation.

2. Materials and methods

In early March 2006 *ex-situ* pulse-chase experiments were carried out using deep-sea sediment cores collected from the central Korsfjord in south-western Norway (Fig. 1) to assess the short- to long-term response of a deep-sea benthic community to a phytodetrital food pulse. The central basin of the Korsfjord (centered at 060^{o} 08' N; 005^{o} 17' E) is approximately 690 m deep and connected to the North Sea at its western tip by a 250 m deep sill. The fjord is well-oxygenated throughout the year and contains an oceanic water body (salinity 35) underlying a surface water mass of a lower salinity (~30, Matthews and Sands, 1973).

A non-axenic clone of the diatom *Skeletonema costatum* (Bacillariophyta) was chosen as a suitable C-source in our experiments, since the spring bloom in the Korsfjord is largely dominated by this species (Erga and Heimdal, 1984). Diatoms were cultured in an artificial seawater medium modified with F/2 (Grasshoff, 1999). The culture medium was amended by replacing 25 % of ^{12}C bicarbonate with $NaH^{13}CO_3$. Diatoms were grown at 15 ^{o}C under a 16: 8 hr light/ dark cycle and harvested by centrifugation (1500 rpm x 5 min), washed 4 times in an isotonic solution to remove excess labelled bicarbonate, and freeze dried. Diatoms possessed a ^{13}C-content of 7.9 ± 0.4 atom % and a C: N ratio of 9 ± 1 (n=6).

Sediment cores were collected from the RV Håkon Mosby using a Smogen box-corer. Sediments used for the tracer addition experiments were recovered from a depth of

688 m (060^{o} 08' 50 N; 005^{o} 17' 70 E), whilst control sediments (i.e. no phytodetritus added) were sampled at a depth of 685 m (060^{o} 09' 2 N; 005^{o} 16' 5 E). Bottom water temperature and oxygen concentration was 7^{o}C and 245 µmol l^{-1}, respectively. Upon retrieval of the box-core, polycarbonate tubes (19 cm dia.) were inserted into the box-cored sediment and dug out. Cores were then carefully covered with filtered 7 ^{o}C seawater to avoid disturbance, sealed with water-tight lids, and maintained at 7 ^{o}C for the 2 h journey back to the University of Bergen's marine biological research station at Espeland. Once at Espeland Research Station, the cores were transferred to a temperature controlled (7 ^{o}C) water bath and allowed to equilibrate for 24 h prior to starting the experiments.

After 24 h, 140 mg of algal C, equivalent to 1 g C_{org} m^{-2}, was injected into each chamber and distributed homogeneously by stirring paddles mounted in the chamber lids. Once a homogeneous algal suspension was observed, stirrers were turned off for 1 h to allow the phytodetritus to sink to the sediment surface. After 1 h, chamber stirrers were switched on again and chamber waters gently mixed at 6 rpm for the remainder of the experiments. Two replicate experiments were run for 2 d, 2 for 7 d and an additional 2 for 14 d. The water O_2 concentration in each chamber was continually monitored and never allowed to decrease by more than 30 % from the bottom water O_2 concentration measured in the Korsfjord. When chamber O_2 concentration decreased to approx. 170 µmol l^{-1}, chamber lids were carefully removed and each chamber aerated using an aquarium pump. At the end of each incubation, two experimental chambers were chosen at random from the water bath and processed.

From each benthic chamber, two 6 cm dia. sub-cores were taken for foraminifera samples (Sweetman and Witte, submitted) and determination of total organic (TO) ^{13}C-signatures through the sediment ($\Delta\delta TO^{13}C$). Each $TO^{13}C$ sub-core was extruded and sectioned at 2 cm intervals from 0 to 10 cm. Cutlets were placed in brown glass bottles and immediately frozen at -20 ^{o}C. Background sediment samples were collected from the control chamber and processed in the same way. Upon return to the laboratory, each cutlet was freeze-dried for 3 d and homogenized using a pestle and mortar. From each homogenized horizon, approximately 50 - 100 mg of freeze-dried sediment was transferred to a pre-combusted glass tube (550 ^{o}C for 5 h) and decalcified by adding 15 ml of 2M HCl and gently stirring overnight. Decalcified sediment was vigorously washed 4 times with Milli-Q water to remove excess acid, concentrated by centrifugation (800 rpm x 4 min), and freeze-dried. Approximately 3.5 mg of post-acidified sediment was then transferred to tin cups for isotope ratio mass spectrometry (IRMS) analysis.

Samples for macrofauna were recovered by sectioning the remaining chamber sediment at 0 - 2, 2 - 5, and 5 – 10 cm horizons. Each horizon was carefully sieved on a 250 μm mesh in cool, filtered seawater, transferred to 4 % formaldehyde solution buffered with sodium tetraborate decahydrate, and stored refrigerated until picked. Macrofauna for natural $\delta^{13}C$-signatures were sampled from the control chamber and processed in the same way.

In the laboratory, sieved samples were picked for macrofauna in cooled artificial seawater (salinity 35) under a binocular microscope and transferred to 4 % buffered formaldehyde solution. To derive information from macrofaunal natural isotopic signatures about potential food sources in the Korsfjord, $\delta^{13}C$-signatures from

'background' macrofauna were corrected for formaldehyde preservation effects by adding 1 ‰ to each $\delta^{13}C$-value (Demopoulos et al., 2007; Sweetman and Witte, in press). However, preservation effects on stable isotope signatures were considered to be negligible compared to tracer uptake (~1 ‰ - C.R. Smith pers. comm.) thus, no corrections were applied to 'background' or 'enriched' signatures when calculating specific uptake of label and C-turnover. Separate picking utensils were used for unlabelled and labelled samples to avoid contamination of stable isotopes. Organisms were identified to major taxon, but polychaetes and crustaceans were identified to family and class or order, respectively. Single organisms were washed of attached organic debris in cooled, clean artificial seawater (salinity 35), placed in tin cups and dried at 35 – 40 ^{o}C for a period of 2 wk. Calcareous shelled organisms were decalcified with 2M HCl in double boated silver caps and dried as above. In order to obtain sufficient biomass for isotope measurements, some individual organisms needed to be combined as in Aberle and Witte (2003), Kamp and Witte (2005), and Sweetman and Witte (in press). Prior to isotopic analysis, all organisms were weighed on an electronic microbalance (Sartorius) for biomass determinations (mg dw).

The isotopic ratios of the macrofaunal organisms were measured using both Europa Integra (enriched isotopes - reproducibility: $\delta^{13}C$ = 0.02 ‰) and Hydra 20/20 (natural isotopes - reproducibility: $\delta^{13}C$ = 0.04 ‰) isotope ratio mass spectrometers at UC Davis, USA. Sediment samples were analysed using a Finnigan Delta plus XP (Thermo) isotope ratio mass spectrometer at MPI Bremen. Macrofaunal C isotopic ratios ($^{13}C/\ ^{12}C$) were measured against a PDB-standard and are expressed as delta notation as relative difference between sample and standard: $\delta^{13}C$ (‰) = ($^{13}C/\ ^{12}C_{sample}$)/ ($^{13}C/$

$^{12}C_{standard}$) -1] x 10^3. Specific uptake of ^{13}C by macrofaunal organisms was calculated as excess (above background) and is expressed in $\Delta\delta^{13}C$ notation: $\Delta\delta^{13}C = \delta^{13}C_{sample} - \delta^{13}C_{background}$. Turnover of ^{13}C was calculated as the product of the excess atom % ^{13}C (difference in atom % ^{13}C between sample and background) and C-content (expressed as unit weight): C-turnover (unit wt C) = [(atom % $^{13}C_{sample}$ – atom % $^{13}C_{background}$) x (unit wt C of organism). Specific labelling of sediment ($\Delta\delta TO^{13}C$) was measured relative to a PDB standard and expressed as excess above background as $\Delta\delta TO^{13}C = \delta TO^{13}C_{sample} - \delta TO^{13}C_{background\ sediment}$.

2.1. Data analysis

Total macrofaunal abundance and biomass estimates from all 7 chambers were analysed for outliers by box-whisker plots. The control chamber contained an unusually high abundance of macrofauna thus, no abundance or biomass data was used from this chamber. Abundance/ biomass vs. depth relationships were analysed using One-Way ANOVA tests for taxa found in all 6 experimental chambers. Kolmogorov-Smirnov tests for normality and Levene's test for homogeneity of variance were conducted prior to carrying out ANOVA. Where data sets failed to meet one or both of these assumptions, a natural log transformation [ln or ln(X + 1) in cases with 0-values] was attempted. In cases where neither assumption of normality and/ or homoscedascity was met following data transformation, a non-parametric Kruskal-Wallis test was performed. The 13 tests of abundance/ biomass vs. depth increased the probability of committing Type I errors (Dytham, 2003) therefore; α-levels were adjusted for multiple testing using a sequential Bonferroni correction (Holm, 1979).

The influence of experimental duration and polychaete feeding guild on specific uptake of ^{13}C-tracer were both tested using Kruskal-Wallis tests after data transformation failed to meet parametric assumptions. C-turnover vs. time was analysed by regression curve estimation, with residuals plotted against line-fit values to assess which model best described the data (Dytham, 2003, Norusis, 2006). An α-level of 0.05 was used as a criterion for statistical significance. All data analysis was conducted using SPSS 15.0 software (SPSS Inc, Chicago, IL).

3. Results

3.1. Macrofaunal Community Structure

Mean macrofaunal abundance and biomass were 4687 ± 965 ind. m^{-2} and 1619 ± 1337 mg dw m^{-2}, respectively. Macrofauna density increased and biomass decreased with sediment depth (Figs. 2a & b), but no statistically significant relationships were found for either mean total abundance/ biomass and sediment depth (Table 1).

Macrofaunal community composition is given in figures 3 to 4. Seven major macrofaunal taxa were identified from the Korsfjord. The crustaceans clearly dominated macrofaunal abundance (Fig. 3a). However, the Bivalvia and Polychaeta contributed most towards macrofaunal biomass (Fig. 3b). The Ostracoda dominated the crustacean community in terms of abundance (99 %) and biomass (98 %) with the Harpacticoida, Tanaidacea, Amphipoda and Isopoda collectively contributing 1 % and 2 % to abundance and biomass, respectively. The polychaeta were numerically dominated by the sub-surface deposit feeding Capitellidae, Opheliidae and Paraonidae (Fig. 4a), but by the Onuphidae and Spionidae in terms of biomass (Fig. 4b). Opheliid polychaetes (*Ophelina*

spp.) were only ever found at 0-2 cm depth and the only taxon to show a statistically significant depth preference (Table 1).

3.2. Isotopic signatures and C-turnover

Natural $\delta^{13}C$- and $\delta^{15}N$-signatures are given in figure 5. An aplacophoran possessed the heaviest natural $\delta^{13}C$-signature (-16.1 ‰), and an ostracod the lowest (-23 ‰). Delta ^{15}N-signatures ranged from 14.3 ‰ to 6.8 ‰ for a sipunculid and capitellid polychaete, respectively (Fig. 5). Delta ^{13}C-measurements ($\delta^{13}C$) of all animals are given in table 2. Mean specific uptake of ^{13}C ($\Delta\delta^{13}C$) increased sharply from 3 ± 10.7 ‰ after 2 d to 25.5 ± 46.3 ‰ after 7 d (Fig. 6). After 14 d, macrofaunal labelling averaged 19.9 ± 32.8 ‰. We did not observe uncorrected natural $\delta^{13}C$-signatures heavier than -17.1 ‰. Thus, in our enrichment experiments, signatures > -15 ‰ where considered as evidence of C-uptake (Levin et al., 1999; Aberle and Witte, 2003; Sweetman and Witte, in press). The percentage of labelled animals showed a sharp increase from 2 to 7 d, but overall macrofaunal enrichment throughout the 2 week experiment was modest, with only 4 % of animals showing $\delta^{13}C$-signatures greater than 100 ‰ (Table 2). There was a large degree of variability in specific uptake evident across the entire 2 week experiment (Fig. 6) and polychaete feeding guild (Fig. 7), and no statistically significant relationships were found for either specific uptake of ^{13}C and: (1) experimental duration (Kruskal-Wallis: $\chi^2_{2\ d.f.} = 5.631$; $p = 0.060$) or (2) polychaete feeding guild (Kruskal Wallis: $\chi^2_{2\ d.f.} = 4.402$, $p = 0.111$).

Of all the polychaetes examined, only the Paraonidae showed an increasing response to our fresh C-source with time (Fig. 8). Both the lumbrinerid polychaetes and

bivalves showed peak mean $\Delta\delta^{13}$C-signatures after 1 wk (Fig. 8). The Onuphidae showed no response during the first 7 d and only negligible uptake after 14 d (Fig. 8). No labelled algae were ever ingested by the Capitellidae, Opheliidae or Ostracoda as demonstrated by δ^{13}C-signatures < -15 ‰ (Table 2, Fig. 8).

Total macrofaunal C-turnover increased significantly ($P < 0.001$) with time from a mean of 4×10^{-2} mg C m^{-2} after 2 d to 7×10^{-1} mg C m^{-2} after 14 d, with comparable amounts of C-turnover between replicates (Fig. 9). Total C-turnover was best described by the logarithmic function, $y = 0.34\text{Ln}(x) - 0.1873$ ($R^2 = 0.986$), where y is C-turnover [mg C m^{-2}] and x is time [d]. On average, 3.3 % of the biomass was involved in C-turnover during the 2 d experiments compared to approximately 61% after 7 and 14 d (Table 2). Sedimentary $\Delta\delta\text{TO}^{13}$C profiles are shown in figure 10. Labelled organic material was found at 4-6 cm depth after 2 d, but was not subducted past 8 cm throughout the entire experiment.

4. Discussion

4.1. Macrofaunal community structure

Mean total macrofaunal density and biomass estimates from the Korsfjord were found to be greater, but within the same order of magnitude as those reported for the Sognefjord by Witte et al. (2003b). Further a field, Flach and Heip (1996) found comparable, but higher mean total abundance values (~ 6000 ind. m^{-2}) to ours at a depth of 670 m along the OMEX transect of the Goban Spur in the NE Atlantic. Flach and Heip (1996) additionally reported biomass estimates of approximately 600 mg C m^{-2}, which, assuming a biomass C: mg dw quotient of 0.5 (Witte et al., 2003b), agree very

well with our mean value of ~ 800 mg C m^{-2}. The close agreement between mean total abundance and biomass estimates found in this study and those from previous investigations (Flach and Heip, 1996; Witte et al., 2003b) indicate that our results are representative of many mid-slope continental margin sediments.

Macrofaunal communities in deep Norwegian fjords tend to be dominated by polychaetes. Witte et al. (2003b) noted that polychaetes numerically dominated (65 %) the macrofauna community at 1265 m in the Sognefjord and Oug (2000) documented densities greater than 80 % from a depth of 185 m in the Balsfjord, northern Norway. Furthermore, Holte (1998) reported high polychaete abundances (~ 90 %) at a number of deep-water sites (90-240 m) in the Holandsfjord and Lie (1978), who carried out a quantitative survey of the benthic macrofauna in the Fanafjord – a branching fjord of the Korsfjord – found the Polychaeta to contribute 70 % of all macrofauna. However, in contrast to these investigations, sediment cores collected from the Korsfjord were mainly dominated by crustaceans (Fig. 3a), of which ostracods where the major crustacean taxon. The different and large crustacean to polychaete abundance ratio found in this study may simply have resulted from spatial patchiness of the macrofauna. High spatial heterogeneity is a common trait in shallow and deep-sea environments and can exist over small spatial scales of centimetres to meter's (e.g. Thrush et al., 1989; Morissey et al., 1992; Drazen et al., 1998; Sweetman and Witte, in press). Processes which drive macrofaunal patchiness in benthic habitats include the presence and possible disturbance effects associated with biogenic structures (Thistle, 1979; Levin et al., 1986; Shaff and Levin, 1994), along with other factors such as sediment excavation by predators, and differences in sediment characteristics (Thrush et al., 1989).

Opheliid polychaetes were confined to the top most 2 cm of sediment where, judging from their relatively heavy $\delta^{13}C$-signatures (Fig. 5), they appear to feed on relatively fresh organic matter (Levin et al., 1999). Approximately half (46 ± 14 %) of all ostracods were found at 5-10 cm depth, and this finding together with the relatively low probability level generated by the One-way ANOVA comparing ostracod abundance and depth (Table 1), suggests that this particular taxon may show a preference for specific ecological conditions found in deeper sediment layers. Earlier studies on ostracods have demonstrated high survival rates under hypoxic/ anoxic conditions indicating that these crustaceans are able to 1) switch to anaerobic pathways and/ or 2) detoxify hydrogen sulphide to non-toxic thiosulphate ($S_2O_3^{2-}$) and sulphite (SO_3^{2-}) in the presence of oxygen (Jahn et al., 1996; Modig and Ólafsson, 1998).

4.2. Natural isotopic signatures and ^{13}C-labelling experiments

Natural $\delta^{13}C$-signatures (-19.2 ± 2.7 ‰) suggested a dependency on a phytoplankton based food-web, assuming a POM $\delta^{13}C$-signature of between -20 to -21 ‰ and a $\delta^{13}C$-enrichment of 1 ‰ per trophic step (Fry and Sheer, 1984). Light natural $\delta^{15}N$-signatures for the Capitellidae indicated selective ingestion of small size classes of POM, of which smaller particles tend to exhibit the lightest $\delta^{15}N$-values (Rau et al., 1990), and/ or microbial food sources. Selective feeding has been observed for the Capitellidae by Neira and Höpner (1994) who demonstrated that fecal pellets produced by the capitellid, *Heteromastus filiformis*, were enriched in both finer particles (< 63 μm) and organic C and proteins. Comparatively light $\delta^{15}N$-values were also measured for the Ostracoda, which, together with light $\delta^{13}C$-signatures indicated preferential ingestion of relatively

small, recalcitrant particles (Rau et al., 1990; Iken et al., 2001). The natural isotopic signatures measured for the Capitellidae and Ostracoda indicate that feeding experiments with microbial cultures and/ or relatively refractory C-sources may yield different response patterns to those seen in this study.

Deductions about deep-sea macrofaunal feeding ecologies are often drawn based on animal mouth morphologies and/ or feeding-guilds of shallow-water analogues (e.g. Mincks and Smith, 2007). But combinations of isotopic tracer and morphological techniques have revealed that a number of these proposed feeding classifications are, in fact, well grounded. For example, polychaete families classified by Jumars and Fauchald (1977), Fauchald and Jumars (1979) and Gaston (1987) as discretely motile, surface- (e.g. cirratulids, and onuphids) and sub-surface deposit feeders (e.g. opheliids, and paraonids) have been shown to rapidly ingest fresh phytodetritus (Levin et al., 1997 & 1999; Aberle, 2001; Aberle and Witte, 2003). In this investigation however, sub-surface deposit feeding opheliid polychaetes did not ingest labelled phytodetritus at all, and surface-deposit feeding onuphids only showed minor enrichment after 14 d. In fact, the only polychaete families which did show ingestion of phytodetritus were the deposit feeding paraonid and cirratulid polychaetes together with the Lumbrineridae - a family largely composed of carnivores (Fauchald and Jumars, 1979). Although feeding reactions may differ depending on the chemical state/ origin of a C-source as previously stated, these latest results also suggest that species- as well as family-specific feeding ecologies may 1) exist and 2) have given rise to the feeding reactions observed. Species-specific feeding behaviours have already been documented for the meiobenthos by Ólafsson et al. (1999) and Modig et al. (2000) who both demonstrated that uptake of diatom C varied not

just amongst major meiobenthic taxa, but also amongst species belonging to the same class or phylum. Ólafsson et al. (1999) showed that amongst the 3 ostracod species, *Candona neglecta, Paracyprideis fennica,* and *Heterocyprideis sorbyana*, total uptake of ^{14}C was significantly different with *C. neglecta* incorporating between 10 to 100 times more ^{14}C than *P. fennica* and *H. sorbyana*. Additionally, Pace and Carman (1996) reported inter-specific differences in the use of microalgal resources by 4 species of harpacticoid copepod in a mudflat habitat, suggesting food-resource partitioning amongst species and van de Bund et al. (2001) demonstrated higher uptake of ^{14}C-labelled phytodetritus by the Baltic Sea amphipod *Monoporeia affinis* compared to *Pontoporeia femorata*. Significant variations in uptake of diatom-C have also been observed between the nematode species *Paracanthonchus* spp. and *Axonolaimus spinosus* (Ólafsson et al., 1999) and distinct inter-specific responses to fresh algal-C have been identified amongst deep-sea foraminifera (Nomaki et al., 2005).

Ontogenetic variability may also explain the different and sometimes unpredictable (e.g. lumbrinerid polychaetes) feeding patterns observed throughout the course of the experiment. Ontogenetic changes in diet/ feeding mode have already been demonstrated in a number of studies for a variety of taxa. For example, Hentschel (1998) found significant body-size-dependent differences in $\delta^{13}C$ for 4 species of tentaculate, surface-deposit feeding polychaetes, suggesting food-resource partitioning amongst individuals, with juveniles assimilating C from benthic diatoms and adults from macro-algal detritus. In addition, Rossi et al. (2004) demonstrated that the diet of the bivalve *Macoma balthica* was directly related to body size, with juveniles feeding entirely on micro-phytobenthos and adults on micro-phytoplankton. Furthermore, in a shallow water

feeding study conducted in the southern German Bight, Kamp and Witte (2005) documented higher incorporation of ^{13}C-labelled algae by juvenile *Fabulina fabula* compared to adults.

$\Delta\delta TO^{13}C$ profiles revealed rapid (< 2 d) burial of algal C below the sediment surface (Fig. 10). Fast (1.5 d) subduction of organic matter by maldanid polychaetes has been reported by Levin et al. (1997) on the North Carolina continental slope, and Sweetman & Witte (in press) found burial of fresh organic C down to 10 cm depth in the abyssal NE Pacific in only 36 h. Jumars et al. (1990) theorized that the limited existence of food reserves; characteristic of deep-sea environments, would force fauna to bury any available food to deeper sediment layers in an effort to store it out of reach of competitors. Paraonid, capitellid and opheliid polychaetes are known for their infaunal, burrowing lifestyles (Fauchald and Jumars, 1979; Neira and Höpner, 1994) and this behaviour, together with their relatively large presence (Fig. 4a) may have contributed to the observed $\Delta\delta TO^{13}C$ distributions. Hoeing of surficial sediments to depth, as observed by the shallow-water maldanid polychaete *Clymenella torquata* (Dobbs and Whitlach, 1982), could also have played a role in creating the profiles seen.

Total C-uptake by the macrofaunal community showed a significant increase over time, but no other data sets exist which describe the long-term (14 d) response of macrofauna to simulated phytodetritus pulses at bathyal depths, which therefore makes a direct comparison of C-cycling rates almost impossible. Comparing macrofaunal C-turnover to that recorded from a 3 d feeding study in the deep Sognefjord (1265 m, Witte et al., 2003b) reveals that total macrofaunal C-turnover in the Korsfjord after 14 d was approximately 1 order of magnitude less than in the Sognefjord. This is most likely

because of the different fractions of the community which ingested significant amounts (i.e. $\delta^{13}C$ >100 ‰) of labelled OM (4 vs. 33 % of specimens, representing 2 vs. 51 % of the biomass in the Korsfjord and Sognefjord, respectively). Based on an annual POC flux estimate of 107 g C m^{-2} yr^{-1} at 90 m in the branch-off Fanafjord (Wassmann, 1984), we introduced 0.93 % of the POC flux the Korsfjord benthos receives in 1 yr, or the equivalent of 3.4 d of POC sedimentation. It is therefore plausible that the C-addition was simply too small to initiate a large response as measured in the Sognefjord by Witte et al. (2003b).

Differences in macrofaunal community structure between the Sognefjord and Korsfjord could offer an alternative explanation for the comparatively small amount of C-turnover by the Korsfjord macrofaunal community. Witte et al. (2003b) and Aberle (2001) documented that surface deposit feeding cirratulid polychaetes and isopods: (1) were the most abundant polychaete and 2nd most abundant crustacean in the Sognefjord, (2) contributed most to polychaete and crustacean biomass, and (3) showed some of the highest $\delta^{13}C$-signatures. Finally and perhaps most importantly, 86 % of all heavily labelled animals (i.e. $\delta^{13}C$ > 100 ‰) inhabited the top-most 5 cm of sediment in the Sognefjord (Aberle, 2001). In the Korsfjord however, the most dominant polychaete families were the sub-surface deposit-feeding Opheliidae, Capitellidae, and Paraonidae, but cirratulids contributed only 3 % to polychaete diversity. In addition, isopods contributed less than 0.4 % to both crustacean density and biomass, and roughly half of all macrofaunal abundance (43 ± 11 %) and a quarter of all biomass (26 ± 28 %) was found at 5-10 cm sediment depth, where labelled organic matter was only observed in 33 % of the chambers (Fig. 10). Collectively, these results demonstrate that the macrofauna

from the Korsfjord had comparatively little access to the supplied C-source and may help to explain the relatively small amount of C-turnover.

Overall, this investigation highlights the variable response to food pulses by macrofaunal taxa and accentuates the need for high taxonomic resolution and a thorough analysis of animal life-histories in future investigations, if we are to understand the role of macrofaunal sedimentary communities in the early diagenesis of OM.

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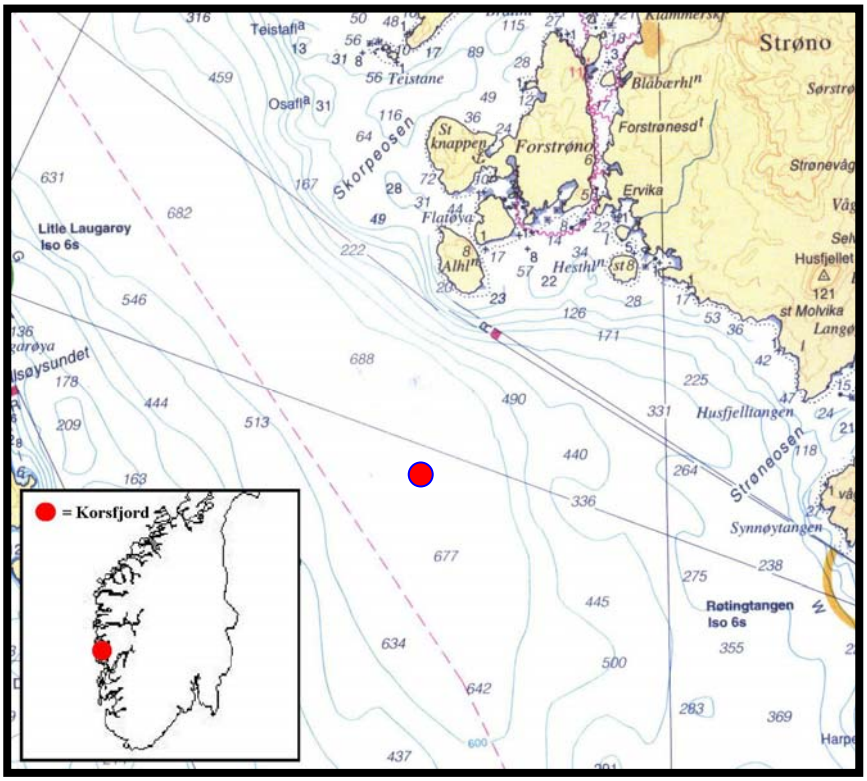
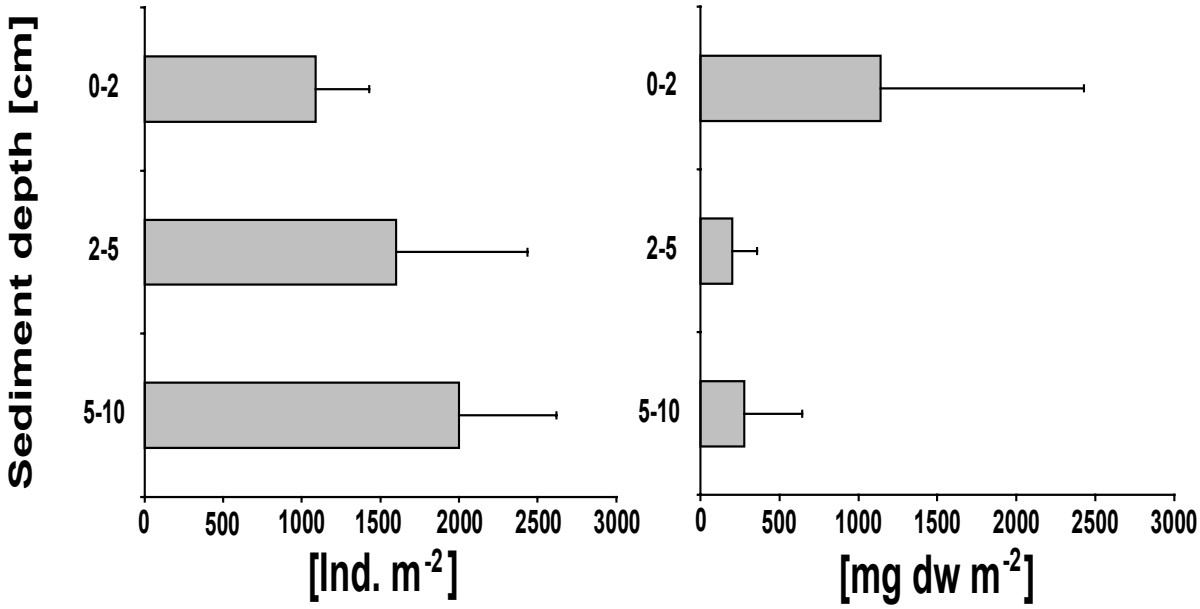
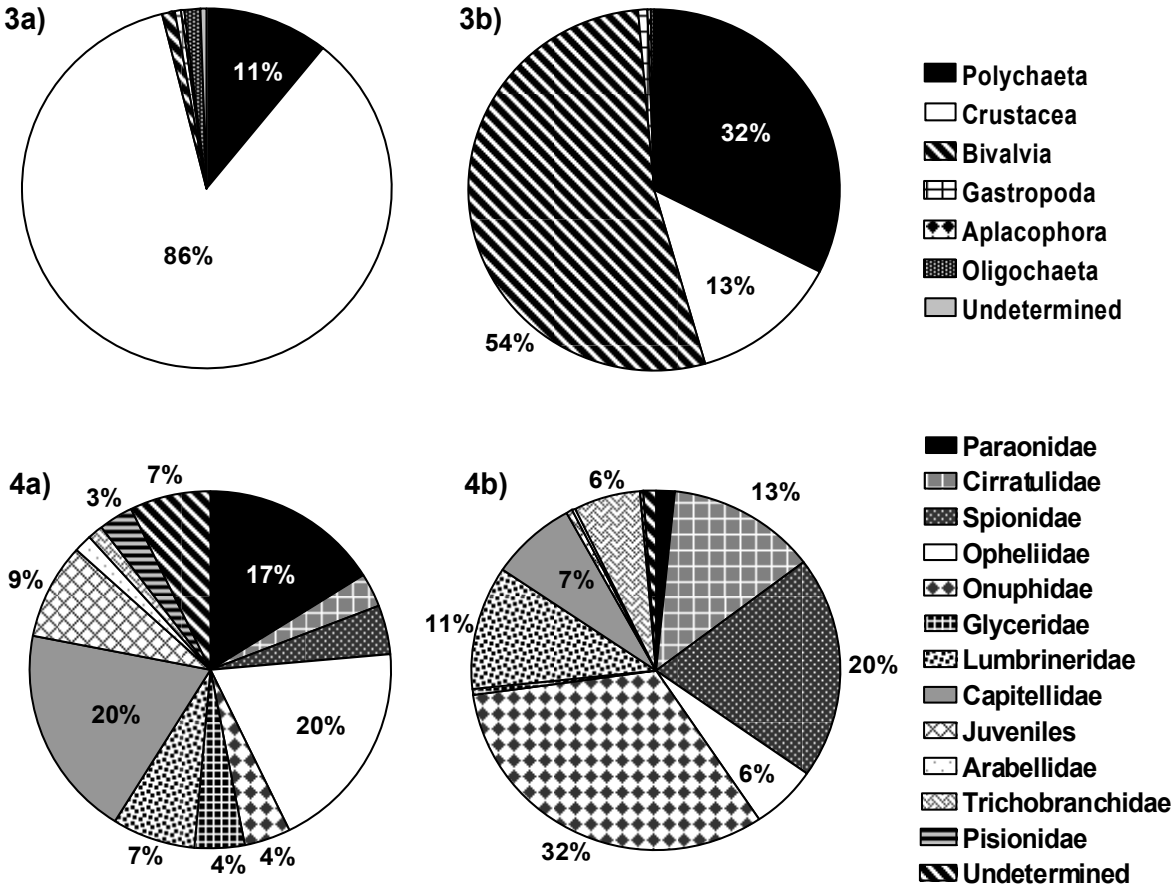


Figure 1. Location of the Korsfjord in western Norway. Red mark denotes sample sites



2 a 2 b

Figure 2. Vertical distribution of (a) total macrofaunal abundance and (b) biomass within the sediment column (0 - 10 cm) in the central Korsfjord. Bars denote +1 standard deviation.



Figures 3-4. Figure 3 (a) Relative abundance (ind. m^{-2}) and (b) biomass (mg dw m^{-2}) of major macrofaunal taxa in the central Korsfjord. Figure 4 (a) Relative abundance (ind. m^{-2}) and (b) biomass (mg dw m^{-2}) of major polychaete families in the central Korsfjord.

Table 1. P-values calculated for abundance/ biomass vs. depth relationships using one-way ANOVAs. Kruskal-Wallis test results in bold. Alpha-level's adjusted using sequential Bonferroni correction (Holm, 1979). ns/ s denotes non-significance/ significance, respectively. Note: biomass vs. sediment depth relationships were not explored for the Paraonidae despite finding individuals in all 6 chambers. This was because of a single individual being accidentally lost during sorting that was included in our abundance, but not our biomass estimate.

Taxa	Abundance vs. depth (p-value)	α-level	Biomass vs. depth (p-value)	α-level
Total macrofauna	0.072 (ns)	0.0063	**0.949** (ns)	0.05
Polychaeta	0.038 (ns)	0.0056	0.855 (ns)	0.025
Capitellidae	0.826 (ns)	0.0167	0.720 (ns)	0.0125
Paraonidae	0.581 (ns)	0.01	…	…
Opheliidae	**0.001** (s)	0.004	**0.001** (s)	0.004
Crustacea	0.01 (ns)	0.0045	0.526 (ns)	0.0083
Ostracoda	0.021 (ns)	0.005	0.495 (ns)	0.0071

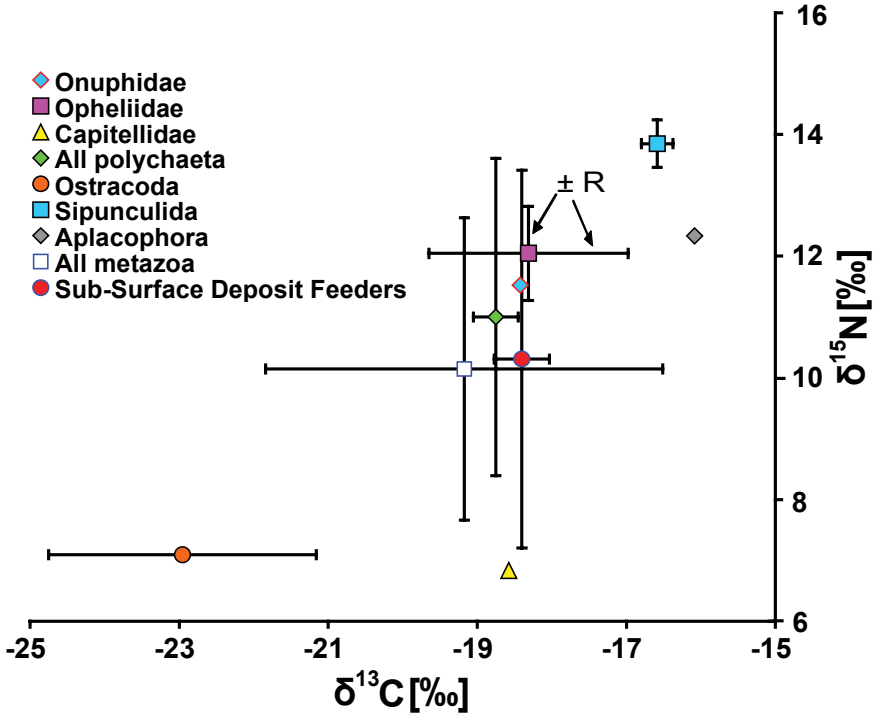


Figure 5. Natural $\delta^{13}C$ and $\delta^{15}N$-signatures of macrofauna from the Korsfjord. Error bars denote standard deviations unless otherwise stated. R denotes range of two measurements. Note: sub-surface deposit feeders refer to only polychaetes.

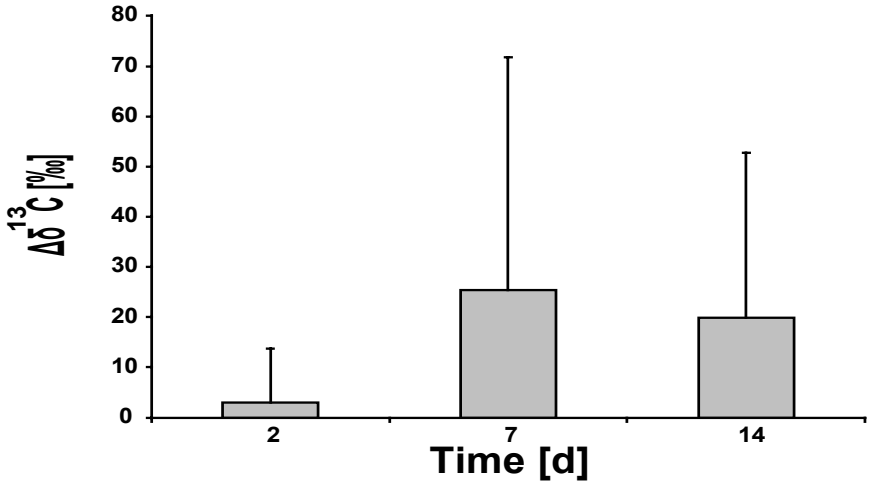


Figure 6. Mean $\Delta\delta^{13}C$-signatures of all macrofaunal organisms after different incubation times. Bars denote +1 standard deviation.

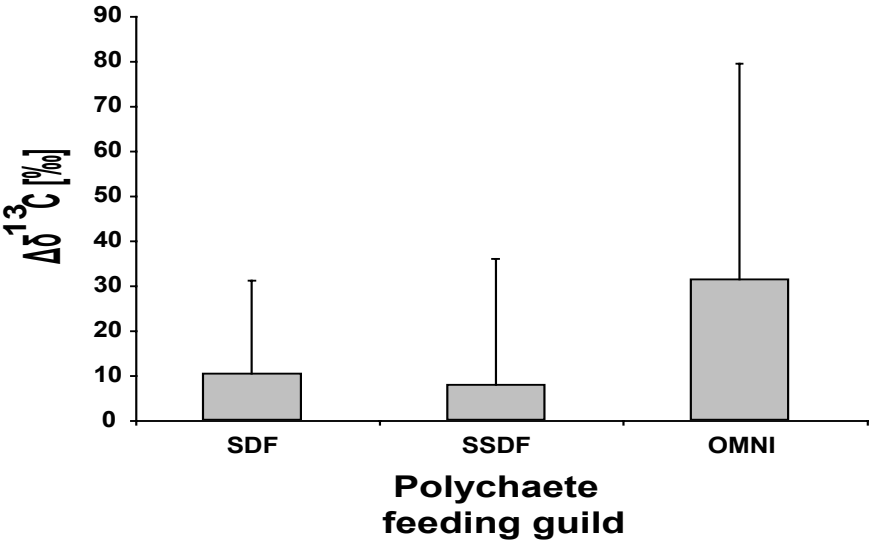


Figure 7. Mean $\Delta\delta^{13}C$-signatures of different polychaete feeding guilds (SDF = surface deposit feeders; SSDF = sub-surface deposit feeders; OMNI = omnivores). Bars denote +1 standard deviation.

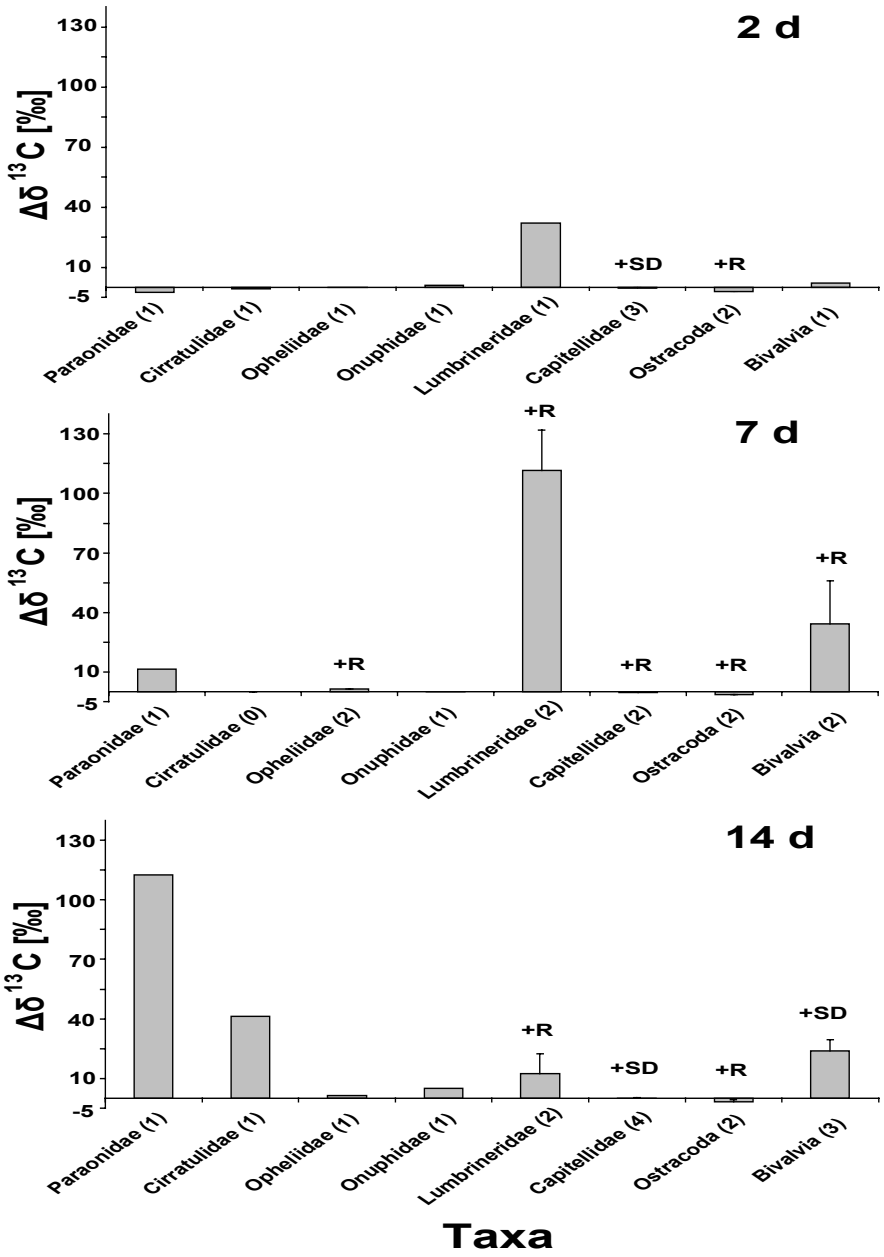


Figure 8. Mean $\Delta\delta^{13}C$-signatures of the most common macrofaunal taxa after different incubation times. Number of samples analysed is given in parentheses. Bars denote +1 standard deviation (SD) or range (R).

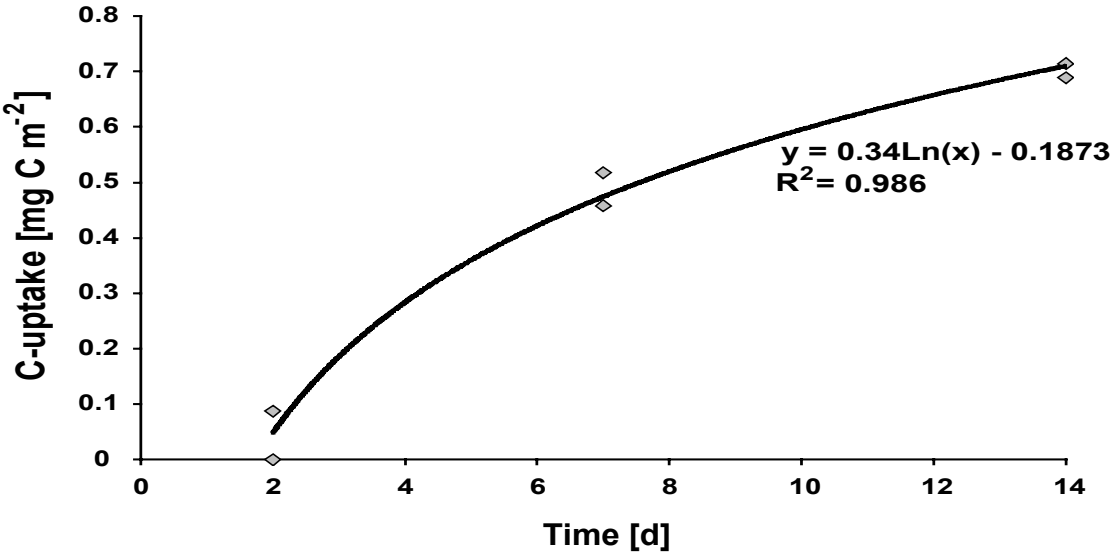


Figure 9. Logarithmic regression of macrofaunal C-uptake vs. time. Data points indicate C-uptake in each replicate incubation chamber after 2, 7 and 14 d.

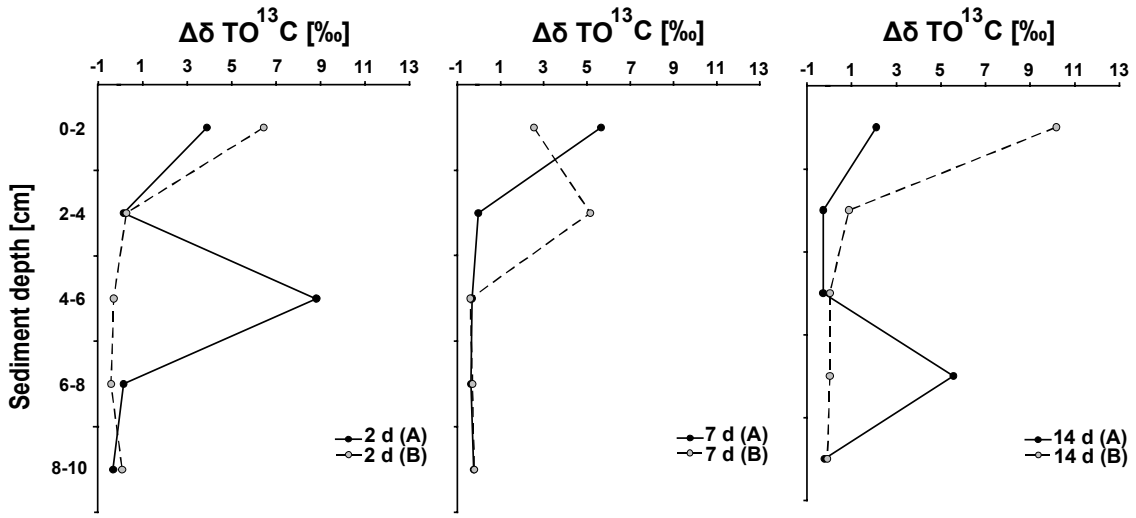


Figure 10. Specific labelling of total organic (TO) ^{13}C in the sediment ($\Delta\delta TO^{13}C$) in each replicate incubation chamber (A or B) after 2, 7 and 14 d.

Table 2. Isotopic signatures and C-uptake of macrofaunal organisms from the central Korsfjord after 2, 7 and 14 d and their vertical position within the sediment column (0 - 10 cm). n denotes number of organisms combined for 1 measurement. A & B denote replicate incubation chamber A or B.

Taxon	n	Incubation	Sediment depth (cm)	Biomass (µg C)	$\delta^{13}C$ (‰)	$\Delta\delta^{13}C$(‰)	C-uptake (x 10^{-3} mg C m^{-2})	C-uptake (% body weight C)	C-processed (% of total C)
Polychaeta									
Cirratulidae	1	2 d A	0-2	697.59	-20.61	…	…	…	…
Paraonidae	2	2 d A	0-2, 5-10	20.14	-21.96	…	…	…	…
Opheliidae	1	2 d A	0-2	740.60	-19.20	…	…	…	…
Onuphidae	1	2 d A	0-2	3178.13	-18.39	…	…	…	…
Glyceridae	2	2 d A	0-2	54.20	-23.56	…	…	…	…
Lumbrineridae	1	2 d A	2-5	382.53	12.51	32.27	76.43	0.45	87.49
Capitellidae	2	2 d A	5-10	76.41	-19.76	…	…	…	…
Capitellidae	1	2 d A	5-10	104.32	-20.17	…	…	…	…
Capitellidae	2	2 d B	0-2	113.20	-20.07	…	…	…	…
Other Polychaeta	4	2 d A	0-2, 5-10	55.37	12.11	31.86	10.93	0.44	12.51
Other Polychaeta	5	2 d B	0-2, 5-10	130.52	-16.33	…	…	…	…
Crustacea									
Ostracoda	56	2 d A	0-2, 2-5, 5-10	44.89	-26.42	…	…	…	…
Ostracoda	91	2 d B	0-2, 2-5, 5-10	45.66	-26.02	…	…	…	…
Other metazoa									
Aplacophora	1	2 d A	5-10	168.78	-18.02	…	…	…	…
Bivalvia	1	2 d A	0-2	714.86	-18.22	…	…	…	…
Gastropoda	3	2 d A	0-2	351.93	-21.37	…	…	…	…
Other Metazoa	6	2 d A	0-2, 2-5, 5-10	51.47	-20.51	…	…	…	…
Other Metazoa	3	2 d B	0-2, 5-10	26.55	-21.17	…	…	…	…
Polychaeta									
Paraonidae	2	7 d A	0-2	36.24	-8.02	11.39	2.56	0.16	0.49
Opheliidae	1	7 d A	0-2	160.01	-17.69	…	…	…	…
Opheliidae	2	7 d A	0-2	77.19	-18.04	…	…	…	…
Onuphidae	1	7 d A	0-2	1814.29	-19.34	…	…	…	…
Lumbrineridae	1	7 d B	2-5	363.27	111.96	131.71	296.29	1.83	64.73
Lumbrineridae	1	7 d B	5-10	117.44	71.28	91.03	66.20	1.26	14.46
Capitellidae	2	7 d A	2-5	180.19	-19.65	…	…	…	…
Capitellidae	1	7 d B	0-2	70.97	-19.58	…	…	…	…
Trichobranchidae	1	7 d A	0-2	1304.01	-19.74	…	…	…	…
Other Polychaeta	2	7 d A	5-10	69.41	-20.45	…	…	…	…
Other Polychaeta	6	7 d B	0-2, 5-10	120.90	107.43	127.19	95.22	1.76	20.80
Crustacea									
Ostracoda	75	7 d A	0-2, 2-5, 5-10	31.62	-25.31	…	…	…	…
Ostracoda	81	7 d B	0-2, 2-5, 5-10	31.11	-25.34	…	…	…	…
Other Crustacea	2	7 d A	0-2	102.77	-10.74	9.43	6.00	0.13	1.16
Other Metazoa									
Bivalvia	1	7 d A	0-2	708.33	-7.81	12.36	54.23	0.17	10.48
Bivalvia	1	7 d A	0-2	1309.75	35.89	56.07	454.73	0.78	87.87
Other Metazoa	2	7 d B	0-2, 2-5	9.39	-25.50	…	…	…	…
Polychaeta									
Cirratulidae	1	14 d A	5-10	1679.65	21.65	41.40	430.65	0.57	60.31
Paraonidae	2	14 d A	0-2, 2-5	81.46	93.06	112.46	56.73	1.56	7.95
Opheliidae	4	14 d B	0-2	102.38	-17.94	…	…	…	…
Onuphidae	1	14 d B	2-5	2658.75	-14.52	4.90	80.72	0.07	11.72
Lumbrineridae	1	14 d A	2-5	1588.28	2.68	22.44	220.66	0.31	30.90
Lumbrineridae	1	14 d B	5-10	361.81	-17.35	…	…	…	…
Capitellidae	1	14 d A	2-5	53.03	-20.12	…	…	…	…
Capitellidae	1	14 d B	0-2	195.75	-19.04	…	…	…	…
Capitellidae	1	14 d B	0-2	160.77	-19.75	…	…	…	…
Capitellidae	2	14 d B	5-10	207.85	-19.52	…	…	…	…
Spionidae	1	14 d A	5-10	5468.46	-18.93	…	…	…	…
Other Polychaeta	2	14 d A	0-2	51.08	-21.08	…	…	…	…
Other Polychaeta	7	14 d B	0-2, 2-5, 5-10	129.75	70.75	90.50	72.71	1.26	10.55
Crustacea									
Ostracoda	125	14 d A	0-2, 2-5, 5-10	44.89	-26.85	…	…	…	…
Ostracoda	105	14 d B	0-2, 2-5, 5-10	47.22	-24.68	…	…	…	…
Other Metazoa									
Bivalvia	2	14 d B	0-2	51.49	-0.46	19.72	6.29	0.27	0.91
Bivalvia	1	14 d B	0-2	1305.17	1.03	21.21	171.41	0.29	24.88
Bivalvia	1	14 d B	0-2	1890.78	10.39	30.56	357.84	0.42	51.94
Oligochaeta	2	14 d B	0-2, 5-10	16.05	-24.04	…	…	…	…
Other Metazoa	2	14 d A	0-2, 2-5	16.29	38.99	59.16	5.97	0.82	0.84

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RETARDED RESPONSE BY DEEP-SEA FORAMINIFERA (> 250 µm) TO A SIMULATED PHYTODETRITAL PULSE IN A WESTERN NORWEGIAN FJORD

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ABSTRACT

The response of a foraminiferal community (> 250 μm) to a simulated phytodetritus sedimentation event was assessed over two weeks in a deep-fjord environment. Sediment cores collected from approx. 700 m depth in the Korsfjord, western Norway were incubated with 1 g C_{org} m^{-2} of labile ^{13}C-labelled *Skeletonema costatum ex-situ* for 2, 7 and 14 d. The foraminiferal community was largely dominated (91 %) by the deep-dwelling species *Globobulimina turgida* and *Melonis barleeanum*, aswell as the shallow infaunal species*Hyalinea balthica*. With the exception of *H. balthica*, foraminiferal average living depths (ALD) were continuously deep, indicating that the majority of foraminifera were not vertically migrating to the surface to feed on the fresh organic matter pulse. *Hyalinea balthica* did migrate towards the sediment surface, but did not feed on our ^{13}C-tracer, suggesting that migration was due to another factor, possibly microhabitat restabilization following initial sub-optimal living conditions. No foraminifera were involved in C-turnover during the first 7 d. After 14 d, 3 % of the foraminifera samples possessed $\delta^{13}C$-signatures indicative of C-uptake, but uptake was confined to *G. turgida*. Foraminifera contributed 2.4 % to faunal C-turnover (foraminifera plus macrofauna), despite them making up 24 % of the combined biomass. The dominance of deep-infaunal species such as *G. turgida* and *M. barleeanum* (68 %) that prefer degraded organic matter over more labile material, as well as the coarse size fraction of foraminifera analysed, which are known to respond slower to phytodetritus deposition than smaller, more opportunistic taxa, are likely reasons for the retarded response to food input observed in this study.

INTRODUCTION

Foraminifera are heterotrophic, amoeboid protists, normally characterised by the presence of granuloreticulose pseudopodia, and tests with at least 1 chamber. They have been found in a variety of deep-sea habitats ranging from abyssal plains to mid-ocean ridges and trenches, where in some instances, they contribute over 50 % of the eukaryotic biomass (Gooday and others, 1992). The widespread occurrence of foraminifera in deep-sea habitats together with their relatively large contribution to overall sedimentary biomass suggests that these protozoans may play a pivotal role in deep-sea carbon-cycling.

Deep-sea sediment dwelling communities rely on the downward flux of exported primary production from the euphotic zone for energy. This flux, once thought to trickle down through the water column in a constant manner, can arrive at the seafloor as large, episodic pulses of labile organic matter (Deuser and Ross 1980; Billet and others, 1983). Once this phytodetritus appears at the seafloor, it can immediately be colonised by a variety of opportunistic foraminifera species (Gooday 1988; Gooday and Lambshead 1989; Gooday and others, 1992; Gooday and Hughes 2002), and feeding studies using environmentally benign stable isotopes have confirmed that deep-sea foraminifera exploit this phytodetritus as a food source (Levin and others, 1999; Nomaki and others, 2005a, 2006; Witte and others, 2003a; Andersson and others, 2007; Woulds and others, 2007). In some instances, foraminifera ingest organic matter faster than other food-web taxonomic groups, for example, the macrofauna (Moodley and others, 2002). Simulated phytodetrital pulses on deep-sea sediments have also demonstrated that opportunistic taxa

vertically migrate from deeper sediment layers to the surface in response to elevated levels of food (Ernst and van der Zwann 2004; Nomaki and others, 2005b).

Being close to land – and research institutes – the deep fjords of western Norway allow easy access for studies of deep-sea benthic communities and their response to phytodetritus deposition. In this study, we examined the temporal response to a simulated ^{13}C-labelled phytodetrital pulse of a foraminiferal (>250 μm) community from the deep Korsfjord, south west of Bergen. Potential changes in overall vertical distribution and average living depth (ALD after Jorissen and others, 1995) as well as the uptake of labelled C were recorded over 14 d. Furthermore, to assess the relative contribution of foraminifera to C-processing, foraminiferal uptake was compared to macrofauna C-turnover.

MATERIAL AND METHODS

In early March 2006 *ex-situ* pulse-chase experiments were carried out using deep-sea sediment cores collected from the central Korsfjord in south-western Norway (Fig. 1). For a short description of the fjord see Matthews and Sands (1973).

A non-axenic clone of the diatom *Skeletonema costatum* (Bacillariophyta) was chosen as a C-source in the experiments since the spring bloom - which in the Korsfjord occurs in late March - is largely dominated by this species (Erga and Heimdal 1984). Diatoms were cultured in an artificial seawater medium modified with F/2 (Grasshoff 1999). The culture medium was amended by replacing 25 % of ^{12}C bicarbonate with $NaH^{13}CO_3$. Diatoms were cultured at 15 ^{o}C under a 16: 8 hr light/ dark cycle and harvested by centrifugation (1500 rpm x 5 min), washed 4 times in an isotonic solution to

remove excess labelled bicarbonate, and freeze-dried. Diatoms possessed a ^{13}C-content of 7.9 ± 0.4 atom % and a C: N ratio of 9 ± 1.

Deep-sea sediment cores were collected aboard the RV Håkon Mosby using a Smogen box-corer. Cores used for tracer addition experiments were taken at 688 m depth (060° 08' 50 N; 005° 17' 70 E), whilst cores for background foraminifera samples were sampled at a depth of 685 m (060° 09' 2 N; 005° 16' 5 E). Bottom water temperature and oxygen concentration was 7°C and 245 μmol l^{-1}, respectively. Upon retrieval of each box-core, a round Plexiglas chamber (20 cm dia.) was inserted into cored sediment and dug out, carefully covered with filtered 7 °C seawater to avoid disturbance, sealed with water-tight lids, and maintained at 7 °C for the 2 h journey back to the University of Bergen's marine biological research station. At Espeland Research Station, each core was transferred to a temperature controlled (7 °C) water bath and allowed to settle for 24 h prior to starting the experiments.

The experiments were started by adding 140 mg of labile algal C, equivalent to 1 g C_{org} m^{-2}, to 6 chambers. Upon injection, the labile algal material was distributed homogeneously by stirring paddles mounted in the chamber lids. Once a homogeneous algal suspension was observed, stirrers were turned off for 1 h to allow the phytodetritus to sink to the sediment surface. After 1 h, chamber stirrers were switched on again and chamber waters gently mixed at 6 rpm for the remainder of the experiments. A 7th chamber was incubated for 7 d without any algal addition thus, acting as a control and a source of natural $\delta^{13}C$ foraminifera signatures. Two enrichment experiments were run for 2d, 2 for 7d and an additional 2 for 14 d. The water O_2 concentration in each chamber was continually monitored and never allowed to decrease by more than 30 % from the

bottom water O_2 concentration measured in the Korsfjord. When chamber O_2 concentration decreased to approximately 170 μmol l^{-1}, chamber lids were carefully removed and each chamber aerated using an aquarium pump. At the end of each incubation, two experimental chambers were chosen at random and removed from the water bath.

Each chamber was processed for foraminifera by taking a 6 cm (dia.) sub-core of sediment. This sub-core was sectioned into 0 – 2, 2 – 4, and 4 – 6 cm horizons. The 0 – 2 cm horizons were immediately sieved on a 250 μm mesh in cool (7 ^{o}C) filtered seawater, and frozen at –20 ^{o}C in plastic 50 ml Falcon tubes. The remaining horizons were frozen un-sieved in sealable plastic bags. Foraminifera for natural δ^{13}C-signatures were sampled from the control chamber and processed in the same way.

In the laboratory, pre-sieved and unsieved samples were thawed one-at-a-time and the un-sieved samples carefully washed on a 250 μm sieve with cooled artificial seawater (salinity 35). Foraminifera were then carefully picked, identified to species under a binocular microscope, washed of attached organic debris, transferred to plastic Petri-dishes and frozen at -20 ^{o}C until isotope ratio mass spectrometry (IRMS) analysis. The criteria used for identifying living foraminifera were tests filled with definite cytoplasm (Moodley and others, 2000, 2002; Nomaki and others, 2005a). While the glassy test of *Globobulimina turgida* allowed direct identification of cytoplasm (yellow to brown colouration), the presence of healthy, living cytoplasm was more difficult to assess through the slightly opaque tests of *Melonis barleeanum* and *Hyalinea balthica*. In these instances, foraminifera were only picked if cytoplasm showed both structure within the chambers, aswell as a yellow-reddish brown colouration when viewed using transmitted

light (P. Heinz communication, 2005; J. Shönfeld communication, 2007). In a limited number of circumstances, it was impossible to identify definite cytoplasm through dense foraminiferal tests, and then only individuals with exposed pseudopodia were picked. Separate picking utensils were used for unlabelled and labelled samples to avoid contamination with stable isotopes.

Prior to IRMS analysis, foraminifera were thawed, dried in silver cups at 50 ^{o}C for 3 d, and weighed using a microbalance (Sartorius) for biomass determinations (mg dw). In order to obtain sufficient biomass for isotope measurements, foraminifera needed to be pooled as in Nomaki and others (2005a). All foraminifera were decalcified by initially adding 20 µl of Milli-Q water, followed by 40 µl of 0.5 M HCl to each sample cup and drying them for 1 wk at 50 ^{o}C. To ensure all calcareous material was dissolved, an additional 20 µl of Milli-Q water and 40 µl of 2 M HCl was then added and dried as before.

The isotopic ratios of the foraminifera were analysed using a Finnigan Delta plus XP (Thermo) isotope ratio mass spectrometer at MPI Bremen. Foraminifera C isotopic ratios (^{13}C/ ^{12}C) were measured against a PDB-standard and are expressed as delta notation as relative difference between sample and standard: δ^{13}C (‰) = (^{13}C/ $^{12}C_{sample}$)/ (^{13}C/ $^{12}C_{standard}$) -1] x 10^3. No δ^{13}C-signatures heavier than -21.8 ‰ were found for any of the foraminifera in the control chamber. Therefore, only foraminifera with signatures greater than -20 ‰ were considered as having been involved in C-uptake as in Levin and others (1999), Aberle and Witte (2003) and Sweetman and Witte (in press). Specific uptake of ^{13}C by foraminifera was calculated as excess (above background) and is expressed in $\Delta\delta^{13}$C notation: $\Delta\delta^{13}C = \delta^{13}C_{sample} - \delta^{13}C_{background}$. Turnover of ^{13}C was

calculated as the product of excess atom % ^{13}C (difference in atom % ^{13}C between sample and background) and C-content (expressed as unit weight): C-turnover (unit wt C) = [(atom % $^{13}C_{sample}$ – atom % $^{13}C_{background}$) x (unit wt C of organism).

To test for vertical migration of foraminifera in response to the added C, ALDs from 0 to 6 cm were calculated for total foraminifera and for the 3 dominant species and 'Other foraminifera' group after 2, 7 and 14 d and compared to those from the control chamber sampled after 7 d. ALDs were analyzed over time since this method provided a quantitative assessment of changing foraminiferal distribution patterns as a function of food supply and time, rather than a qualitative measure (Jorissen and others, 1995). ALDs were calculated using the equation of Jorissen et al. 1995:

$$ALD_x = \sum_{i=1,\,x} (n_i d_i)\, N^{-1}$$

Where x is the depth of the deepest layer, n_i is the number of foraminifera in the ith sediment layer, d_i is the depth mid-point of the ith layer and N is the total number of foraminifera in all layers.

Data analysis

Uptake of C from phytodetritus ($\delta^{13}C$-signatures > -20 ‰) was analysed using Two-way ANOVA tests on natural log transformed [X+2] data with sediment depth and experimental duration set as factors. Kolmogorov-Smirnov tests for normality and Levene's test of Equality of Error variances were carried out prior to conducting ANOVA. Tukey HSD post-hoc tests were used to further explore significant results of

ANOVA. An α-level of 0.05 was used as a criterion for statistical significance. Data analysis was conducted using SPSS 15.0 software (SPSS Inc, Chicago, IL).

RESULTS

Foraminiferal community structure

A total of 4015 foraminifera were picked with 3688 (92 %) identified to species level. The central Korsfjord foraminifera (>250 μm) were characterised by low species diversity with only 3 main species, *G. turgida*, *H. balthica*, and *M. barleeanum* contributing 91 % of all foraminifera (Figs. 2). The 'Other foraminifera' category was made up of an assortment of genera, notably *Cibicidoides* spp., *Bulimina* spp., and *Reophax* spp. Mean total foraminiferal abundance and biomass were 574 ± 84 ind. 28.3 cm^{-2} and 25.5 ± 5 mg dw 28.3 cm^{-2}, respectively.

Species patterns and average living depth (ALD)

Depth distributions and ALDs of the foraminifera throughout the 2 wk experiment are given in figures 3 and 4, respectively. With the exception of *H. balthica*, depth distributions and mean ALDs implied that the majority of foraminifera were not vertically migrating to the surface to feed on the fresh organic matter (OM) pulse. After 14 d, *H. balthica* had a shallower ALD in both fed incubation chambers compared to the un-fed control (Fig. 4C) indicating that these protozoans may have been responding to the added C or migrating because of an additional factor. Variation in ALD between replicates decreased with experimental duration, with the exception of *H. balthica*, suggesting that the ALDs for *G. turgida*, *M. barleeanum* and the 'Other foraminifera'

group after 7 and 14 d were most optimal (Figs. 4A-C). Based on the ALDs found, *G. turgida* and *M. barleeanum* and the protists that comprise the 'Other foraminifera' group are considered deep-infaunal taxa, whilst *H. balthica* is an intermediate infaunal taxon.

Isotopic signatures and response to added carbon

Background δ^{13}C-signatures ($\delta^{13}C_{bkd}$) averaged -24.7 ± 1.9 ‰ and are indicated for all foraminifera, together with specific uptake ($\Delta\delta^{13}$C) signatures at the end of the experiments in figure 5. Only a minor fraction of samples (3 %) possessed δ^{13}C-signatures indicative of ^{13}C ingestion, and uptake was confined to *G. turgida*, which showed a slight increase in mean $\Delta\delta^{13}$C-signatures with experimental duration (Fig. 5A). Delta δ^{13}C-signatures of *G.turgida* were significantly related to sediment depth (Two-Way ANOVA, $F_{2, 18} = 6.883$, $p = 0.006$) with higher mean specific uptake at 0-2 cm compared to 4-6 cm (Fig. 5B, Tukey HSD, $p = 0.02$). A statistically significant result was also found for the interaction between depth and time ($F_{4, 18} = 4.242$, $p = 0.014$) with increasing specific uptake with time at the surface compared to 4-6 cm depth. *Hyalinea balthica*, *M. barleeanum* and the 'Other foraminifera' samples showed no δ^{13}C-signatures greater than -20 ‰ throughout the entire experiment (Fig. 5C-G). Overall, foraminifera did not turn over C during the first 7 d (Fig. 6B). *G. turgida* had processed an average of 0.02 mg C m^{-2} after 14 d. Macrofaunal and foraminiferal biomass and C-uptake are compared in figures 6A and 6B.

DISCUSSION

As stated above, the foraminifera community was dominated by the 3 species, *G. turgida*, *M. barleeanum*, and *H. balthica*, which is indicative of eutrophic to mesotrophic conditions within the Korsfjord (Van Weering and Qvale 1983; Fontainer and others, 2003). Intriguingly the only species common to this and the only other study of Korsfjord foraminifera (Aarseth and others, 1975) was *H. balthica*, where it contributed approximately 20 % of the >200 μm assemblage in both studies. Instead, Aarseth and others (1975) noted that in addition to *H. balthica*; the foraminifera species *B. marginata*, *Uvigerina peregrina*, *Cibicides lobatulus* and *Planulina ariminensis* comprised the majority of the community (>212 μm) in the Korsfjord. One plausible reason for these different findings could be the presence of individual foraminiferal assemblages in different areas of the fjord, resulting from distinct hydrodynamic and sedimentary characteristics (e.g. C_{org}-content), as also witnessed in Bergen harbour by Johansen and others (2001). A direct comparison of foraminiferal community structure from this study with others that focus on Norwegian fjord foraminifera is troublesome however, since for this study only specimens that contained identifiable cytoplasm were picked. In cases where foraminifera possessed dense tests, it was impossible to assess cytoplasm content and visible pseudopodia were used as a criterion for cytoplasm content. But foraminifera may retract their pseudopodia on sampling (Bernhard and Alve 1996), making it practically impossible to identify cytoplasm-containing individuals. This may result in a slight underestimate of foraminiferal abundance and biomass and the results that deal with community structure may not be 100 % representative of the entire community. However, the primary goal of this study was to investigate C-cycling through the

foraminiferal community and the picking techniques used 1) ensured that no dead foraminifera were mistaken for ones inactive in terms of ^{13}C-uptake, and 2) were analogous to those used in previous foraminifera feeding investigations (e.g. Moodley and others, 2000, 2002; Nomaki and others, 2005a, 2006).

Average living depths for *Globobulimina* spp. and *M. barleeanum* at a 550 m site in the Bay of Biscay (> 2 cm - Ernst and van der Zwann 2004) agreed with the ALDs calculated for *G. turgida* and *M. barleeanum* in this study. Oxygen often does not penetrate more than a few millimetres in most eutrophic to mesotrophic sediments (Rasmussen and Jørgensen 1992), so the rather deep ALDs measured for these two species suggest both taxa prefer hypoxic to anoxic conditions. Additional evidence for this comes from Fontanier and others (2002) who noted that *M. barleeanum* generally occurs in the lower part of the sediment oxic zone where nitrate production occurs, and *G. affinis*, in the anoxic zone where denitrification takes place.

With the exception of *H. balthica*, no obvious vertical migration towards the surface was observed by any foraminifera when supplied fresh OM. *Globobulimina* spp. and *Melonis* spp. are known to prefer deeper infaunal habitats (Corliss 1985; Goldstein and Corliss 1994; Ohga and Kitazato 1997; Ernst and van der Zwann 2004; Nomaki and others, 2005b), which would explain their lack of vertical migration towards the surface since deep-dwelling foraminifera generally react slower to added food compared to shallow infaunal species. For example, in an *ex-situ* feeding study, *G. affinis* only migrated into surficial sediments from deeper horizons 14 d after being fed with fresh OM, compared to less than 1 wk for shallow infaunal taxa (Nomaki and others, 2005b). Rudnick (1989) also showed that food-assimilation times differed between surface- and

sediment-dwelling metazoan meiobenthos. *H. balthica*, on the other hand has been described as a shallow infaunal taxon (Corliss and Chen 1988), which fits well to its upward migration. But the rather deep ALDs calculated for this species after 2 d are somewhat surprising. Subduction of foraminifera by bioturbation has been reported in the literature (Ernst and others, 2002) and might explain the initially rather deep ALDs calculated for this taxon. In this case, the observed migration may have resulted from microhabitat restabilization - a process that can take up to 20 d following sediment mixing (Nomaki and others, 2005b).

In previous investigations, the genus *Globobulimina* has shown variable response times to food additions ranging from 2-10 d (Nomaki and others, 2005a, b). The late response observed by *G. turgida* in this study adds to this variability, but it must be kept in mind that we did not sample the long-term chambers after 10 d. Nonetheless, the retarded response by *G. turgida* suggests that this particular species may prefer more decomposed organic matter. Fontanier and others (2002) concluded that certain species of *Globobulimina* rely more on refractory vs. labile OM, and as OM generally becomes more refractory with increasing sediment depth, the deep ALDs and relatively light natural δ^{13}C-signatures (-22.8 ± 0.8 ‰) found for *G. turgida* in this study provide further evidence for this. *Melonis barleeanum* also shows a preference for altered OM as a food source (Caralp 1989; Fontanier and others, 2002), and the relatively light natural δ^{13}C-signature measured for this species (-27 ‰) suggests that feeding experiments using labelled refractory OM may have resulted in different feeding patterns being observed for *M. barleeanum*.

The statistically significant relationship between uptake of ^{13}C by *G. turgida* and sediment depth, plus the significant interaction between depth and time indicate that individuals living closer to the sediment surface are able to exploit phytodetritus to a greater degree than those living in deeper sediment layers. Previous investigations have also demonstrated higher uptake of C by shallow infaunal foraminifera and macrofauna compared to deeper-dwelling animals (Aberle and Witte 2003; Kitazato and others, 2003; Nomaki and others, 2005a; Sweetman and Witte in press).

Macrofauna from our experimental cores were analysed in a separate study (Sweetman and Witte, submitted), and in view of the minor amount of tracer ingested by the large foraminifera studied here, it is not surprising that the macrofaunal community processed far more C than the foraminifera. Moodley and others (2002) carried out two *in-situ* incubation experiments at a deep-sea site in the NE Atlantic (2170 m) and found that despite comparable foraminiferal and macrofaunal biomass, macrofaunal C-uptake was on average 12 % of that of the foraminifera. In this study, although macrofaunal biomass was only 2 to 3 times greater than foraminiferal biomass, the foraminifera played no part in overall C-turnover during the first 7 d and only contributed 2.4 % to faunal C-turnover (foraminiferal plus macrofaunal) after 14 d. Macrofauna are known to dominate C-cycling at the base of oxygen minimum zones, whereas under hypoxic conditions foraminifera tend to be the lead-players (Andersson and others, 2007; Woulds and others, 2007). Bottom waters in the Korsfjord and the NE Atlantic are well-oxygenated throughout the year thus; oxygen availability is an unlikely explanation for this difference. C-cycling pathways can differ dramatically depending on faunal community structure (Levin and others, 1999) and the dominance (68 %) of deep-infaunal species

(i.e. *G. turgida* & *M. barleeanum*) that tend to prefer degraded over fresh OM (Caralp 1989; Fontanier and others, 2002) may be one explanation for the comparatively low degree of foraminiferal C-turnover.

In addition, it is important to bear in mind that we focussed on a coarse size fraction of foraminifera (> 250 μm). Intriguing studies by Gooday and Hughes (2002), Fontanier and others (2003), and Duchemin and others (2007) have all shown that small sized fractions (e.g. 63-150 μm) of foraminifera respond faster to OM inputs than more coarse ones (>150 μm). For example, Fontanier and others (2003) demonstrated that opportunistic species, such as *Epistominella exigua*, which are largely confined to <150 μm fractions, exhibit higher density increases after spring and autumn phytoplankton bloom periods in the southern Bay of Biscay (550 m) compared to larger protists (>150 μm). Duchemin and others (2007) also revealed a faster response to phytodetritus deposition by the small-sized foraminifera species, *E. exigua* and *Nuttallides pusillus* compared to larger taxa, again suggesting that small-sized foraminifera react stronger to POM input than larger individuals. Results from this and previous investigations indicate that the role of foraminifera in deep-sea C-cycling is highly variable and in all likelihood is driven by differences in foraminiferal community composition and structure, with large (> 250 μm), deep-infaunal species showing a lesser response to phytodetritus deposition than smaller-sized (30-250 μm), shallow-infaunal opportunistic species.

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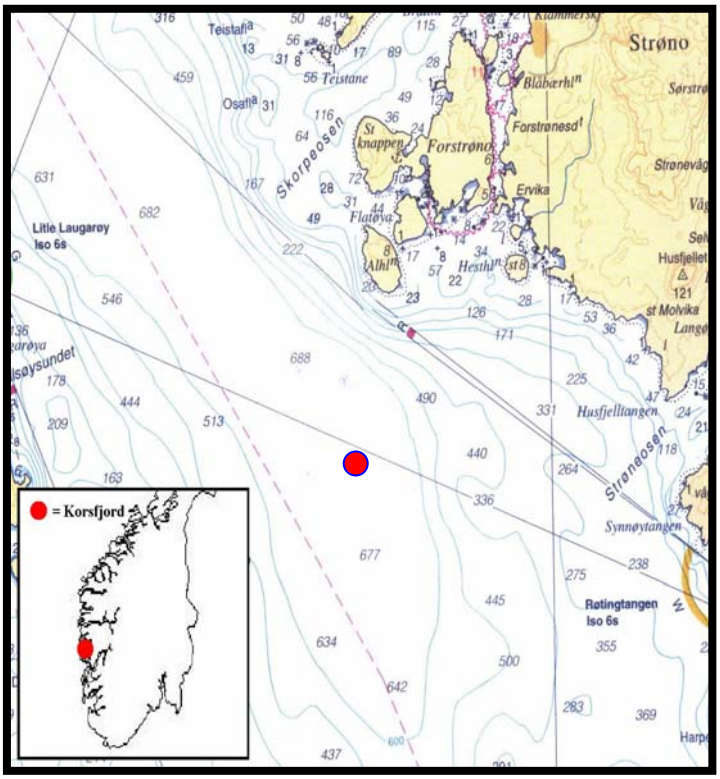
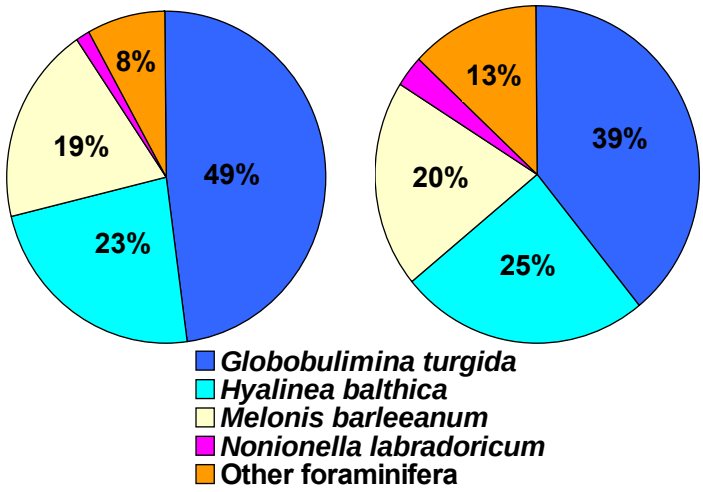
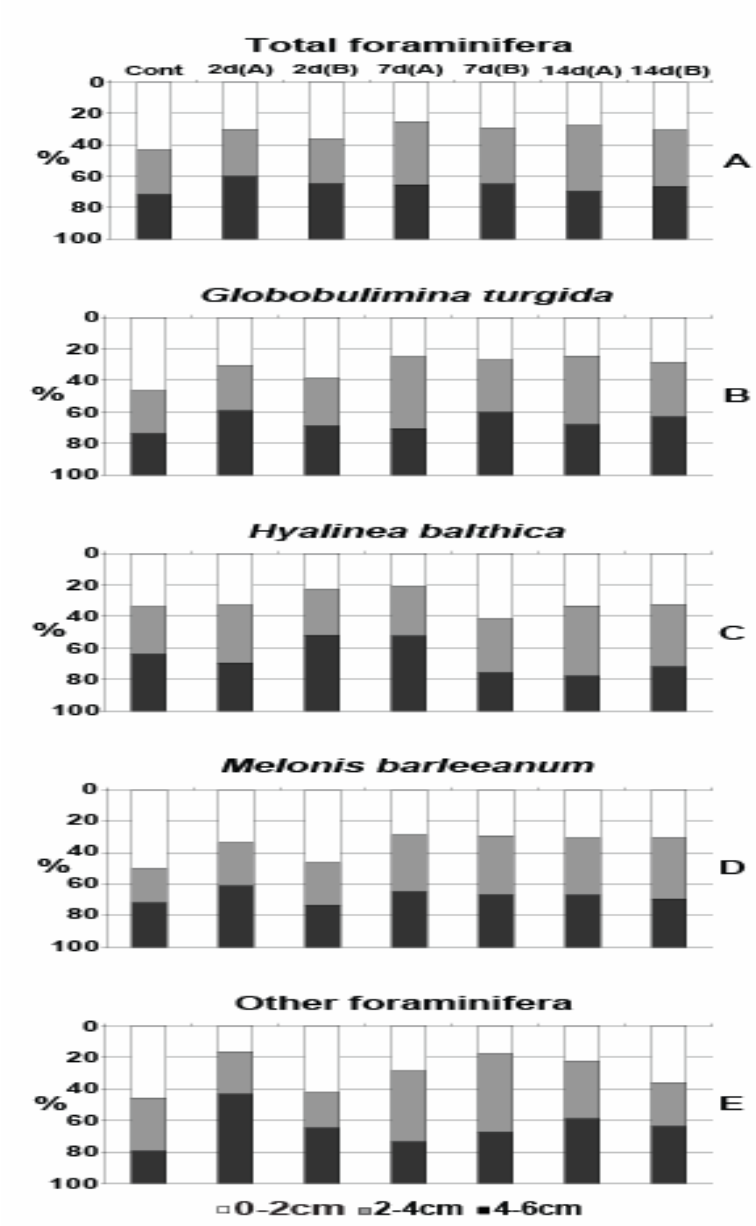


FIGURE 1. Location of the Korsfjord in western Norway. Red marker denotes sampling sites.

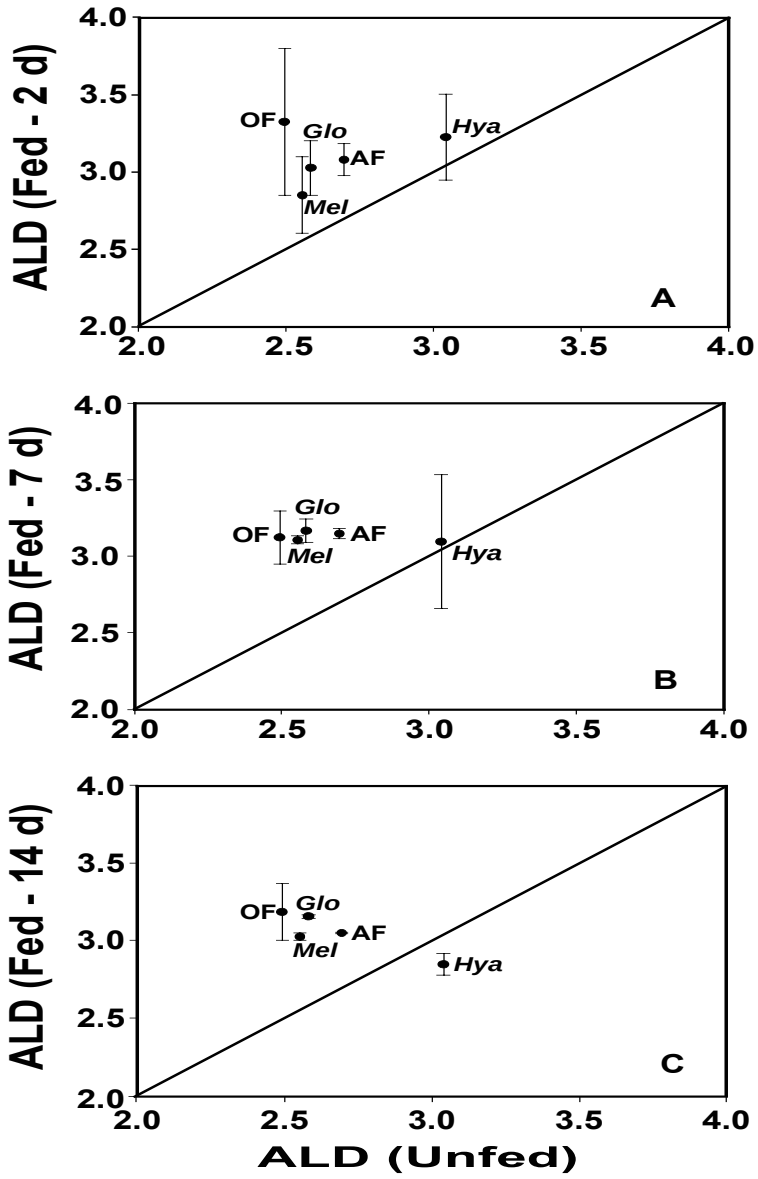


2a **2b**

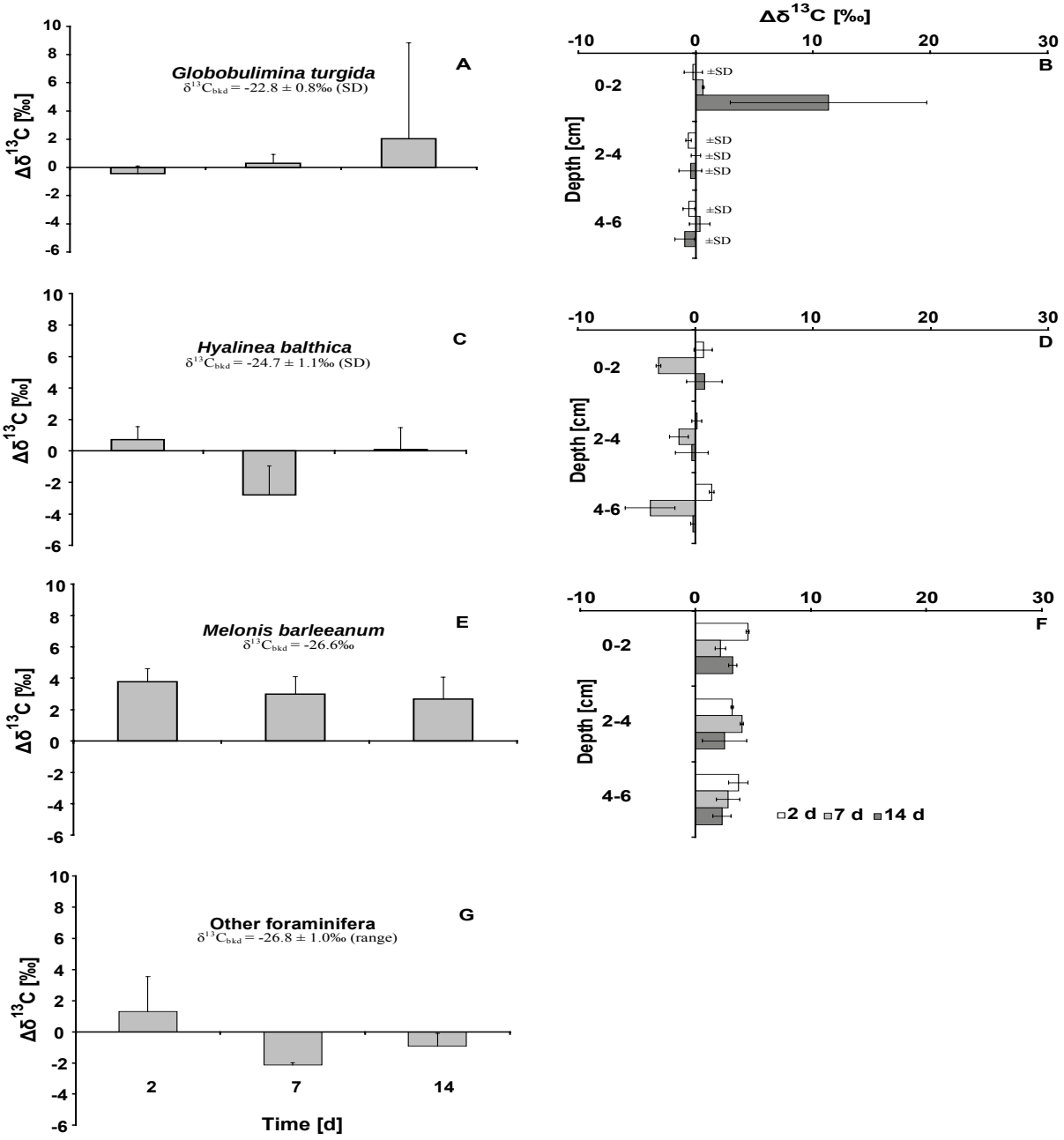
FIGURES 2a-b. Relative (a) abundance (ind. m^{-2}) and (b) biomass (mg dw m^{-2}) of major foraminiferal taxa in the central Korsfjord.



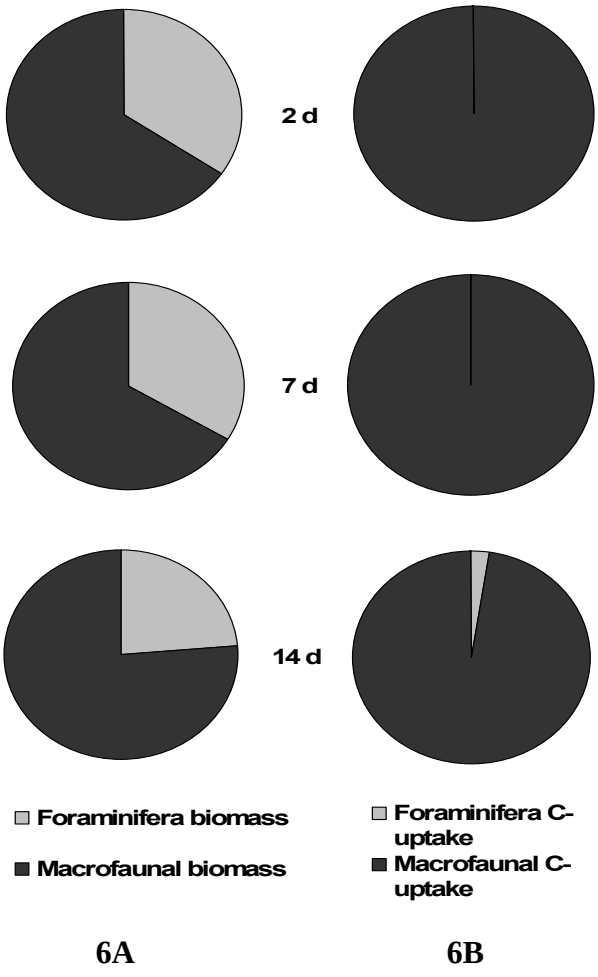
FIGURES 3a-e. Relative distribution of foraminifera as a function of depth and experimental duration. Note: 2, 7 and 14 d (A/B) denote replicate chambers (A/B) processed after 2, 7, and 14 d.



FIGURES 4a-c. Average Living Depths (ALD) of foraminifera (0-6 cm) compared between fed (2, 7, & 14 d) and unfed treatments (AF = All foraminifera, *Glo* = *Globobulimina turgida*, *Mel* = *Melonis barleeanum*, *Hya* = *Hyalinea balthica*, OF = Other foraminifera). Bars denote ± range of two replicates.



FIGURES 5a-g. Specific uptake ($\Delta\delta^{13}C$) by foraminifera as a function of depth and time (a, c, e, g = specific uptake vs. time, bars denote +1SD; b, d, f = specific uptake vs. depth and time, bars denote ± range unless otherwise stated; a & b = *Globobulimina turgida*, c & d = *Hyalinea balthica*, e & f = *Melonis barleeanum*). Natural $\delta^{13}C$-signatures are shown.



FIGURES 6a-b. Comparison between macrofauna and foraminifera biomass (mg C m^{-2}) and C-turnover over time (mg C m^{-2}).

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Conclusions and Outlook

Marine ecosystems, especially those found in the deep-sea, are subjected to a variety of natural and/ or man-made perturbations such as disturbance events (e.g. as a result of polymetallic mining), pollution and climate change, and each of these stressors has the potential to substantially modify deep-sea biodiversity and ecosystem functioning. In order to elucidate the potential impacts of such stressors, it is important to first understand baseline ecosystem dynamics. Deep-sea environments are notoriously challenging environments to work in and as a result of the technical difficulties and large expense associated with this particular field of research, very little is known about its ecosystems. In an effort to learn more about deep-sea ecosystem functioning, this thesis has focused on elucidating the role of macrofauna and foraminifera in deep-sea C-cycling. Whilst the results presented and discussed are the outcome of only a relatively small set of experiments, they do reveal some interesting insights into the role of macrofaunal and foraminiferal communities in C-cycling and suggest avenues for further exploration.

The 2nd chapter of this thesis describes macrofaunal community structure (>250 μm) at Station M and for the first time in the Pacific documents the short-term response of an abyssal macrofaunal community to a pulse of phytodetritus. Despite macrofaunal community structure being similar to other deep-sea sites, the labelling study revealed a different response pattern to that seen by Witte et al. (2003a) in the abyssal NE Atlantic. Although some animals - mainly the smaller-sized macrofauna - showed rapid ingestion of labelled phytodetritus, total macrofaunal C-turnover in late October 2004 in the NE Pacific was approximately 1 % of that processed in the abyssal NE Atlantic in May/ June

2000 (Witte et al. 2003a). Comparing both Pacific and Atlantic data sets thus reveals that abyssal macrofaunal communities do not always respond immediately to phytodetritus deposition as seen in the Atlantic (Witte et al. 2003a), but instead ingest OM at a variety of rates. The different response patterns of two abyssal communities seen at different times of year also suggests that macrofaunal response times may vary seasonally (Fig. 1), from very fast immediately prior to the spring bloom as observed by Witte et al. (2003a) and Aberle and Witte (2003), to relatively slowly in late autumn when this study was carried out.

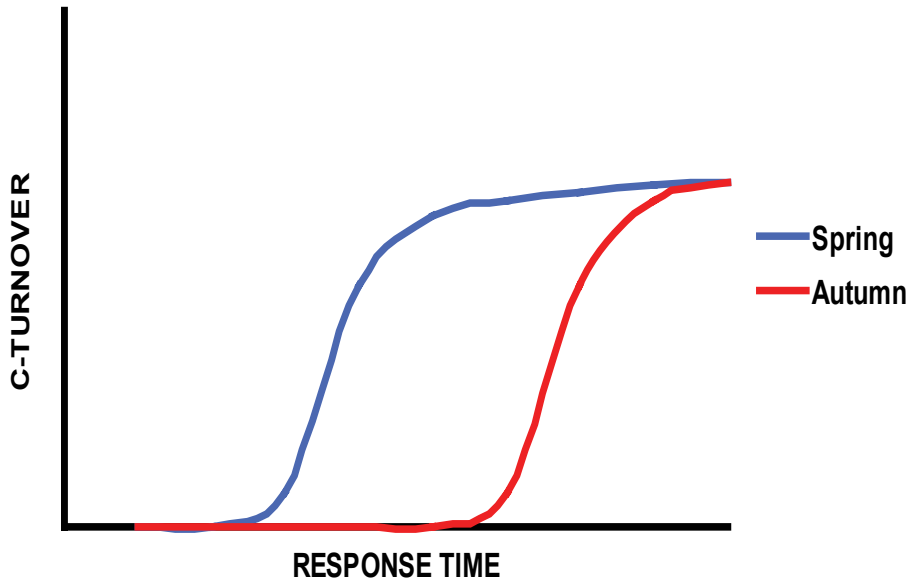

Figure 1 – The Seasonally-Dependent Response Time Hypothesis

The third chapter describes the short-to-long term response of a deep Norwegian fjord macrofaunal community to a simulated food pulse. The 14 day experiment highlighted the shear variability in response by certain macrofaunal taxa and provided evidence that functional group classifications (e.g. surface-deposit feeders) are, in some

instances, a poor indicator of an organism's ability to process C. For example, of the 7 deposit feeding polychaete families identified in the study, only 2 - the Paraonidae and Cirratulidae, together with the largely carnivorous Lumbrineridae - were seen to respond and ingest labelled OM. The results generated by this study therefore suggest that species-specific feeding ecologies and/ or ontogenetic changes in diet may play an important role in macrofaunal C-cycling and C-burial and therefore warrant rigorous testing in future studies.

The fourth chapter details for the first time the response of a deep Norwegian fjord foraminifera community (>250μm) to a pulse of fresh, labile organic matter. Overall, the results generated showed that in contrast to previous foraminifera feeding studies (e.g. Moodley et al. 2002), foraminifera sometimes play an almost negligible role in benthic C-cycling compared to metazoan macrofauna. One of the most plausible reasons for the retarded response of foraminifera demonstrated here was due to the coarse-size fraction of foraminifera analyzed. Previous studies have shown that small, opportunistic species, such as *Epistominella exigua*, which are normally <150 μm in size, exhibit higher density increases after spring and autumn phytoplankton bloom periods compared to larger foraminifera (>150 μm) (Fontanier et al. 2003, Duchemin et al. 2007).

Finally and collectively, all three studies highlighted the potential importance of biodiversity and benthic community structure in modifying benthic C-cycling rates in the deep-sea. For example, results from both macrofaunal feeding studies when compared to previous abyssal (Witte et al. 2003a, Aberle & Witte, 2003) and fjord (Aberle 2001, Witte et al. 2003b) investigations suggest that low C-turnover rates may result from a lack of surface-deposit feeding animals. What's more, comparatively low macrofaunal

C-processing rates in the Korsfjord when compared to other fjords could be due to the rather deep-dwelling macrofaunal community in the Korsfjord as opposed to largely surface dwelling macrofaunal assemblages in other previously studied fjord environments (Aberle 2001, Witte et al. 2003b). In addition, this thesis has provided evidence that foraminiferal communities dominated by deep-dwelling taxa, such as *Globobulimina turgida* and *Melonis barleeanum*, generally respond slowly to phytodetritus deposition as a result of largely deep-infaunal lifestyles, and possible preferences for recalcitrant organic material over fresh, more labile resources. Results from this thesis therefore imply that changes in deep-sea biodiversity and benthic community structure as a result of natural and/ or man-made perturbations, may have profound impacts on C-cycling and hence C-sequestration rates - as seen in other studies (e.g. Cardinale et al. 2006) - and thus emphasize the need for thorough, long-term biodiversity and ecosystem monitoring studies in the deep-sea.

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